APOMIXIS AND SPECIATION IN THE

BOTHRIOCHLOININAE

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Submitted to the Faculty of the Graduate School of
the Oklahoma State University
in partial fulfillment of the requirements
for the degree of
DOCTOR OF PHILOSOPHY
May, 1963

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PREFACE

Each chapter in this thesis is presented here, with minor modifications, in the form and style of the various biological journals to which they will be submitted for publication. It is believed that this method of presentation will allow for more accurate interpretation of the data.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER I

INTRODUCTION

Apomixis is genetically controlled. Ernst (1918) suggests that this mode of reproduction is the result of hybridization. Meiotic disturbances are commonly encountered, and apomictic groups are usually highly polymorphic. Hybridization evidently promotes apomixis in that gene combinations which can produce apomixis are brought together. The fact that most apomicts are polyploids further indicates that hybridization may have played a role in the wide distribution of apomixis in the plant kingdom. Stebbins (1950) suggests that the close association between apomixis, polyploidy, interspecific hybridization, and polymorphism may be explained on an indirect rather than on a direct basis. Both diploid and polyploid apomictic taxa are known, and although most apomicts are polyploids, strictly sexual polyploid species are commonly encountered.

The genetic basis of apomixis is poorly understood. Levan (1937) demonstrates that bulbil production in Allium carinatum is controlled by a single gene, although the expression of this character may be modified by other genes, as well as environmental factors. Muntzing and Muntzing (1945), from studies in Potentilla, suggest that apomixis is controlled by multiple genes. This also appears to be true in Hieracium (Christoff, 1942). Gerstel and Mishanec (1950) indicate that apomixis is inherited as a recessive character in Parthenium argentatum, but acts as a dominant when two genomes carrying the genes for apomixis are combined with a single set of genes controlling sexuality.

1

Evidently, the genes controlling apomixis may either be dominant or recessive over those inducing sexuality in various plant groups. Furthermore, its manifestation may often be related, in quantitative terms, to the number of genomes bearing the genes for apomixis. Stebbins (1950) indicates that the complexity and multiformity of disturbances that accompany apomixis can only be explained if we assume that normal sexuality requires a synchronized balance between a series of developmental processes. Such a balance, one would expect, could be upset by a number of different factors, not only genetical but also environmental. On this basis, Clausen (1954, 1961) suggests that apomixis must be controlled by a whole constellation of genes.

Stebbins (1950) points out that the different disturbances, characteristic of apomicts, probably are controlled by completely different groups of genes. Evolution towards apomixis must have been initiated through wide crossing. Thus, a genetic system which enforces cross-fertilization is almost essential. Similarly, a perennial habit is important. Hybrids in which the apomictic mode of reproduction is not yet completely established will be highly sterile and become extinct if annual. This probably (Stebbins, 1950) explains the fact that known sexual ancestors of nearly all apomicts are perennial and cross-fertilizing. Apomixis apparently, therefore, developed stepwise under the rigorous controls of natural selection.

The present study is an attempt to determine the genetic basis of apomixis, as well as the evolutionary potential of the apomictic complex Bothriochloininae. This generic-complex follows the classical pattern where diploids ($2n=20$) are sexual, tetraploids ($2n=40$) are facultative apomicts, and higher ploids are

essentially obligate apomicts. However, some Australian and New World polyploid representatives of Bothriochloa are sexual, and all the polyploids produce functional pollen. Harlan et al. (1961), Celarier et al. (1961), de Wet et al. (1961), indicate that the three genera Bothriochloa, Dichanthium, and Capillipedium form an interrelated generic-complex. Among the apomictic members reproduction by pseudogamous apospory is prevalent. Sexual species, sexual forms of the tetraploid D. intermedia and D. annulatum, as well as facultative and obligate apomictic species were crossed in various combinations. The nature of inheritance of apomixis in the F_1, F_2, and back cross generations was studied. Chromosome association during first metaphase was studied and its possible effect on the recombination of genetical factors will be discussed. Cytological and morphological studies were conducted on parents and their hybrids. Hybrids were also produced between sexual and sexual forms, sexual and apomictic forms, and apomictic and apomictic forms at different ploidy-levels.

The Bothriochloininae provides an unique opportunity to study the nature of inheritance of those genes controlling apomixis and sexuality. Both diploid and polyploid sexual species are available. Under experimental conditions, and possibly also in nature, scaling from one ploidy-level to the other does not severely affect the formation of cytologically balanced gametes. The diploid sexual species D. annulatum can give rise to a completely sexual and largely self-sterile auto-tetraploid. Hybrids between facultative apomictic tetraploids, and crosses with sexual tetraploids often produce strictly sexual tetraploids and hexaploids.

CHAPTER II

DISTRIBUTION OF APOMIXIS IN PLANTS

The term apomixis is recognized to include all types of asexual repro-
duction. This may either be purely vegetative, or seeds may be produced without
fertilization. Seed formation without fertilization was first described by Smith
(1839) for Alchornea ilicifolia, a dioecious member of the Euphorbiaceae. The
embryo of this species develops directly from adventitious buds of the nucellar
tissue. Juel (1900) demonstrates apomictic seed formation in Antennaria alpina,
and shortly afterwards Murbeck (1902) described a similar phenomenon in
Alchemilla. Cytological abnormalities during macrosporogenesis in apomictic
representatives of Hieracium were observed by Rosenberg (1917). Ostenfeld and
Raunkiaer (1903) earlier demonstrate that seed set is normal in this genus, as
well as in Taraxacum, after emasculation and prevention of pollination.

Winkler (1920, 1934) indicates the relationships between apomictic pheno-
mena and the corresponding sexual processes. Types of apomictic reproduction
are fully discussed by Stebbins and Jenkins (1939), Fagerlind (1940), Gustafsson
(1946, 1947 a, 1947 b) and Stebbins (1941, 1950). These authors recognize two
principal types of apomixis.

One type is vegetative reproduction where seed formation is completely
absent or forms only a secondary means of reproduction. This is particularly
well demonstrated in Elodea canadensis which in northern Europe reproduces

4

strictly by asexual means, but elsewhere is normally sexual. The most common mode of vegetative reproduction in higher plants is by means of bulbs, runners, layers, and buds. In Polygonum viviparum and some members of the genera Allium, Festuca and Poa the vegetative propagules occur within the inflorescence and replace the flowers. This type of vegetative reproduction is commonly referred to as vivipary.

The second recognized type of apomixis is agamospermy, where the embryos and seed are formed by asexual means, through the circumvention of meiosis and fertilization. Two major types are recognized by Stebbins (1950). The embryo may develop directly from the diploid, sporophytic tissue of the nucellus or ovule integument, and the gametophytic stage is consequently completely omitted. This, adventitious embryony is often encountered in the genus Citrus, and is common in some representatives of the families Euphorbiaceae, Ochnaceae, Myrtaceae, and Liliaceae. More common are methods of reproduction which, phenotypically at least, include a complete alternating of generations. The diploid gametophyte, however, is formed without fertilization as a result of some method by which meiosis is circumvented.

Two principal ways of circumventing meiosis are recognized. Apospory is recognized to include types where the embryo sacs are formed directly from a cell of the nucellus or the inner integument of the ovary by a series of somatic divisions. When the embryo sacs arise from a cell of the archesporium, in which meiosis is either omitted or so modified that chromosome reduction does not occur, the process is referred to as diplospory.

Diploid gametophytes, formed either by apospory or diplospory, may give rise to embryos through parthenogenesis by means of the multiplication of the egg cell, or by apogamety where some other cell gives rise to the embryo. These processes, apogamety and parthenogenesis, as well as adventitious embryony may be autonomous. In pseudogamous apomicts, however, pollination without fertilization is required to initiate these processes of embryo development.

Plants are often facultative apomicts, both diploid and haploid embryo sacs are formed in the same ovary. The latter usually function sexually and the other develop parthenogenetically. In experimental material, at least, the diploid embryo sac may occasionally function sexually and the haploid one often developes parthenogenetically. Most gametophytic apomicts are characterized by essentially normal chromosomal behaviour during microsporogenesis. Thus, the absence of chromosome pairing, and irregular chromosome reduction during macrosporogenesis can not be due to a lack of chromosome homology. Potentially, therefore, most apomicts should be able to reproduce sexually under certain conditions. Stebbins (1950) suggests that the meiotic disturbances during macrosporogenesis are both genetically and environmentally controlled.

Apomixis is neither necessary, nor is it an effective means for promoting phylogenetic development. Nevertheless, apomixis is widespread among members of the plant kingdom and recurs over and over again in unrelated groups. Recent reviews, by Stebbins (1941, 1950) Gustafsson (1946, 1947 a, 1947 b), Myers (1947), Nygren (1954), Steil (1951), Manton (1952), Rousi (1956), and Carnahan and Hill (1961), indicate that apomixis occurs in at least 40 families of Angiosperms, and that this mode of reproduction is widespread in the

Pteridophytes. Among the Angiosperms an apomictic mode of reproduction is commonly encountered in three of the largest and perhaps most successful families of flowering plants, the Rosaceae, Compositae and Gramineae. These reviews make a survey of literature superfluous. Table I lists species reported by recent workers to reproduce apomictically.

Apomixis was so far reported for at least 39 genera of the family Gramineae (Table II). Although poorly sampled as a whole, it may be of significance to note that this mode of reproduction was reported only in genera belonging to the more advanced subfamilies (Table III), being particularly well represented in the Panicoideae.

Generally speaking, agamic complexes consist of several basic diploid species together with a superstructure of interrelated apomicts. In the genera Festuca and Poa, however, apparently basic diploid species reproduce by means of vivipary (Nygren, 1954). Gametophytic apomixis was reported in diploid species of Potentilla and Ranunculus (Gustafsson, 1947 a), and also among the Gramineae in Panicum, Pennisetum and possibly Brachiaria (Table II).

Classically, apomixis was regarded as a process that shuts off all sources of genetic variability except for mutation, produces clones incapable of adapting to changing environments, and eventually leads to extinction. Clausen (1961), however, points out that apomictic groups represent balanced genetic systems in which some degree of sexual reproduction is maintained indefinitely. Completely obligate apomicts appear to be rare or absent among the Gramineae (Harlan et al., 1961; Price, 1959). The diploids usually reproduce sexually and the polyploids exhibit various degrees of sexuality. Even those that produce

TABLE I

RECENT REPORTS ON APOMICTIC ANGIOSPERMS AND GYMNOSPERMS

Name	Type of apomixis*	$2n$	Authority
Amaranthaceae			
Aerva tomentosa			Murgai, 1959
Bombacaceae			
Pachira oleaginea	AE	72	Baker, 1959, 1960
Buxaceae			
Simmondsia chinensis			Gentry, 1955
Casuarinaceae			
Casuarina distyla	Ps	22, 23	Barlow, 1958, 1959
C. nana	Ob	22, 23, 44	Barlow, 1958, 1959
Compositae			
Cichorium intybus	A		Plumier, 1960
Helianthus annum	A		Ustinova, 1951
Townsendia incana		28, 30	Beaman, 1954
T. montana		36	Beaman, 1954
T. parryi		36	Beaman, 1954
T. rothrockii		36	Beaman, 1954
T. spathulata		36	Beaman, 1954
Liliaceae			
Allium odorum	D	32	Hakansson and Levan, 1957
Lilium longiflorum	P	48	Emsweller and Uhring, 1962
Paris tetraphylla	V	10	Kurabayashi and Somejima, 1953
Meliaceae			
Lansium domesticus			Bernardo et al., 1961
Orchidaceae			
Dactylorchis			Heslop-Harrison, 1959
Zygopetalum mackayi		ca. 96	Afzelius, 1959
Pinaceae			
Pseudotsuga menziesii	Ag		Orr-Erwing, 1957

10

TABLE II

APOMIXIS IN THE GRAMINEAE

Name	Tribe	Type*	2n	Authority
Agropyron Gaertn.	Hordeae			
A. scabrum		D	42	Hair, 1956
Agrostis Linn.	Aveneae			
A. stolonifera		V	28, 35, 42	Nygren, 1954
A. tenuis				
= A. vulgaris		V	28-42	Nygren, 1954
Anthephora Schreb.	Paniceae			
A. pubescens		A	40	Brown and Emery, 1958
Bothriochloa O. Ktze.	Andropogoneae			
B. acidula		A	40	
B. caucasica		A	40	
B. decipiens		A	40	Brown and Emery, 1958; Celarier and Harlan, 1957
B. ewartiana		A	50, 60	Brown and Emery, 1958 Celarier and Harlan, 1957
B. glabra		A	40	Covas, 1952; Brown and Emery, 1958
B. grahamii		A	40	
B. intermedia		A	40, 50, 60	Brown and Emery, 1958 Celarier and Harlan, 1957
B. insculpta		A	50, 60	
B. ischaemum		A	40, 50, 60	Brown and Emery, 1958; Celarier and Harlan, 1957
B. kuntzeana		A	40	
B. odorata		A	40	
B. oryzetorum		A	40	
B. pertusa		A	40	Brown and Emery, 1958; Celarier and Harlan, 1957
B. radicans		A	40	Brown and Emery, 1958; Celarier and Harlan, 1957
Bouteloua Lag.	Chlorideae			
B. curtipendula		A, Ob	20-102	Harlan, 1949; Brown and Emery, 1958; Gould, 1959

Table II (Continued)

Name	Tribe	Type*	2n	Authority
Brachiaria Griseb	Paniceae			
B. brizantha		A	18, 36, 54	Brown and Emery, 1958
B. serrata		A	18, 36	Brown and Emery, 1958
Buchloe Engelm.	Chlorideae			
B. dactyloides		A		Brown and Emery, 1958
Calamagrostis Roth.	Aveneae			
C. canadensis		D	42-66	Nygren, 1954
C. chalybaea		D	28, 42	Nygren, 1946, 1954
C. inexpansa		D	28, 56, 58	Nygren, 1954
C. langsdorfii		D	84-104, 28	Nygren, 1954
C. lapponica		D	42-112	Nygren, 1946, 1954
C. purpurascens		D	28, 42-56, 58, 84	Nygren, 1946, 1954
C. purpurea		D	56-91	Nygren, 1946, 1949b, 1954
Capillipedium Stapf				
C. arachnoideum		A	40	
C. kwashotense		A	40	
C. parviflorum		A	40	Brown and Emery, 1958; Celarier and Harlan, 1957
C. spicigerum		A	40, 50	
Cenchrus Linn.	Paniceae			
C. setigerus		A, Ps	34, 36	Bashaw and Fisher, 1953; Fisher, Bashaw, & Holt, 1954.
Chloris Sw.	Chlorideae			
C. gayana		A		Brown and Emery, 1957
Deschampsia Beauv.	Aveneae			
D. alpina		V	26, 39-56	Nygren, 1949
D. caespitosa		V	26, 26-28	Nygren, 1949
D. rhenana		V		Nygren, 1949
Dichanthium Willem.	Andropogoneae			
D. annulatum		A	40	Brown and Emery, 1958; Celarier and Harlan, 1957
D. aristatum = D. nodosum		A	40	Brown and Emery, 1958; Celarier and Harlan, 1957
D. caricosum		A	40	Brown and Emery, 1958; Celarier and Harlan, 1957

Table II (Continued)

Name	Tribe	Type*	2n	Authority
D. fecundum		A	40	
D. pallidum		A	40	
D. papillosum		A	60	
D. tenue		A	40	
Echinochloa Beauv.	Paniceae			
E. frumentacea		A	54	Yabuno, 1953
Eleusine Gaertn.	Eragrosteae			
E. coracana		A		Nygren, 1954
Eragrostis Beauv.				
E. chloromelas		D	40, 60-63	Brown and Emery, 1958
E. curvula		D	50	Brown and Emery, 1958
E. heteromera		D	40	Brown and Emery, 1958
Eremepogon (Hack.) Stapf Andropogoneae				
E. foveolatus				
Eriochloa Kunth	Paniceae			
E. borumensis		A		Brown and Emery, 1958
E. sericea		A	54	Brown and Emery, 1958
Euclasta Franch.	Andropogoneae			
E. condylotricha		A		
Festuca Linn.	Festuceae			
F. ovina		V	28, 35	Piotrowicz, 1954; Nygren, 1954
F. rubra		V	28, 42	Piotrowicz, 1954; Takeoka, 1954; Nygren, 1954
Fingerhuthia Nees.	Chlorideae			
F. africana		D	40	Brown and Emery, 1958
Heteropogon Pers.	Andropogoneae			
H. contortus		A	40, 60	Brown and Emery, 1958
Hordeum Linn.	Hordeae			
H. vulgare		P	14	Foriani, 1950
		MP		Davies, 1958
Hyparrhenia Anderss.	Andropogoneae			
H. hirta		A	40, 44, 45, 60	Brown and Emery, 1958

Table II (Continued)

Name	Tribe	Type*	2n	Authority
H. rufa		A	30, 40	Brown and Emery, 1958
Melinis Beauv.	Paniceae			
M. minutiflora		Fa		Bumpus, 1960
Nardus Linn.	Nardeae			
N. stricta		D		de Coulon, 1923
Panicum Linn.	Paniceae			
P. antidotale		A	18	Shama Kumari, 1960
P. deustum		A	36	Brown and Emery, 1958
P. maximum		A	18, 32, 36, 44	Warmke, 1954; Brown and Emery, 1958
P. obtusum		A	20, 36, 40	Brown and Emery, 1958
P. purpurascens				Warmke, 1951
P. virgatum		A	21, 25, 30	Brown and Emery, 1958
Paspalum Linn.	Paniceae			
P. dilatatum		Ps, A, Ob	40, 50	Smith, 1948; Hayman, 1956; Brown and Emery, 1958; Bashaw and Forbes, 1958
P. hartwegianum		A	60	Brown and Emery, 1958
P. malacophyllum		A		Brown and Emery, 1958
P. notatum		A	20	Burton, 1948; Burton and Forbes, 1960
P. scrobiculatum		A	40	Warmke, 1954
P. secans		A, Ob, Ps	40	Snyder, 1957
Pennisetum Rich.	Paniceae			
P. ciliare		A, Ps, Ob	32, 34, 36, 40, 43, 48, 54	Bashaw and Fisher, 1953; Snyder et al., 1955; Fisher et al., 1954; Bashaw, 1962
P. cladestinum		A		Narayan, 1951, 1955
P. dubium		A	66	Gildenhuys and Brix, 1959
P. latifolium			36	Narayan, 1955 b
P. orientale		Fa, A	35, 36	Hrishi, 1952, Narayan, 1955
P. purpureum		A	27, 56	Brown and Emery, 1958
P. ramosum		A?	10	Narayan, 1955
P. ruppellii		A	27	Narayan, 1955
P. setaceum		A	27	Narayan, 1955
P. typhoides		P	28	Raman, et al. 1962

Table II (Continued)

Name	Tribe	Type*	2$\underline{n}$	Authority
P. villosum		A	18, 27, 36, 54	Narayan, 1955
Poa Linn.	Festuceae			
P. alpina		V, D	14	Nygren, 1950, 1953, 1954
P. ampla		A	100 ca.	Nygren, 1950
P. arachnifera		V	54-56	Nygren, 1954
P. arctica		V, A	72	Nygren, 1950
P. arida		A	63-103	Nygren, 1950
P. bulbosa		V	39	Nygren, 1950
P. compressa		A	50	Nygren, 1953
P. depauperata		A		Nygren, 1950
P. elongata		A		Nygren, 1950
P. glauca		D	49, 56, 62	Nygren, 1953
P. gracillima		A	81-86	Nygren, 1953
P. herjedalica		V	47-64	Nygren, 1954
P. jemtlandica		V	37-39	Nygren, 1950
P. nemoralis		D	35	Nygren, 1953
P. nervosa		D	62-70	Nygren, 1953
P. palustris		D		Nygren, 1954
P. pratensis		A	22-147	Nygren, 1954
var. vivipara		V	42/4B	Nygren, 1954
P. scabrella		A	44/f-104	Nygren, 1953
P. secunda		A	74-87	Nygren, 1953
P. stricta		V	38, 39	Nygren, 1950
Saccharum Linn.	Andropogoneae			
S. officinarum		D		Nygren, 1954
S. spontaneum		D	40-128	Nygren, 1954
Schmidtia Steud.	Pappophoreae			
S. bulbosa			36	Brown and Emery, 1958
S. kalahariensis				Brown and Emery, 1958
Secale Linn.	Hordeae			
S. cereale				Kljucareva, 1957
Setaria Beauv.	Paniceae			
S. leucopila		A	54, 68, 72	Emery, 1957
S. villosissima		A	54	Emery, 1957
S. viridis		V		Nygren, 1954
Themeda Forssk.	Andropogoneae			
T. quadrivalis		A	40	Brown and Emery, 1958
T. triandra		A	20, 40, 71	Brown and Emery, 1958

Table II (Continued)

Name	Tribe	Type*	2n	Authority
Tricholaena Schrad.	Paniceae			
T. monachne		A	36	Brown and Emery, 1958
Tripsacum Linn.	Maydeae			
T. dactyloides		Fa, Ps, D	45, 54, 72 90, 108	Farquharson, 1954, 1955; Brown and Emery, 1958
Urochloa Beauv.	Paniceae			
U. bolbodes		A	36	Brown and Emery, 1958
U. mosambicensis		A	30	Brown and Emery, 1958
U. pullulans		A	28 E	Brown and Emery, 1958
U. trichopus		A	14, 30	Brown and Emery, 1958
X Triticale	Hordeae	P	20	Nakajima, 1956
Zea Linn.	Maydeae			
Z. mays		P	20	Yarnell and Hills, 1959

*A = Apospory, D = Diplospory, Fa = Facultative apomict, MP = Male Parthenogenesis, Ob = Obligate Apomict, P = Parthenogenesis, Ps = Pseudogamy, V = Vivipary.

TABLE III

DISTRIBUTION OF APOMICTIC GENERA AMONG

TRIBES OF THE GRAMINEAE

Sub-family	Tribe	Number of Apomictic genera
Eragrostoideae	Chlorideae	4
	Eragrosteae	2
	Pappophoreae	1
Festucoideae	Aveneae	3
	Festuceae	2
	Hordeae	3/1 artificial
	Nardeae	1
Panicoideae	Andropogoneae	9
	Maydeae	2
	Paniceae	12

TOTAL 39 genera and one
intergeneric
hybrid

predominantly apomictic embryo sacs usually produce functional pollen (Celarier and Harlan, 1957). Recently, Harlan and de Wet (1962) demonstrated that in the generic-complex Bothriochloa and Dichanthium facultative apomixis actually promotes hybridization, giving rise to a highly adaptable system capable of rapid evolution. In such a system mechanisms which maintain a sexual potential, others which insure cross-fertilization, and still others which insure the formation of balanced gametes are nicely checked the one against the other. Apomixis, on the other hand, provides an escape from sterility and a means for rapid colonization of new habitats.

CHAPTER III

CHROMOSOME NUMBER AND MODE OF
REPRODUCTION IN THE BOTHRIOCHLOININAE

The grass tribe Andropogoneae is one of immense morphological varia-
tion, subdivided into six subtribes by Pilger (1954). The Andropogoninae remains
a large subtribe, and was subdivided by de Wet (1963) into seven smaller, appar-
ently more natural, generic-complexes.

Seven genera, Bothriochloa O. Kuntze, Capillipedium Stapf, Dichanthium
Willemet, Euclasta Franchet, Eremopogon (Hack.) Stapf, Spathia Ewart, and
Indochloa Bor, form such a complex, and is referred to for convenience, as
the Bothriochloininae. The genera Bothriochloa, Capillipedium, Dichanthium, and
Eremopogon are widely distributed throughout the tropics and the subtropics of
the Old World. Some species of Bothriochloa also extend into the warmer parts
of Europe, and a few species are confined to the New World. The monotypic
genus Euclasta is present in both tropical Africa and tropical America and India.
The genus Indochloa is confined to India, and Spathia is endemic to northern
Australia. The latter two genera are unknown cytologically. Embryological
studies (Brown and Emery, 1958; Celarier and Harlan, 1957; Harlan et al. 1958),
as well as cytogenetical studies summarized by Harlan et al. (1961) indicate
that diploid ($2n=20$) representatives of the Bothriochloininae reproduce sexually,
while polyploids are usually apomicts. Exceptions are some Australian and
American polyploid species of Bothriochloa which appear to reproduce sexually.

18

Chromosome numbers were determined for species belonging to the genera Bothriochloa, Capillipedium and Dichanthium. These data will be correlated with mode of reproduction and geographic distribution.

MATERIAL AND METHODS

Chromosome numbers were determined from developing microspore mother cells stained with acetocarmine. Degree of sexuality was determined by means of emasculation and pollination experiments. At least 40 florets of each species were emasculated and pollinated with pollen from a related species or from a morphologically different collection of the same species. Embryological studies were conducted on some species at different ploidy-levels.

RESULTS

The cytogenetical data are summarized in Table IV. The diploid species ($2n=20$) are regular in their chromosomal behavior. The chromosomes associate strictly into bivalents during microsporogenesis, and regular chromosome reduction takes place. The tetraploids are characterized mostly by bivalent formation, although some chromosomes occasionally fail to pair or associate into multivalents. Higher polyploids are usually more irregular in their cytological behavior than the tetraploids. Bivalent formation and regular chromosomal distribution, however, is the rule, and functional pollen is always produced. The strictly sexual Old World tetraploids and hexaploids, are characterized strictly by bivalent formation during microsporogenesis.

Cytological abnormalities are closely correlated with an apomictic mode of reproduction. Harlan et al. (1961) indicate that after staining with aceto-carmine (Bradley, 1948) the embryo sacs of the diploid species have two conspicuous polar nuclei and a group of antipodal cells. The asexual embryo sacs, of apomictic species, are characterized by a single polar nucleus and no antipodal cells. Sexual embryo sacs were observed in all the species studied. Those characterized by a facultative apomictic mode of reproduction (Table IV) have both sexual as well as apomictic embryo sacs at the time of anthesis. In those classed as obligate apomicts the sexual embryo sacs are crowded out by numerous apomictic ones at the time of anthesis.

Mode of reproduction is based, in the majority of species, on cytogenetical observations. Emasculations, and pollination with pollen from a related species, or morphologically different collection of the same species will give rise to the production of hybrids, or result in the absence of seed set in the sexually reproducing species. This is true in all the diploids ($2n=20$) as well as the American polyploids B. alta, B. barbinodis, B. edwardsiana, B. exaristata, B. hassleri, and B. saccharoides. The American species B. hybrida ($2n=120$) B. palmeri ($2n=180$), B. springfieldi ($2n=120$), and B. wrightii ($2n=120$) were not available for study. Cytological behavior (Gould, 1956, 1957), however, suggests that these species also reproduce sexually. The only Old World polyploid species that reproduce strictly by sexual means are the Australian B. decipiens ($2n=40$) a cleistogamous species, B. erianthoides ($2n=60$), and B. ambigua ($2n=60$). These species are all characterized strictly by bivalent formation during microsporogenesis.

TABLE IV

CHROMOSOME NUMBER AND MODE OF

REPRODUCTION IN THE BOTHRIOCHLININAE.

Name	No.	2n	No. Emasc.	No. Plants	% Maternal	Mode of Reproduction
Bothriochloa O. Kuntze						
B. acidula (Stapf) de Wet	4158	40	55	11	100	Obl
B. alta (Hitchc.) Henr.	6094	60	81	0	0	Sex
B. ambigua S. T. Blake	6137	60	350	9	0	Sex
B. barbinodis (Lag.) Henr.	6097	180	196	0	0	Sex
var. perforata (Trin.)Gould	3700	180	44	0	0	Sex
B. compressa (Hook.f.) Henr.	9086	20	44	0	0	Sex
B. concanensis (Hook.f.) Henr.	9101	20	48	0	0	Sex
B. decipiens (Hack.) Hubb.	5498	40	256	0	0	Sex
var. cloncurrensis (Domin)Hubb.	6510	40	160	0	0	Sex
B. edwardsiana (Gould) Parodi	3682	60	44	0	0	Sex
B. erianthoides (F. Meull.)Hubb.	5786	60	80	0	0	Sex
B. ewartiana (Domin) Hubb.	5803	50	531	8	100	Obl
	6137	60	480	128	99.2	ƒObl
B. exaristata (Nash) Henr.	6591	60	84	0	0	Sex
B. foulkesii (Hook.f.) Henr.		20				Sex
B. glabra (Roxb.) A. Camus	5297	40	90	53	86.5	Fac
	6580	40	44	12	100	Obl
	7699	40	180	40	100	Obl
	7010	40	195	24	92.3	Fac.
B. grahamii (Haines) Bor	2655	40	1366	907	86.7	Fac
	4028	40	302	117	91.7	Fac
	4393b	40	140	72	98.6	Fac
	5400	40	154	62	96.9	Fac
	5450	40	160	42	89.6	Fac
	8860	60				
B. hassleri (Hack.) Henr.	3145	60	40	0	0	Sex
B. hybrida (Gould) Gould		120				Sex
B. insculpta (Hochst.) A. Camus	4090	50	350	30	100	Obl
	3704	60	160	24	100	Obl
var. vegetior (Hack.) Hubb.	5470	40	156	18	99.8	ƒObl
B. intermedia (R.Br.) A. Camus	6587	40	120	60	100	Obl

Table IV (Continued)

Name	No.	2n	No. Emasc.	No. Plants	% Maternal	Mode of Reproduction
	5496	60	84	58	100	Obl
	4607	80	44	10	100	Obl
B. ischaemum (Linn.)Keng	5704	40	150	23	100	Obl
	1359	60	1672	182	100	Obl
var. songarica(Rupr.)Cel.&Hari.	6459	50	379	58	99.2	/Obl
	7055	50	179	61	100	Obl
	1347	60	867	192	100	Obl
B. kuntzeana (Hack.) Henr.	9106	20	88	0	0	Sex
	8299	40	79	31	100	Obl
B. longifolia (Hack.) Bor	8300	20	45	0	0	Sex
B. odorata (Lisboa) A. Camus	5409	40	45	27	100	Obl
	7232	40	93	18	100	Obl
B. oryzetorum (Hack.) Bor	8894d	40	44	14	96.5	Ap
B. palmeri (Nash) Pilger		180				Sex
B. pertusa (Linn.) A. Camus	5431	40	44	15	100	Obl
B. radicans (Lehm.) A. Camus	3055	40	184	61	94.6	Fac
B. saccharoides (Sw.) Rydb.	2579	60	324	0	0	Sex
var. longipaniculata (Gould)Gould	3133	120	685	3	0	Sex
var. pulvinata (Gould) Gould	7302	60	315	0	0	Sex
var. torreyana (Steud.) Gould	4396	60	44	7	0	Sex
	4085	80	81	0	0	Sex
B. springfieldii (Gould) Gould		120				Sex
B. woodrowii (Hook.f.)A.Camus	9114	40				Ap
B. wrightii (Hack.) Henr.		120				Sex
Capillipedium Stapf						
C. arachnoideum Henr.	8428	40				Obl
	4788	50	61	4	100	Obl
C. assimile (Steud) A. Camus	9116	20				Sex
C. caucasicum (Trin.) de Wet	7700	40	185	10	100	Obl
C. huegelii (Hack.) A. Camus	5794	20	90	0	0	Sex
C. kwashotense (Hyata) de Wet	6156	40	64	10	100	Obl
C. parviflorum (R.Br.) Stapf	3054	40	67	15	100	Obl
	6460	20	44	0	0	Sex
C. spicigerum S. T. Blake	4599	40	100	18	100	Obl
Dichanthium Willemet						
D. annulatum (Forssk.) Stapf	3234	20	156	35	0	Sex
	3965	20	89	17	0	Sex
	5396	20	263	63	0	Sex
	3182	40	372	121	93.5	Fac
	4099	40	263	93	78.5	Fac

Table IV (Continued)

Name	No.	2n	No. Emasc.	No. Plants	% Maternal	Mode of Reproduction
	4393	40	897	253	100	Obl
	5296	40	136	66	97.0	Fac
	5430	40	493	136	88.2	Fac
D. aristatum (Poir.) Hubb.	7199	20	311	0	0	Sex
	2571	40	321	33	89.1	Fac
	4086	40	239	49	98.5	Fac
	4098	40	38	4	100	Obl
D. caricosum (Linn.) A. Camus	1529	40	140	52	96.4	Fac
D. fecundum S. T. Blake	6525	40	252	102	100	Obl
D. humilius J. M. Black	3723	20	44	0	0	Sex
D. maccanii Blatt.	9049	20				Sex
D. pallidum (Hook.f.) Henr.	6178	40	64	12	96.6	Fac
D. panchganiense Blatt. et McCann	9040	20				Sex
D. sericeum (R. Br.) A. Camus	4610	20	93	0	0	Sex
D. setosum S. T. Blake	7784	20	44	0	0	Sex
D. superciliatum (Hack.) A. Camus	6527	20	88	0	0	Sex
D. tenue (R. Br.) A. Camus	2583	40	212	53	87.2	Fac

*Reproduction: Sex = Sexual, Fac = Facultative apomict, Obl = essentially obligate apomict.

The apomictic representatives are classified in Table IV, as either facultative or obligate apomicts, on the basis of breeding behavior. Embryological studies, however, indicate that even in those species classed as obligate apomicts sexual embryo sacs, as well as functional pollen, are always produced. Some degree of sexuality is therefore always maintained. In the facultative apomicts the degree of sexuality varies between 0.1 and 25 percent. Completely sexual representatives of the predominantly apomictic tetraploid species may occur in nature, but were not observed among our collection. The data on mode of reproduction, however, is based only on a selected number of plants used in hybridization experiments.

DISCUSSION

The basic diploid species of Dichanthium are restricted endemics, one group in India and the other in Australia. The Indian diploids D. panchganiense and D. maccannii are annuals closely related morphologically, and may represent relics of the original basic stock that gave rise to the widely distributed polyploids. Morphological data suggest that the diploid races of D. annulatum and D. aristatum are naturally occurring polyhaploids. Experimentally produced polyhaploids, from tetraploid representatives of these two species, resemble the naturally occurring diploids in detail cytologically as well as morphologically. The Australian diploids are annuals and mostly self pollinated. This could give rise to a number of distinct biotypes, each adapted to a rather narrow ecological area. It was suggested by de Wet and Harlan (1962) that the species D. humilius, D. setosum and D. superciliatum may represent ecobiotypes of the more widely

distributed D. sericeum.

The diploid species of Bothriochloa are perennials and endemic to India.
Bor (1960) indicates that B. compressa is confined to Deccan, B. concanensis
to the western Ghats, B. kuntzeana to Madhya Pradesh, B. longifolia to the
vicinity of Madras, and B. foulkesii is endemic to the Nilgiris.

The diploid annual C. huegelii is extremely variable morphologically, and
widely distributed in, but restricted to central and western India. The diploid
races of C. parviflorum extend from India to Hong Kong. Capillipedium assimile
is widely distributed, extending from India to southeast Asia, China and Japan.
The collections available for study are Indian in origin and diploid.

Polyploid species of Bothriochloa, Capillipedium and Dichanthium are widely
distributed. The sexually reproducing representatives, as well as those which
are essentially obligate apomicts are usually characterized by a more limited
range of distribution than the facultative apomictic species. Polyploid sexual
species, all belonging to the genus Bothriochloa, are confined to Australia and
America. Singh and de Wet (1961) demonstrate cytogenetically that the Australian
and American species are closely related. This would suggest a once world
wide distribution of the genus. The obligate apomict, B. ewartiana is confined
to Australia, B. insculpta to Africa, B. ischaenum is typically a Eurasian species,
and B. pertusa extends from India to southeast Asia. Similarly, in the genus
Dichanthium the two obligate apomictic species D. fecundum and D. papillosum
are confined to Australia and Africa respectively.

Harlan et al. (1961), Harlan, Chheda, and Richardson (1962), Harlan (1963),
and de Wet, Harlan, and Faruqi (1963) demonstrate that the genera Bothriochloa,

Capillipedium, and Dichanthium form an interrelated hybrid-complex. The species B. intermedia, widely distributed throughout the tropics and subtropics of the Old World, hybridizes in nature with B. ischaemum, C. parviflorum, and D. annulatum wherever their ranges of distribution overlap. The latter species further forms a hybrid-complex with D. caricosum which in turn hybridizes in nature with D. aristatum. These hybrid combinations are usually referred to as species, but survive in nature only due to their apomictic mode of reproduction. Chromosome association is not severely affected by hybridization, be it intraspecific, interspecific or intergeneric. Studies on artificially produced hybrids indicate that the chromosomes usually pair preferentially within genomes derived from each parental species (de Wet, Mehra, and Borgaonkar, 1961). Harlan and Chheda (1962) indicate that this mode of chromosome association is genetically controlled.

Cytogenetical and morphological studies indicate that derivatives of introgression between B. ischaemum and B. intermedia extend from Kashmir through China. Hybrid derivatives between the latter species and C. parviflorum are referred to taxonomically as B. glabra, C. caucasica, and C. spicigerum. The latter species is confined to Australia, C. caucasica to the Caucasus region, and B. glabra is widely distributed from southern Africa to Australia. Hybridization and introgression between B. intermedia and D. annulatum also gave rise to a number of distinct biotypes. Typically, D. annulatum is a tropical Indian species. Hybridization products between this species and B. intermedia are particularly common in the Gangetic plains of India, but present over the complete range of sympatric distribution of these two species. Taxonomically

these plants are referred to as B. grahamii. Experimentally produced hybrids

between D. annulatum and B. grahamii resemble the Mediterranean ecotype of

D. annulatum described by Mehra and Celarier (1958), and Mehra (1962) in

detail. The hexaploid, D. papillosum, a derivative out of an apparent cross

between the Tropical and Mediterranean ecotypes of D. annulatum, extends

across the whole of tropical and subtropical Africa. This species was synthe-

sized (Harlan et al. 1961) by fertilizing the cytologically unreduced female

gamete of the Mediterranean ecotype with pollen from the Tropical ecotype.

From a biosystematic point of view a number of species within each genus

should be united into large heteromorphous hybrid complexes. Harlan and

de Wet (1963) include all the hybrid derivatives between B. intermedia and other

representatives of Bothriochloa, as well as Capillipedium and Dichanthium,

into a single taxonomic unit, the compilospecies B. intermedia. Gardner (1952)

and Roberty (1960), purely on the basis of gross morphological data, combine

the genera Bothriochloa and Dichanthium, but retain Capillipedium as a

distinct genus. For the present, however, these genera are regarded as distinct.

A revision at this time will not be complete, and will lead to further rearrange-

ment as more data become available.

The genera Eremopogon and Euclasta appear to be genetically isolated from

each other, as well as the remainder of representatives belonging to the

Bothriochloininae. The species studied are tetraploid and appear to reproduce

strictly by gametophytic apomixis. Eremopogon foveolatus is widely distri-

buted in the drier regions of India and Africa. The species Euclasta condylo-

tricha is present in both tropical Africa, America, and India. Morphological

data suggest affinities with Dichanthium.

The genera included in the tribe Andropogoneae, although usually sub-divided into subtribes, are so interlinked morphologically as to form a single coherent group. Cytological data (Celarier, 1956, 1957, 1958, 1959; and Brown, 1950, 1951) suggest that the tribe needs revision. Morphological observations presented by Roberty (1960) coincide with these cytogenetical data, and this revision may serve as a guide for future biosystematic studies.

SUMMARY

The genus Bothriochloa is characterized by chromosome numbers ranging almost continuously in multiples of 10 from $2n=20$ to $2n=180$. Chromosome numbers of $2n=20$, 40 and 60 were encountered in Dichanthium. The genus Capillipedium is characterized by $2n=20$, 40, and 50 chromosomes, whereas representatives of the genera Euclasta and Eremopogon which were studied are tetraploids ($2n=40$).

In these genera diploids ($2n=20$) reproduce sexually, tetraploids are mostly facultative apomicts, and higher polyploids are essentially obligate apomicts. Exceptions are the American and some Australian polyploid representatives of Bothriochloa ($2n=60$, 80, 120, 180) which reproduce sexually.

The diploids are all narrow endemics, the facultative apomicts are widely distributed, and the sexually reproducing as well as apomictic polyploids are usually restricted in their distribution range.

CHAPTER IV

ANEUPLOIDY AND SEXUAL BALANCE IN

THE BOTHRIOCHLOININAE

Morphological and cytogenetical data indicate that interspecific as well as intergeneric hybridization takes place among, and between some facultative apomictic representatives of the genera Bothriochloa O. Kuntze and Dichanthium Willemet (Harlan et al. 1958; and Harlan et al. 1961). Classically, apomixis was regarded as a process leading to a phylogenetic dead end. Increase of genetic variability is limited to mutation, and changing environment should eventually lead to extinction.

Recently, Clausen (1954, 1961) points out that in all apomictic groups studied in detail, contact with sexuality is maintained indefinitely. Apomictic groups should, therefore, be regarded as potential sources of genetic variability. The present paper reports some of the cytogenetical data on hybrids produced between facultative apomictic species and biotypes of Bothriochloa and Dichanthium.

MATERIAL AND METHODS

Plants were grown in a uniform nursery as described by Celarier and Harlan (1956). Morphological data are based on as many plants as were available for study, both in the field and in the herbarium. Chromosome number and

chromosome association were determined from developing microspore mother cells stained with acetocarmine. Hybrids were produced by W. L. Richardson, using the technique described by Richardson (1958). Second generation populations were obtained from self-pollinating selected hybrids.

RESULTS

More than 1000 hybrids, representing intraspecific, interspecific and intergeneric combinations within, and between the genera Bothriochloa, Capillipedium, and Dichanthium have so far been produced. Among the 300 second generation populations grown, 25 exhibit a large degree of morphological variation. The majority reproduce strictly maternal progenies, and in some others the second generation populations were not large enough for cytogenetical studies.

The chromosome numbers and cytological behavior of the plants used as parents are discussed by Harlan, de Wet, and Richardson (1961). The cytology of the hybrids, and the second generation populations is summarized in Table V. The hexaploid ($2n=60$) B. ambigua reproduces sexually, and is characterized strictly by bivalent formation during microsporogenesis. The remaining parental species, B. grahamii, B. intermedia, D. annulatum, D. aristatum, and D. caricosum are facultative apomictic tetraploids exhibiting various degrees of sexuality. These behave cytologically like segmental allopolyploids as defined by Stebbins (1947). The chromosomes usually associate into bivalents during meiosis, although some chromosomes often fail to pair or these form multivalents. Chromosomal behavior of the hybrids is variable, but functional

TABLE V

CYTOLOGY OF SOME SEGREGATING HYBRID POPULATIONS

Hybrid	$2n$	No. Plts.	Chromosome Association*			
			I	II	III	IV
B. ambigua 5643 (6$\underline{n}$) x B. grahamii 5450 (4$\underline{n}$)	50	2	9.24 4-14	19.68 17-23	0.28 0-1	0.20 0-1
F$_2$ progeny	43	1	2.77 1-5	19.00 17-20	0.77 0-2	
	46	1	3.15 0-8	21.00 19-23		0.20 0-1
	49	1	5.25 2-9	21.18 19-23		0.56 0-2
	50	6	5.45 2-14	21.29 14-24	0.65 0-4	0.22 0-2
	60	1	3.25 2-8	27.60 26-29		0.20 0-1
	65	1	7.50 5-10	28.75 26-29		0.50 0-1
B. grahamii 5450 (4$\underline{n}$) x B. intermedia 3965 (4$\underline{n}$)	60	1	12.77 0-36	23.45 12-30	0.04 0-1	
F$_2$ Progeny	57	1	2.80 1-5	27.10 26-28		
	49	1	2.20 0-5	27.50 22-29	0.13 0-3	0.43 0-2
	60	4	2.42 0-6	27.60 22-30	0.18 0-3	0.45 0-2
	62	1	2.89 0-6	29.55 28.31		
	65	1	7.20 3-15	28.80 25-31		

Table V (Continued)

Hybrid	2n	No. Plts.	Chromosome Association*			
			I	II	III	IV
D. annulatum x-98 (4n) x D. annulatum 4390 (4n)	60	1	3.10 0-4	24.20 22-26	0.4 0-2	1.8 0-2
F$_2$ progeny	60	14	2.28 2-12	26.54 22-30	0.25 0-3	0.95 0-3
	30	2	2.68 0-6	13.14 7-14	0.13 0-2	0.18 0-2
B. intermedia 6573 (4n) x B. intermedia 5410b (4n)	40	1		15.50 12-20		2.25 1-4
F$_2$ progeny	40	10	1.52 0-2	17.57 12-20	0.05 0-3	0.40 0-4
D. aristatum 4084 (4n) x D. caricosum 2583 (4n)	40	1	1.53 0-4	15.20 13-20	0.46 0-2	1.53 0-3
F$_2$ progeny	40	1	0.63 0-2	18.80 16-20	0.09 0-1	0.27 0-1
	42	1	1.44 0-4	19.83 17-21		0.22 0-2
B. grahamii 4028 (4n) x B. grahamii X-750 (4n)	40	1	2.41 0-8	17.06 15-20	0.77 0-2	0.29 0-1
F$_2$ progeny	39	1	1.26 1-3	18.86 18-19		
	40	3	1.55 0-8	18.95 16-20	0.13 0-1	0.01 0-1
	42	1	1.5 2-4	20.10 18-21	0.10 0-1	
	46	1	4.33 4-5	19.66 19-21	0.33 0-1	0.33 0-1
D. annulatum X-98 (4n) x (B. grahamii 2655 x D. annulatum 5398) (6n)	50	1	7.38 4-12	19.23 17-21	0.15 0-2	0.92 0-2

Table V (Continued)

Hybrid	2n	No. Plts.	Chromosome Association*			
			I	II	III	IV
F₂ progeny	40	3	2.18 0-6	18.83 17-20		0.36 0-1
	41	2	2.83 1-5	18.50 16-20	0.25 0-2	0.1 0-1
	42	1	3.83 2-6	18.08 14-20		0.50 0-2
	43	1	1.00 1	20.30 19-21		0.30 0-1
D. annulatum 4099 (4n) x (D. annulatum 5797 x D. annulatum 4099) (4n)	40	1	1.53 0-4	15.20 13-20	0.46 0-2	0-3 0-3
F₂ progeny	40	5	1.21 0-4	19.30 18-20	0.01 0-1	0.04 0-1

*Average and range of chromosome association at first metaphase are given. I = univalent, II = bivalent, III = trivalent, and IV = quadrivalent.

pollen is always produced. This is true of intraspecific, interspecific, as well as intergeneric hybrids. Chromosome pairing, as demonstrated by de Wet, Mehra, and Borgaonkar (1961), takes place preferentially between genomes derived from each parental species. Harlan and Chheda (1962) demonstrate that this mode of chromosome association is genetically controlled.

Degree of morphological variation among second generation populations is graphically presented in Plate I. The majority of hybrids produce strictly maternal progenies, and consequently reproduce apomictically. Those hybrids that exhibit genetical segregation in the second generation must reproduce sexually. Those sexually reproducing hybrids selected for detailed studies are all euploids. Many of the artificially produced hybrids (Harlan and Chheda, 1962) are aneuploids. This could be expected, as the facultative apomictic parental species are characterized by irregular chromosome behavior during microsporogenesis.

Variation in chromosome number was never observed among the maternal progenies of both euploid as well as aneuploid hybrids. Aneuploidy was commonly encountered among the segregating progenies of hexaploid and pentaploid hybrids. Among the segregating progenies of tetraploid hybrids, aneuploidy is common only among those hybrids characterized by extremely variable chromosome association during microsporogenesis (Plates II and III).

The tetraploid B. grahamii numbers 5450 from Delhi, India, 2655 from British Guiana, and 4028 from Mt. Abu, India, when emasculated and pollinated with a morphologically different biotype of the same species, produce approximately 10 hybrids among a progeny of 100 plants. The parental plant designated

LEGEND FOR PLATE I

Figure 1. Morphological variation in the F_2 population of B. ambigua x B. grahamii sexual hybrid.

Figure 2. Morphological variation in the F_2 population of B. intermedia x B. intermedia sexual hybrid.

Figure 3. Morphological variation in the F_2 population of B. grahamii x B. intermedia sexual hybrid.

Figure 4. Morphological variation in the F_2 population of D. annulatum x (B. grahamii x D. annulatum) sexual hybrid.

Figure 5. Morphological variation in the F_2 population of B. grahamii x B. grahamii apomictic hybrid.

Figure 6. Morphological variation in the F_2 population of D. annulatum x D. annulatum sexual hybrid.

Plate I

86

1

20 18 16 14 12 10 8 6 4 2

○ B. ambigua 5643
▲ B. grahamii 5450
■ F_1
● F_2

0 1 2 3 4 5 6 7 8 9 10 11

2

24 22 20 18 16 14 12 10 8 6

○ B. intermedia 6573b
▲ B. intermedia 5410b
■ F_1
● F_2

1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4 2.6 2.8 3.0

NUMBER OF PRIMARY RACEMES

3

62 25 23 21 19 17 15 13 11 9

○ B. grahamii 5450
▲ B. intermedia 3965
■ F_1
● F_2

0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0

4

○ D. annulatum X-98
▲ B. grahamii 2655 X D. annulatum 5398
■ F_1
● F_2

13 11 9 7 5 3

1.8 2.2 2.6 3.0 3.4 3.8 4.2 4.6 5.0 5.4 5.8 6.2

5

○ B. grahamii 5400
▲ B. grahamii 5450
■ F_1
● F_2

24 22 20 18 16 14

0.1 0.3 0.5 0.7 0.9 1.1 1.3 1.5

6

○ D. annulatum X-98
▲ D. annulatum 4390
■ F_1
● F_2

12 10 8 6 4 2

3.2 3.6 4.0 4.4 4.8 5.2 5.6 6.0 6.4 6.8 7.2 7.6

RATIO LENGTH LONGEST RACEME/LENGTH PRIMARY AXIS

Morphological variation in the F_2 populations

LEGEND FOR PLATE II

Cytology of parents and some hybrids

Figure 1. Metaphase I in D. annulatum 3242 ($2n=20$).

Figure 2. Metaphase I in D. annulatum 4565 ($2n=40$).

Figure 3. Metaphase I in a F_2 plant ($2n=60$) showing 4 univalents and 28 bivalents.

Figure 4. Metaphase I in a F_2 plant ($2n=57$) showing 5 univalents and 26 bivalents (one overlapping).

Figure 5. Metaphase I in a F_2 plant ($2n=40$) showing 1 univalent, 18 bivalents, and 1 trivalent.

Figure 6. Metaphase I in a F_2 plant ($2n=42$) showing 21 bivalents.

Figure 7. Metaphase I in a F_2 plant ($2n=60$) showing 30 bivalents.

Figure 8. Early Anaphase I in a F_2 plant ($2n=42$) showing delayed separation of some chromosomes.

Figure 9. Metaphase I in a F_2 plant ($2n=50$) showing 9 univalents, 19 bivalents, and 1 trivalent.

Figure 10. Metaphase I in D. papillosum 3716 ($2n=60$).

Plate II
Cytology of parents and some hybrids

39
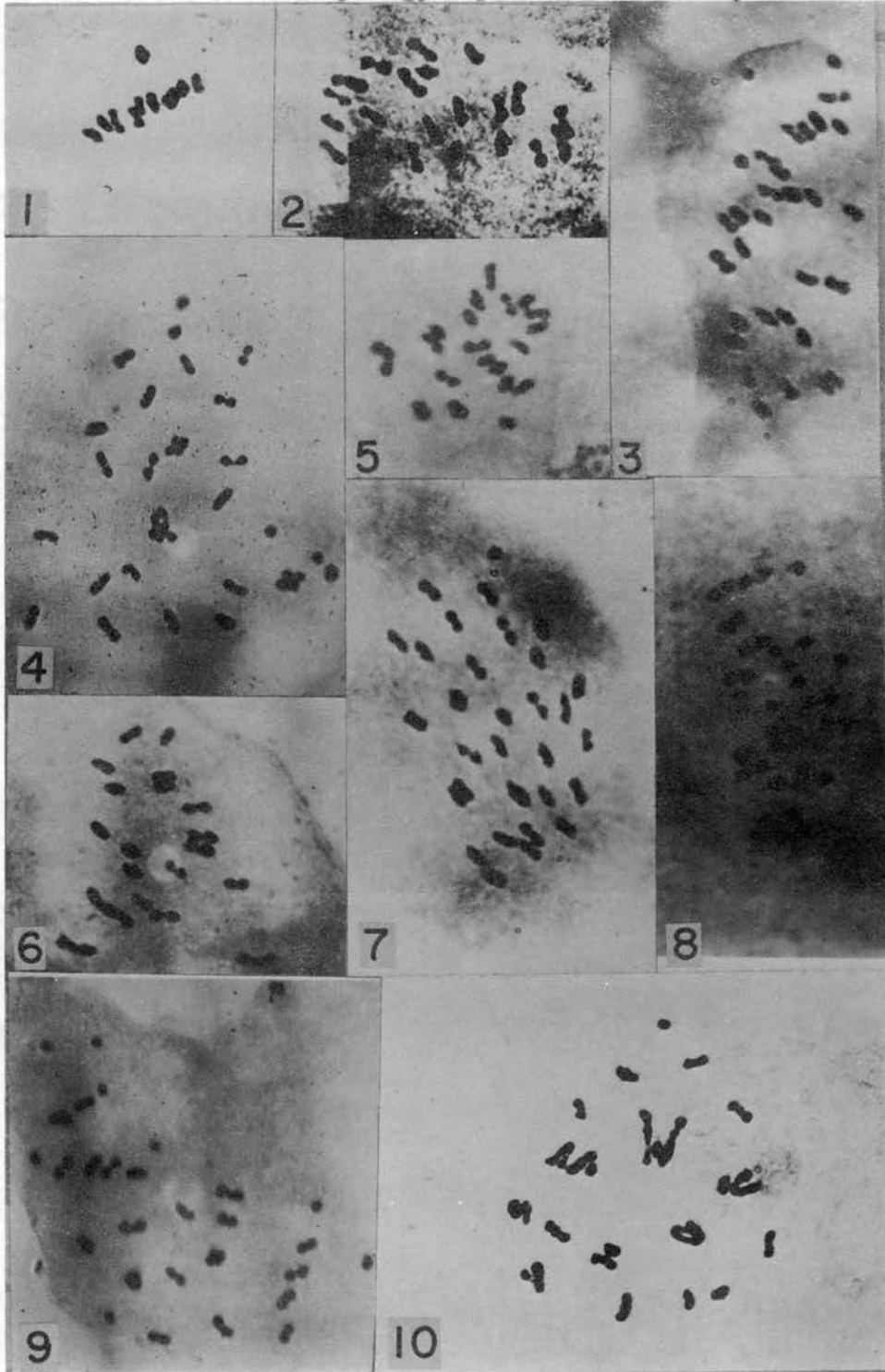
LEGEND FOR PLATE III

Figure 11.   Anaphase I in a F_2 plant ($2n=42$).

Figure 12.   Anaphase I in a F_2 plant ($2n=60$).

Figure 13.   Anaphase I in a F_2 plant ($2n=60$) showing 31 and 28 chromosomes

at poles and 1 laggard.

Figure 14.   Anaphase I in a F_2 plant ($2n=46$).

Figure 15.   Anaphase I in a F_2 plant ($2n=43$).

Figure 16.   Telophase I in a F_2 plant ($2n=60$) showing 7 dividing laggards.

Figure 17.   Telophase I in D. papillosum 3716 ($2n=60$) showing 2 dividing and

2 non-dividing laggards.

Plate III
Cytology of parents and some hybrids
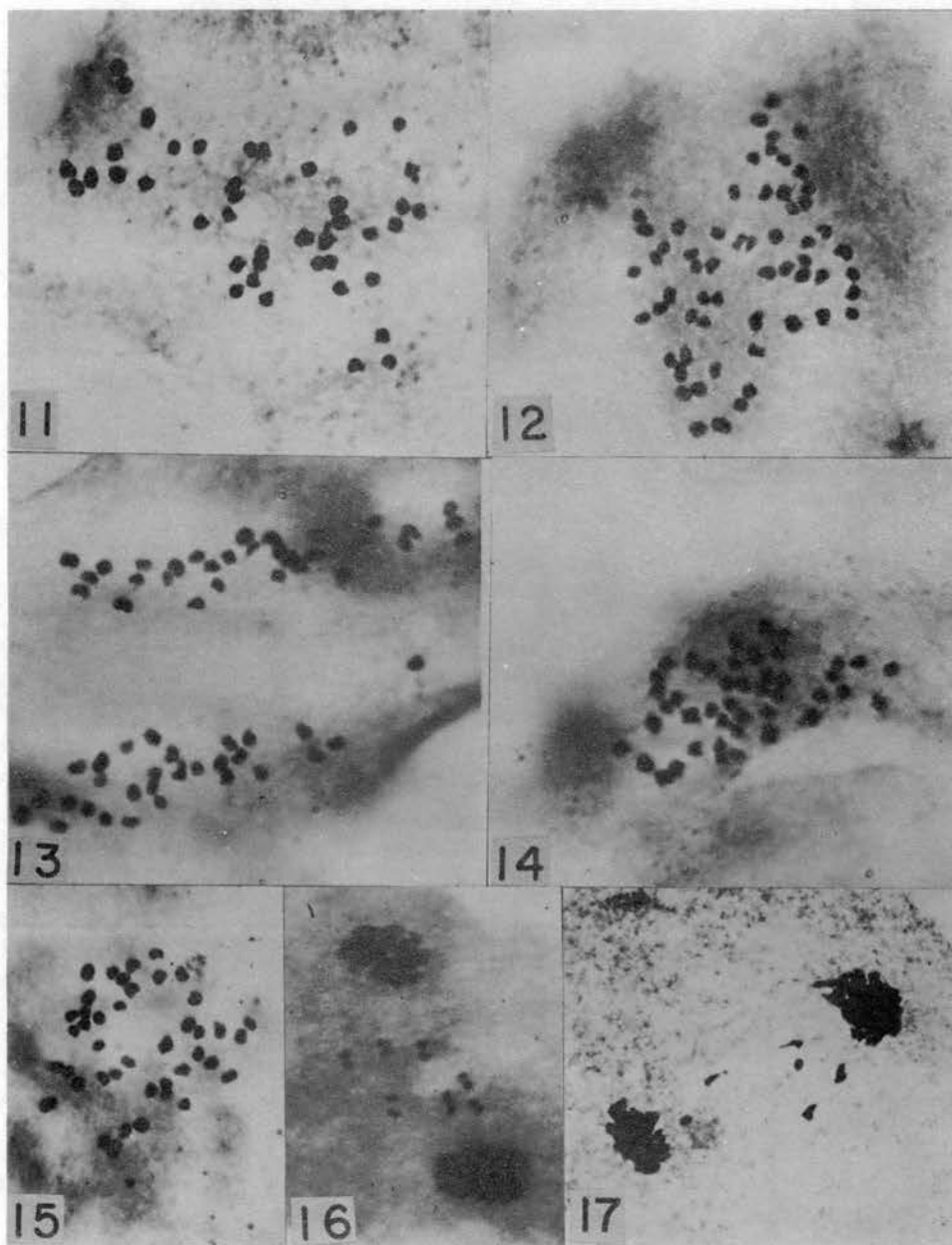
X-750 in Table V represents a completely sexual and self-sterile hybrid between two facultative apomictic biotypes of this species.

Two hybrid plants were obtained when a facultative apomictic tetraploid B. grahamii was crossed with a sexual hexaploid B. ambigua. Both hybrids are pentaploid, characterized by numerous univalents and uneven chromosome distribution during microsporogenesis. Eleven second generation plants were obtained, six of which are pentaploid and the others are aneuploids ranging in chromosome number from $2n=43$ to $2n=65$.

Hybrids between facultative apomictic tetraploids of B. grahamii mostly reproduce apomictically, but occasionally some of these hybrids are characterized by genetical segregation in the second generation. The populations may either be aneuploid or have the same chromosome number as the hybrid parents.

The B. intermedia parental plants, numbers 5410-b from Matiana, India, 6573 from Kandahar, Afghanistan, and 3965 from Calcutta, India, when used as the female parent exhibit approximately 7% sexuality. These cross readily with each other, as well as with B. grahamii. The latter species can also be crossed with D. annulatum. The D. annulatum parents, numbers 4099, 5398, and 5797, are Indian in origin, whereas number 4390 was collected in Tunisia. These exhibit from 10-20% sexuality. The plant designated X-98 is a completely sexual autotetraploid derived from natural doubling of the chromosomes of an Indian diploid race of D. annulatum.

When a tetraploid facultative apomict is used as the female parent, both the cytologically reduced as well as unreduced female gamete may function sexually. When the male parent is also tetraploid, the hybrids are either

tetraploid or hexaploid. Apomictic, as well as sexually reproducing plants were obtained among both tetraploid and hexaploid hybrids. The latter, when reproducing sexually, are characterized by large numbers of aneuploid plants in the second generation.

DISCUSSION

Harlan et al. (1961) demonstrate experimentally that Bothriochloa intermedia hybridizes in nature with both Capillipedium parviflorum and Dichanthium annulatum. Cytogenetical data indicate that B. grahamii represents a natural hybrid between D. annulatum and B. intermedia. Experimentally B. grahamii crosses readily with both D. annulatum and B. intermedia. These artificially produced hybrids resemble assumed natural hybrids in detail. The hexaploid B. ambigua resembles B. intermedia in gross morphological characters, and cytomorphological observations suggest that these two species hybridize in nature. Harlan (1963) demonstrates natural hybridization between B. ischaemum, and both B. intermedia and B. grahamii.

Experimentally produced hybrids, as indicated by Chheda, de Wet, and Harlan (1961), are often characterized by aneuploidy. Natural hybridization should, therefore, also produce aneuploid plants. For this reason aneuploidy was expected to be common among polyploid members of the Bothriochloininae. Harlan et al. (1958, 1961), however, demonstrate that among approximately 600 collections studied, representing most of the genera and species included in the Bothriochloininae, aneuploidy is almost completely absent. Artificially produced aneuploids are usually less vigorous than the euploid hybrids. Natural selection

for complete genomes could, therefore, explain the rare occurrence of aneuploid plants in nature.

Completely sexual races of the predominantly apomictic polyploid species appear to be rare or absent in nature. Artificially produced hybrids between facultative apomicts are sterile, reproduce apomictically, or are sexual to various degrees. Crosses between a facultative apomict, and the artificially produced sexual plant (X-750) of B. grahamii produce hybrids which are either facultative apomicts or they reproduce sexually. When the sexual plant is used as the female parent and crossed with a race that is essentially an obligate apomict, the progeny always reproduces as facultative apomicts. Apomixis in this group must, therefore, be inherited as a dominant character over sexuality.

Naturally occurring hybrids are euploids, and either facultative or essentially obligate apomicts. Hybridization at the polyploid level apparently became possible after the establishment of an apomictic mode of reproduction. Genetically controlled preferential chromosome pairing, demonstrated by Harlan and Chheda (1962), insures the formation of balanced gametes, and the possibility of further hybridization as well as introgression. Plants that reproduce strictly by sexual means are at a disadvantage. Their progenies are characterized by a large percentage of aneuploids, which will be eliminated by natural selection. Being completely sexual, and under experimental conditions largely self-sterile, these hybrids will cross readily with apomictic races. Apomixis, being dominant over sexuality, will give rise to introgressive derivatives which again reproduce apomictically. The ability of the facultative races to cross and produce strictly sexual plants, which in turn get swamped by apomicts, will increase

genetic variability. According to the population models of Wright (1935), such a breeding system should be close to maximum in evolutionary efficiency.

The maintenance of a sexual potential and the genetically induced preferential chromosome pairing are integrated systems. This, together with apomixis, permit the maximum amount of variability to be maintained in a population. Harlan and de Wet (1963) indicate that at this stage of evolutionary development, such a system is better designed for the destruction of species rather than the production of new ones. Such a population, however, has unlimited evolutionary potentialities. Combining genes from various species of different genera, adapted to a wide array of ecological and climatic niches, such a hybrid population is widely distributed over the range of the Bothriochloininae. Distinct biotypes, localized in particular ecological regions, and which maintain their unity of type by means of essentially obligate apomictic reproduction, are commonly encountered. The strictly African hexaploid D. papillosum, an introgressive hybridization derivative between D. annulatum and D. intermedia is an example.

For biotypes to become genetically isolated from each other, however, a change over to sexuality is necessary. This will be a long term project. Ecological, seasonal, or geographic isolation will lead to the formation of locally inbreeding populations. Selection will favor only apomicts or cytologically balanced sexually reproducing clones. Harlan and Chheda (1962) demonstrate that the genes controlling preferential chromosome pairing also induce nonhomologous pairing when close homologues are absent. Segmental interchange will eventually lead to the establishment of new karyotypes. Drastic environmental changes could eliminate the apomicts and new sexually reproducing

populations will evolve.

SUMMARY

1. Hybrids between facultative apomictic representatives, and between sexual and apomictic species within and between the genera <u>Bothriochloa</u> and <u>Dichanthium</u> reproduce either sexually or are apomicts.

2. Chromosome association during microsporogenesis in these hybrids is irregular, but degree of irregularity is not correlated with mode of reproduction.

3. Second generation progenies of sexually reproducing hybrids are characterized by a high degree of aneuploid plants.

4. As aneuploidy is rare in nature, although natural hybridization is commonly encountered, this cytological condition is selected against in nature.

5. Indirectly, therefore, plants that reproduce apomictically have a selective advantage over their sexual counterparts.

6. Such an apomictic population, which has the ability to hybridize, will be highly variable genetically, and should consequently be close to maximum in evolutionary potential.

CHAPTER V

THE GENETIC BASIS OF APOMIXIS IN THE BOTHRIOCHLOININAE

The grass genera Bothriochloa O. Kuntze, Capillipedium Stapf, and Dichanthium Willemet form an interrelated agamic-complex referred to as the Bothriochloininae for convenience. The various types of apomixis are fully discussed by Gustafsson (1946) and Stebbins (1950). Seeds in apomictic representatives of the Bothriochloininae are produced by means of pseudogamous apospory. Stebbins (1950) indicates that gametophytic apomixis must be controlled by a number of genes forming a genetically balanced system in sexually reproducing races. Interaction between these genes in different hybrid combinations may result in apomixis or sterility. The available data discussed by Gerstel and Mishanec (1950), Stebbins (1950), and Muntzing (1958) suggest that the apomictic condition is recessive to sexuality, but an increase in chromosome number often increases the tendancy towards sexuality.

The genetic basis for inheritance of apomixis and sexuality was studied in intraspecific, interspecific and intergeneric hybrids produced among representatives of the Bothriochloininae.

MATERIAL AND METHODS

Approximately 1000 hybrids were available for study. The majority of these were produced by W. L. Richardson, using facultative apomictic races of

46

various species as the female parent (Harlan et al. 1961). These include intra-specific, interspecific as well as intergeneric hybrids. Hybrids in which a sexual race of B. grahamii was used as the female parent were produced by H. R. Chheda (Harlan et al. 1961), while those having sexual D. annulatum as the female parent were supplied by A. P. Singh (Harlan et al. 1961).

Self pollinated progenies of 555 hybrids, as well as backcross populations in various combinations, were grown in a uniform nursery. These were studied cytologically and morphologically in order to determine the degree of sexuality.

RESULTS

Harlan et al. (1961) demonstrate that, in the Bothriochloininae, diploids reproduce sexually, tetraploids are facultative apomicts, and higher polyploids are essentially obligate apomicts. Exceptions are the high polyploid American representatives of Bothriochloa and some Australian tetraploid and hexaploid species of the same genus. Species that reproduce sexually are characterized strictly by bivalent formation among the chromosomes during microsporogenesis. Apomictic species behave cytologically like segmental allopolyploids. The chromosomes usually form bivalents during meiosis, although some chromo-somes often associate into multivalents or fail to pair at all. Hybridization between facultative apomicts, be it interspecific or intergeneric, does not severely affect chromosome pairing. Studies by de Wet, Mehra, and Borgaonkar (1961) indicate that the chromosomes usually pair preferentially between genomes derived from each parental species. Harlan and Chheda (1962) demonstrate that this mode of pairing is genetically controlled, and that nonhomologous pairing is

induced when close homologues are absent. Hybrids between naturally occurring sexual species, in which preferential chromosome pairing does not take place, are sterile due to an almost complete absence of chromosome homology.

Hybrids were produced between sexual plants as well as facultative apomicts, natural as well as artificially produced sexual plants, within and between ploidy levels. The apomictic species and hybrids exhibit from 0-22% sexuality. These are divided into obligate, and facultative apomicts. Obligate apomicts exhibit less than 1% segregation in the second generation, or less than 1% of the seed from emasculated florets of a female parent produce hybrid offspring. Facultative apomicts, in this classification, exhibit from 1-22% sexuality. Truly sexual plants produce strictly hybrid populations after emasculation and pollination, and 100% segregation in the second generation. Hybrid plants that are sterile produce no seed on selfing, and no functional pollen.

The data are summarized in Table VI. The majority of the second generation populations are strictly maternal, while a few appear to be fully sexual, and some are facultative apomicts. Many of these classed as obligate apomicts may represent facultative apomicts. The second generation populations only rarely exceeded 40 plants. The probability of observing genetic segregation among facultative apomicts in such a small population is limited.

The sexual tetraploid D. annulatum was obtained from doubling the chromosome number of a sexual diploid race. Hybridization between two facultative apomictic races gave rise to the sexual tetraploid B. grahamii. When the chromosome number of a facultative apomictic tetraploid plant of B. grahamii was doubled, the resulting octoploid is almost completely sexual in its breeding

TABLE VI

MODE OF REPRODUCTION OF HYBRIDS IN THE BOTHRIOCHLOININAE

Hybrid		$2n$	Number of Hybrids*			
			Ster	Sex	Fac	Obl
Sexual	**Sexual**					
D. annulatum (2n)	x D. annulatum (2n)	20		5		
D. annulatum (4n)	x D. annulatum (2n)	30	10			
		50	1			
	x D. panchganiense (2n)	30	7			
	x B. grahamii (4n)	40		20		
B. grahamii (4n)	x D. annulatum (2n)	30	3			
	x D. annulatum (4n)	40		20		
	x D. aristatum (2n)	30	5			
	x D. panchganiense (2n)	30	2			
	x B. longifolia (2n)	30	3			
B. saccharoides (6n)	x B. exaristata (6n)	60	6			
B. saccharoides (8n)	x B. decipiens (4n)	60	1			
B. saccharoides (12n)	x B. ambigua (6n)	90	3			
	x B. erianthoides (6n)	90	1			
	x B. saccharoides (6n)	90	8			
Fac. Apomict	**Sexual**					
D. annulatum (4n)	x D. annulatum (4n)	40		1	9	
		60			2	3
	x D. annulatum (2n)	30	2			
		50				4
B. grahamii (4n)	x B. grahamii (4n)	40			6	2
		60			1	
	x D. annulatum (2n)	50				3
		30	2			
	x D. annulatum (4n)	40		1	4	10
		60			1	2
B. ischaemum (5n)	x D. annulatum (4n)	70				1
Sexual	**Fac. Apomict**					
D. annulatum (4n)	x D. annulatum (4n)	40		1	4	10
		60		1	1	
	x D. aristatum (4n)	40			4	
	x D. caricosum (4n)	40		1	1	8

Table VI (Continued)

Hybrid		2n	Number of Hybrids*			
			Ster	Sex	Fac	Obl
	x B. grahamii (4n)	40		1	4	15
B. ambigua (6n)	x B. grahamii (4n)	50			2	
B. grahamii (4n)	x B. grahamii (4n)	40		1	5	24
	x B. glabra (4n)	40			3	1
	x B. intermedia (4n)	40			1	6
	x D. annulatum (4n)	40			2	18
	x D. aristatum (4n)	40				3
	x D. caricosum (4n)	40			1	2
D. annulatum (4n)	x (D. annulatum x D. fecundum) (4n)	40			5	
	x (B. grahamii x D. annulatum) (6n)	50			1	12
B. grahamii (4n)	x (B. grahamii x C. parviflorum) (4n)	40				8
Sexual	**Obl. Apomict**					
D. annulatum (4n)	x D. fecundum (4n)	40			3	
	x D. papillosum (6n)	50				14
B. ambigua (6n)	x D. ischaemum (4n)	50	2			
B. grahamii (4n)	x B. ewartiana (6n)	50				5
	x B. ischaemum (4n)	40				5
	x B. ischaemum (5n)	45	2			1
	x B. ischaemum (6n)	50				4
	x B. kantzeana (4n)	40				5
	x B. odorata (4n)	40				2
	x B. pertusa (4n)	40				2
	x C. caucasica (4n)	40	5			1
	x C. parviflorum (4n)	40				4
	x C. spicigerum (4n)	40				3
	x D. fecundum (4n)	40			1	4
	x D. papillosum (6n)	50				5
Fac. Apomict	**Fac. Apomict**					
D. annulatum (4n)	x D. annulatum (4n)	40			2	18
	x D. aristatum (4n)	40				4
		60				2
D. aristatum (4n)	x D. annulatum (4n)	40				2
	x D. caricosum (4n)	40	1		3	
		60				3
D. caricosum (4n)	x D. aristatum (4n)	40			1	1
		60				2

Table VI (Continued)

Hybrid		2n	Number of Hybrids*			
			Ster	Sex	Fac	Obl
B. grahamii (4n)	x D. annulatum (4n)	40				1
	x B. grahamii (4n)	40			1	7
	x B. grahamii (4n)	40	1		6	23
		60				8
	x D. intermedia (4n)	40			4	16
		60				2
	x D. annulatum (4n)	40			2	15
		60				1
D. annulatum (4n)	x (D. annulatum x D. annulatum) (4n)	40			1	6
	x (B. grahamii x D. annulatum) (4n)	40			1	
		60			1	

Fac. Apomict	Obl. Apomict	2n	Ster	Sex	Fac	Obl
D. annulatum (4n)	x D. papillosum (6n)	50				5
B. grahamii (4n)	x B. ewartiana (6n)	70				8
	x B. ischaemum (4n)	40			4	16
		60				3
	x B. ischaemum (6n)	50				2
		70				1
	x B. odorata (4n)	40				1
	x B. pertusa (4n)	40				1
		60				1
	x B. radicans (4n)	60				1
	x C. parviflorum (4n)	40				7
	x C. spicigerum (4n)					2

*Ster = Sterile; Sex = Sexual; Fac = Facultative Apomict; Obl = Obligate apomict.

behavior.

Hybrids between facultative apomicts usually reproduce apomictically. Occasionally the hybrid is completely sexual. More frequently the hybrids are facultative apomicts. The hybrids often exhibit no more sexuality than their parents, while in other crosses a range of hybrids, varying from almost completely sexual to essentially obligate apomicts, are obtained.

Both the cytologically reduced as well as unreduced female gamete of tetraploid facultative apomicts may function sexually or develop parthenogenetically. The hexaploid hybrids are usually facultative apomicts, although occasionally a completely sexual hybrid is obtained. Polyhaploids are always completely sterile. When facultative apomicts are crossed with an obligate apomict as the male parent the hybrids are always apomictic.

Hybrids between facultative apomicts as the female parent, and sexual races of the same or a related species, are apomicts, or they reproduce sexually. When the cytologically unreduced gamete of the facultative apomict is fertilized with a male gamete of a sexual tetraploid, the hexaploid hybrid reproduces apomictically. Similarly, pentaploid hybrids between a facultative apomictic tetraploid and a sexual diploid are apomictic, but the triploid hybrids are sterile. Using the sexual species as the female parent, the progeny is sterile when pollinated with a distantly related apomict, completely apomictic when the male parent is a related obligate apomict, and either sexual or apomictic when the male parent is a related facultative apomict.

Hybrids between distantly related sexual species are sterile due to the absence of chromosome homology. Artificially produced sexual races of

predominantly apomictic species, when crossed, gave rise to strictly sexual offspring. Triploid hybrids between sexually reproducing tetraploid, and sexually reproducing diploid races of the same or a related species are either sterile or lethal.

Backcross populations are either apomictic or reproduce sexually. The mode of reproduction being determined by both chromosome number, and breeding behavior of the parental species.

DISCUSSION

At the same ploidy level, hybrids between a sexual and essentially obligate apomict always reproduce apomictically. When crossed with a facultative apomict the hybrids either reproduce sexually or apomictically. Hybrids between sexually reproducing species are either sterile, due to absence of chromosome homology, or reproduce sexually when functional gametes are produced. These observations indicate that the apomictic mode of reproduction is dominant over sexuality.

Cytologically the apomicts behave like segmental allopolyploids as defined by Stebbins (1947). Bivalent formation is the rule, and functional gametes are always produced. The truly sexual species are characterized strictly by bivalent formation during microsporogenesis. Diploid species always reproduce sexually, and polyploids are either apomicts or strictly sexual. These observations indicate that polyploidy by itself does not induce apomixis. Furthermore, the artificially produced autotetraploid, derived from a sexually reproducing diploid, is sexual. Mode of chromosome pairing among the predominantly

apomictic polyploids is genetically controlled (Harlan and Chheda, 1962). In hybrids, the chromosomes usually pair preferentially between genomes derived from each parental species.

Genetic segregation will therefore follow the pattern described by Muller (1914), based on random distribution of chromosomes. Harlan et al. (1961) indicate that the apomictic species of Bothriochloa, Capillipedium, and Dichanthium form an interrelated generic-complex. The observed data indicate that the genes controlling mode of reproduction are present in each basic genome of the polyploids. Stebbins (1950) and Powers (1945) suggest that apomixis must be controlled by a number of different genes. These act in correlation with each other to produce a series of developmental disturbances. Only in one particular combination will all the requirements for sexual reproduction be met. This appears to be true also in members of the Bothriochloininae, and the genes controlling mode of reproduction, present on each basic genome, is inherited as a unit. Crossing over and chromatid segregation, as long as the chromosomes pair preferentially and are distributed at random, will not severely affect genetic ratios. For these reasons apomixis is assigned the symbol A and sexuality a. Each genome is assigned a number. The possible gene combinations are listed in Table VII.

Obligate apomictic tetraploids will have the genetic constitution AAAA. Facultative apomicts are divided into four classes, AAAa (II), AAaa (III), AaAa (IV), and Aaaa (V). Harlan et al. (1961) point out that sexual embryo sacs are always formed in the obligate apomicts, but that these are usually crowded out by numerous apomictic ones. Occassionally, less than 1%, hybrids are obtained

TABLE VII

GENE COMBINATIONS DETERMINING

MODE OF REPRODUCTION

Ploidy level	Genome	Reproduction	Possible Gametes*	Class
$2n$	a^1a^1	Sex	a^1	
$4n$	$A^1A^1A^2A^2$	Obl	$A^1A^2,\ A^1A^1A^2A^2$	I
	$A^1a^1A^2A^2$	Fac	$A^1A^2,\ a^1A^2,\ A^1a^1A^2A^2$	II
	$A^1A^1A^2a^2$	Fac	$A^1A^2,\ A^1a^2,\ A^1A^1A^2a^2$	II
	$a^1a^1A^2A^2$	Fac	$a^1A^2,\ a^1a^1A^2A^2$	III
	$A^1A^1a^2a^2$	Fac	$A^1a^2,\ A^1A^1a^2a^2$	III
	$A^1a^1A^2a^2$	Fac	$A^1A^2,\ a^1A^2,\ A^1a^2,\ a^1a^2,\ A^1a^1A^2a^2$	IV
	$A^1a^1a^2a^2$	Fac	$A^1a^2,\ a^1a^2,\ A^1a^1a^2a^2$	V
	$a^1a^1A^2a^2$	Fac	$a^1A^2,\ a^1a^2,\ a^1a^1a^2A^2$	V
	$a^1a^1a^2a^2$	Sex	a^1a^2	VI
$6n$	$A^1A^1A^2A^2A^3A^3$	Obl		
	$a^1a^1a^2a^2a^3a^3$	Sex	$a^1a^2a^3$	

*Based on chromosome distribution following preferential chromosome pairing, and on function of unreduced gametes.

when obligate apomicts are used as the female parent. These may have the genetic constitution AAAa. Facultative apomicts exhibit from 1-22 percent sexuality, but this does not seem to be correlated with the genetic constitution of the plants. Parental species showing 3% and another with 10% sexuality when crossed to a sexual female parent behave exactly alike in later generations.

Strictly sexual tetraploids, when crossed among each other, never produce apomictic offspring. Assuming genetic contitutions, and segregation as indicated in Table VII, crosses between sexual and facultative apomictic races will only rarely produce truly sexual hybrids (Table VIII). Homozygous recessive hybrids will result from crosses between sexual plants and facultative apomicts of classes IV and V (AaAa, Aaaa). The hexaploid hybrids behave as facultative, or obligate apomicts, except for one of the two hexaploids obtained when the cytologically unreduced female gamete of the sexual D. annulatum functioned sexually. This hybrid may represent a homozygous recessive, while the other combines one or two dominant genes with recessive ones. Hybrids between sexual and obligate apomictic tetraploids reproduce apomictically as could be expected. Similarly hybrids between facultative apomicts and obligate apomicts will reproduce apomictically.

Hybridization among facultative apomicts can produce truly sexual offspring only when representatives of class IV or class V cross among themselves, or between each other (Table VIII). All the other hybrids will either be facultative or obligate apomicts. Not a single truly sexual hexaploid was obtained experimentally when two facultative apomicts were crossed. This would suggest that even in a hexaploid, a single genome dominant for apomixis will induce

apomictic reproduction.

Triploid hybrids, representing crosses between either sexual or facultative apomictic tetraploids, and a sexual diploid, are always sterile. When the cytologically unreduced female gamete of a facultative apomict is fertilized by a sexual diploid, the pentaploid hybrids are always apomicts. Experimentally produced polyhaploids from tetraploid as well as hexaploid facultative apomictic hybrids are similarly sterile. Why apomixis cannot function in triploid hybrids as well as diploid and triploid polyhaploids, is difficult to explain. The diploids are characterized essentially by bivalent formation during microsporogenesis, although functional pollen is never produced. Sterility may be due to a physiological unbalance in both diploids and triploids.

The phylogenetic potential of such a partially apomictic population is unlimited, as pointed out by Clausen (1954, 1961). Within the Bothriochloininae, facultative apomixis makes possible, not only interspecific, but also intergeneric hybridization. Harlan and de Wet (1963) demonstrate that in such a breeding system, mechanisms which insure cross fertilization, others which promote the formation of balanced sexual gametes, together with apomixis, form a balanced genetic system. The result is a polymorphous population, adaptable to a large array of environmental conditions, and consequently capable of rapid evolution.

At this stage, however, species barriers are being broken down, and an unlimited number of biotypes are present in nature. Many of these are often regarded as species (de Wet, 1962), while others defy classification. Many of these are adapted to specialized ecological regions, are essentially obligate apomicts and form hybrid complexes which are referred to by Harlan and de Wet (1963) as compilospecies. These are apomicts that maintain contact with sexuality.

TABLE VIII

GENETIC CONSTITUTION OF AN INTERBREEDING TETRAPLOID

POPULATION CONSISTING OF SEXUAL, FACULTATIVE, AND

OBLIGATE APOMICTS

Class	Parents		$2\underline{n}$	Hybrid Genotypes*
	Sex	Obl		
VI x I	aaaa	AAAA	40	AAaa
	Fac	Sex		
II x VI	AAAa	aaaa	40	1AAaa, 1Aaaa
			60	AAAaaa
III x VI	AAaa	aaaa	40	Aaaa
			60	AAaaaa
IV x VI	AaAa	aaaa	40	1AAaa, 2Aaaa, 1aaaa
			60	AaAaaa
V x VI	Aaaa	aaaa	40	1Aaaa, 1aaaa
			60	Aaaaaa
	Fac	Fac		
II x II	AAAa	AAAa	40	1AAAA, 2AaAA, 1AaAa
			60	1AAAaAa, 1AAAaAA
II x III	AAAa	AAaa	40	1AaAa, 1AAAa
			60	1AAAaAa, 1AAaaAa, 1AAaaAA
II x IV	AAAa	AaAa	40	1AAAA, 3AAAa, 2AaAa, 1AAaa, 1Aaaa
			60	1AAAaAA, 2AAAaAa, 1AaAaAA, 1AAAaaa, 1AaAaAa
II x V	AAAa	Aaaa	40	1AAAa, 1AaAa, 1AAaa, 1Aaaa
			60	1AAAaAa, 1AAAaaa, 1AaaaAA, 1AaaaAa
III x III	AAaa	AAaa	40	AaAa
			60	AAaaAa
III x IV	AAaa	AaAa	40	1AAAa, 2AaAa, 1Aaaa
			60	1AAaaAA, 1AaAaAa, 2AAaaaA, 1AAaaaa
III x V	AAaa	Aaaa	40	1AaAa, 1Aaaa
			60	1AAaaAa, 1AAaaaa, 1AaaaAa
IV & IV	AaAa	AaAa	40	1AAAA, 4AAAa, 4AaAa, 2AAaa, 4Aaaa, 1aaaa
			60	1AaAaAA, 2AaAaAa, 1AaAaaa
IV & V	AaAa	Aaaa	40	1AAAa, 2AaAa, 1AAaa, 3Aaaa, 1aaaa
			60	1AaAaAa, 1AaaaAA, 1AaAaaa, 2AaaaAa, 1Aaaaaa
V & V	Aaaa	Aaaa	40	1AaAa, 2Aaaa, 1aaa,
			60	1AaaaAa, 1Aaaaaa

*Include combinations from reciprocal crosses.

Truly sexually reproducing plants must occasionally be produced, but are immediately swamped by the apomitts.

SUMMARY

The nature of inheritance of apomixis was studied in the generic-complex Bothriochloa, Capillipedium, and Dichanthium. Apomixis is inherited as a dominant character over sexuality.

Genes controlling mode of reproduction appear to be present in each basic genome of the polyploids. These genes are inherited as units, and the presence of one such unit in a polyploid ($4\underline{n}$, $5\underline{n}$, $6\underline{n}$) is sufficient to induce apomixis.

Polyhaploids derived from tetraploid facultative apomictic tetraploids, as well as triploid hybrids obtained from crossing facultative tetraploids and sexual diploids, are completely sterile. This may be due to a physiological unbalance which prevents these plants from reproducing apomictically.

Partial apomixis allows introgressive hybridization to take place within species, between species, as well as between some representatives of the three genera Bothriochloa, Capillipedium, and Dichanthium. Such a breeding system is polymorphic, highly adaptable, and consequently capable of rapid evolution.

At this stage of phylogenetic development, however, this genetic system is better designed for the destruction of species, than the production of new ones.

CHAPTER VI

THE RELATIONSHIPS BETWEEN DICHANTHIUM
ANNULATUM AND D. FECUNDUM

The species Dichanthium annulatum (Forssk.) Stapf and D. fecundum S.
T. Blake are closely related morphologically. Blake (1944), when describing the
latter species, indicates that it is usually regarded to be identical with D. annu-
latum, or else it is treated as a variety by Hackel (1889) and Domin (1915).
These two species are similar in habit, but D. fecundum differs conspicuously
from D. annulatum in having, except in the homogamous spikelet pairs at the base
of each raceme, bisexual sessile as well as pedicellate spikelets. This develop-
ment of a bisexual pedicellate spikelet is of particular interest, as it represents
the key character by which Pilger (1954) and de Wet (1962) distinguish some of
the assumed more primitive subtribes of the Andropogoneae.

The species D. fecundum, an obligate apomict, was crossed with a sexual
race of D. annulatum in an attempt to determine the relationships of these two
species and the mode of inheritance of the distinguishing character of pedicellate
spikelet.

MATERIAL AND METHODS

Hybrids were produced as described by Richardson (1958). The sexual
race of D. annulatum was used as the female parent. The hybrid obtained was

60

self pollinated, and the second generation grown and studied morphologically.

Backcrosses to D. annulatum were also produced, and the progeny of these
were also studied.

<div align="center">RESULTS</div>

The sexually reproducing D. annulatum is a tetraploid derived from
doubling the chromosome number of a diploid sexual plant of the same species.
The apomictic D. fecundum is a tetraploid, and behaves cytologically like a
segmental allopolyploid (Borgaonkar and de Wet, 1960). The autotetraploid D.
annulatum is characterized mostly by bivalent formation and normal chromo-
some reduction during microsporogenesis (de Wet, Mehra, and Borgaonkar, 1961).
These cytological data are summarized in Table IX.

The salient morphological characteristics of the parents and the hybrid
are summarized in Table X. In general appearance, this hybrid resembles the
male parent closely, except for inflorescence structure, and is characterized by
bisexual pedicellate spikelets. When this hybrid was self-pollinated, 18 plants
were obtained. These exhibit no or very little morphological variation and
resemble the F_1 hybrid in detail (Plate IV, Fig. 1). Apomixis, in this hybrid,
evidently behaves as a dominant over sexuality, and the second generation pro-
geny is consequently completely maternal. When backcrossed to D. annulatum,
116 plants were obtained. These were extremely variable morphologically
(Plate IV, Fig. 2), with 64 plants characterized by male pedicellate spikelets,
and 52 had bisexual pedicellate spikelets. Degree of sexuality among these plants
were not determined, but it could be assumed that some of them will reproduce

TABLE IX

CYTOLOGICAL DATA OF DICHANTHIUM ANNULATUM AND

D. FECUNDUM AND THEIR HYBRIDS

Species	2n	Chromosome Association*			
		I	II	III	IV
D. annulatum	40	0-4	12-20	0-1	1-4
		0.75	15.50	0.08	2.16
D. fecundum	40	0-3	15-20	0-1	0-2
		0.46	18.42	0.03	0.65
Hybrid (D. ann. x D. fec.)	40	0-4	17-20		0-1
		0.73	19.50		0.07
Backcross	40	0-2	18-20	0-1	0-1
D. ann. x (D. ann. x D. fec.)		0.25	19.58	0.08	0.08

*Range and average number of various configurations observed are listed.

63

TABLE X

MORPHOLOGY OF D. ANNULATUM, D. FECUNDUM AND THE

ARTIFICIALLY PRODUCED HYBRID

Character	D. annulatum	Hybrid	D. fecundum
Pedicellate Spikelet	Male	Bisexual	Bisexual
Raceme number	3-20	2-10	1-5
Average	5.5	3.7	3.2
Primary axis length	7-17 mm.	4-13 mm.	5-15 mm.
Average	11.6 mm.	9.5 mm.	10.9 mm.
Raceme length	59-76 mm.	63-80 mm.	56-104 mm.
Average	68.5 mm.	63.6 mm.	94.1 mm.

Plate IV

Morphology of Dichanthium annulatum, D. fecundum and their hybrids
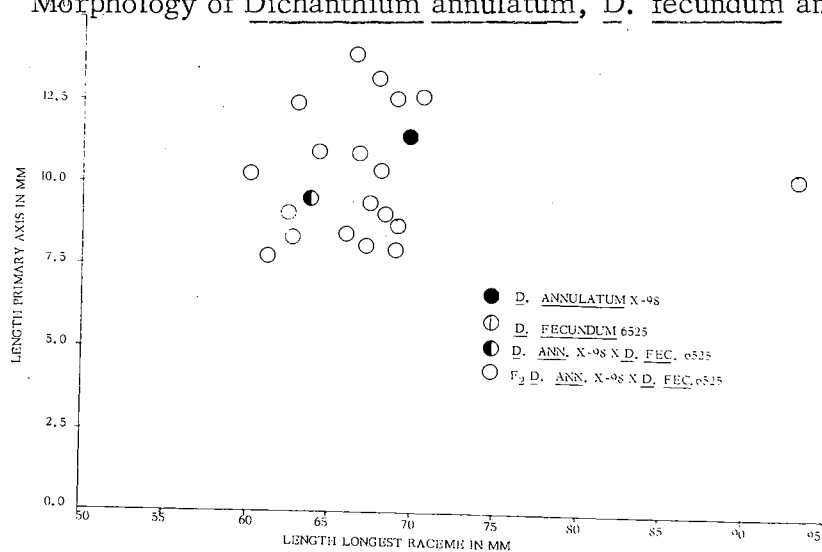
Figure 1. Morphological variation in the F_2 population of D. annu-
latum x D. fecundum apomictic hybrid.
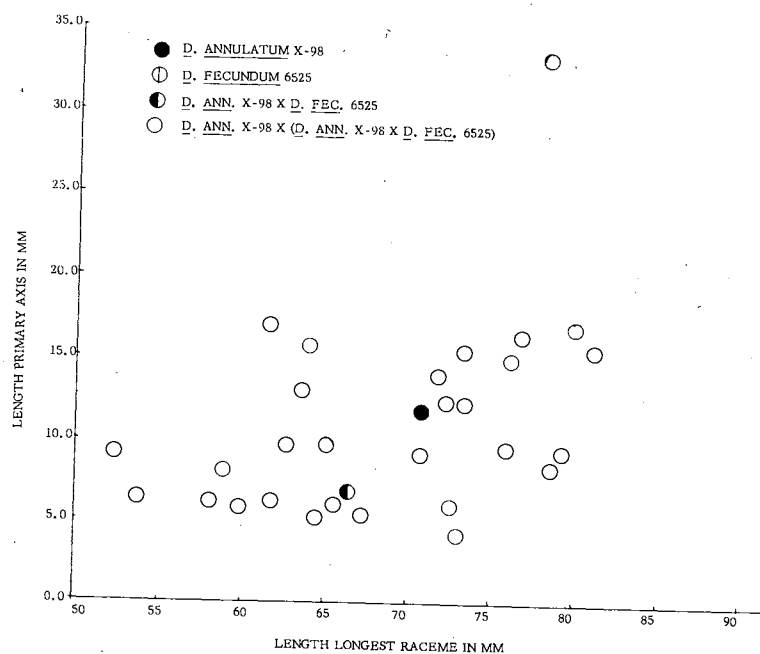
Figure 2. Morphological variation in the back-cross population
D. annulatum x (D. annulatum x D. fecundum).

sexually (cf. Chapter V).

The gene determining bisexual pedicellate spikelets is inherited as a simple dominant character over male pedicellate spikelets. This might have been expected. Within the genus Dichanthium, as well as the whole subtribe Andropogoninae, D. fecundum is the only species characterized by bisexual pedicellate spikelets. This change evidently came about, in this facultative apomictic tetraploid, through mutation. The sexual D. annulatum, being an autotetraploid, must have the recessive gene in four doses and may be assigned an ssss genetic consitution. The segmental allotetraploid D. fecundum may be homozygous dominant SSSS, or heterozygous SSSs, SSss, Ssss for this char- acter. If this mutation took place at the tetraploid level, which appears to be the case, the chances are that only one locus mutated. Being essentially an obligate apomict, no or very little genetic segregation will take place and the natural population will be strictly bisexual in respect to pedicellate spikelets. Functional pollen is always produced by D. fecundum. Assuming a genetic constiution of Ssss, both Ss and ss gametes can be produced. The hybrids between this species and D. annulatum should therefore be characterized either by bisexual or male pedicellate spikelets. Only three hybrids were obtained from 300 emasculated florets and these are all characterized by bisexual pedi- cellate spikelets.

Natural hybridization apparently takes place in Australia between plants of D. fecundum as well as between this species and D. annulatum. Some of the

Australian specimens filed with the herbarium of the Royal Botanic Gardens at Kew, England resemble D. fecundum in inflorescence structure, but are characterized by male pedicellate spikelets. Others again resemble D. annulatum more closely but have bisexual pedicellate spikelets (de Wet, 1962).

Be that as it may, the hybrid between D. annulatum and D. fecundum has at least one dominant gene for bisexuality of the pedicellate spikelet. This hybrid is highly apomictic and produces no genetic segregation in the second generation progeny. Backcrossed to D. annulatum, the expected segregation into plants with bisexual, and others with male pedicellate spikelets were observed. Assuming a genetic constitution of Ssss in the hybrid, the gametes will either be Ss or ss. Phenotypically, 50% of the back-cross generation plants should be male, and 50% bisexual in respect to pedicellate spikelet structure. This, essentially was the ratio obtained experimentally.

Numerous other morphological characters, such as pubescence, raceme number, raceme length, number of nodes of the inflorescence and racemes, and length of the primary axis of the inflorescence were also studied. These are variable within individual plants, and averages are used in constructing the scatter diagrams (Plate IV, Fig. 1, 2). For these reasons, these characters do not lend themselves to a cytogenetical study. They serve, however, to indicate that genetical segregation takes place, and that the distinguishing characters between these two species, except for bisexuality of the pedicellate spikelet, are only a matter of degree.

Cytological data do not serve to indicate clearly the relationships between these two species. Chromosome association in hybrids between species, and

also between races of the same species in the genus Dichanthium takes place preferentially between genomes derived from each parental plant (de Wet, Mehra, and Borgaonkar, 1961). When close homologues are absent, Harlan and Chheda (1962) demonstrate that non-homologous chromosome pairing is genetically induced.

From a biosystematic point of view, D. annulatum and D. fecundum should be combined into a single taxonomic unit. Valentine and Love (1958) point out that, in apomictic groups, a species concept based on the absence of gene exchange cannot be applied. Mutation will give rise to a number of distinct biotypes (Baker, 1959), each one often adapted to a distinct ecological niche. Although morphologically, and often also ecologically distinct, these should not be recognized as biological species. This study indicates that as soon as the apomictic barrier is broken down, the characters separating these two species have no taxonomic significance. The species concept in apomictic groups is fully discussed by Gustafsson (1947b), Stebbins (1950), Rollins (1950) and Valentine and Love (1958). From a practical point of view D. fecundum should be regarded as a variety of D. annulatum. The latter species is widely distributed in India, extends eastward to Australia and westward to central Africa. The other, D. fecundum, appears to be endemic to Australia. Logically the varietal name D. annulatum var. monostachya F. Meull. (ex Bentham, Fl. Austral. 7, 531. 1878) should be adopted. The name, however, suggests a plant with a single raceme, whereas raceme number in D. fecundum varies from one to five. Domin's varietal name, D. annulatum var. gradispiculatus (in Biblioth. Bot. 20, 85, 269. 1915) also does not describe this plant in detail.

For these reasons Blake (1944) bases his description of D. fecundum on a new type. The varietal combination D. annulatum var. fecundum (Blake) comb. nov. is therefore proposed to include all plants resembling D. annulatum, but which differ from this species in the bisexuality of the pedicellate spikelets.

CONCLUSIONS

1. The major distinguishing character between Dichanthium annulatum (Forssk.) Stapf and D. fecundum S. T. Blake, bisexuality of the pedicellate spikelet, is inherited as a simple dominant.

2. Dichanthium fecundum is predominantly apomictic, and consequently may have arisen from D. annulatum through mutation.

3. The new taxonomic combination D. annulatum var. fecundum (S. T. Blake) comb. nov. is proposed to include plants presently referred to as D. fecundum.

CHAPTER VII

APOMIXIS AND SPECIATION IN THE BOTHRIOCHLOININAE

The Andropogoneae, subtribe Andropogoninae (Pilger, 1954), includes a diverse group of genera subdivided by de Wet (1962) into a number of generic-complexes. The Bothriochloininae is characterized by sessile spikelets with 2-keeled lower glumes having inflexed margins, and the stipitiform lemma of the bisexual floret passes directly into an awn. In these respects it differs from other generic groups. Seven genera are included. The monotypic Australian endemic Spathia neurosa Ewart et Archer was not available for cytogenetical studies. M_0 rphological data, however, suggest affinities with Dichanthium. The genus Indochloa Bor is represented by two species, I. clarkei (Hack.) Bor and I. oligantha (Hochst.) Bor, both localized endemics in India. These species are unknown cytologically and their phylogenetic affinities within the Bothriochloininae are not clear. Two species of Eremopogon Stapf are recognized by de Wet (1962). One, E. tuberculatus (Hack.) A. Camus is an Indian endemic, and the other, E. foveolatus (Del.) Stapf is widely distributed in the drier regions extending from India to Africa. Harlan et al. (1961) indicate that this genus is genetically isolated from the others included in the Bothriochloininae. Morphological data suggest affinities with Schizachyrium Nees belonging to the generic group Andropogoninae. The monotypic Euclasta condylotricha (Hochst.) Stapf is present in both tropical Africa and tropical America. Spikelet morphology suggests affinities with Dichanthium, but these two genera are isolated

genetically. The three genera Bothriochloa O. Kuntze, Capillipedium Stapf and Dichanthium Willemet each includes a large and diverse group of interrelated species. The latter genus extends throughout the tropics and subtropics of the Old World. The greatest concentration of species belonging to Capillipedium is in India and southeast Asia. One species, the morphologically variable C. parviflorum (R. Br.) Stapf, extends from India to Japan, Australia, and southern Africa. Only this species and its close relatives were studied in detail. Two distinct species groups are evident in the genus Bothriochloa. The members of the group, confined to the warmer parts of the Americas, are high polyploids, reproduce sexually and appear to be closely related to some Australian species. The other group is widely distributed throughout the tropics and subtropics of the Old World and mostly reproduces apomictically.

The relationships within and between the genera Bothriochloa, Capillipedium, and Dichanthium will be discussed.

MORPHOLOGY

The generic limits of these three genera are not always distinct. Classically, Hackel (1889) includes them with the genus Andropogon Linn. as sections. Stapf (1917), however, indicates that they differ so conspicuously from Andropogon, and except for some dubious species also from each other, that each of these deserves generic rank. From Andropogon they differ most conspicuously in respect to lemma characteristics. The bisexual florets are awned from the sinus of a bilobed lemma in Andropogon, while the lemma forms the hyaline base of the awn in members of the Bothriochloininae. Two Australian species,

Bothriochloa biloba S. T. Blake and B. eriantholdes (F. Meull.) C. E. Hubbard, resemble Andropogon in having bilobed lemmas. They, however, resemble Bothriochloa more closely in respect to inflorescence structure. The species Dichanthium polyptychuun (Steud) A. Camus with bilobed lemmas was referred to Andropogon by de Wet (1962).

The two genera, Bothriochloa and Dichanthium may be subdivided into a number of morphologically similar species-complexes. Four major groups are recognized in the genus Dichanthium and six groups in Bothriochloa.

RELATIONSHIPS WITHIN DICHANTHIUM. -- Relationships within this genus are discussed by de Wet and Richardson (1963). Two diploid complexes are recognized. The Australian group includes D. humilius J. M. Black, D. sericeum (R. Br.) A. Camus, D. setosum S. T. Blake and D. superciliatum (Hack.) A. Camus. These are characterized by sessile or subsessile racemes which are fasciculate, and the lower glume of the sessile spikelets is long ciliate above the middle, usually forming a subapical arch. They are distinguished, the one from the other, mostly by raceme number and distribution of cilia on the lower glumes. It was suggested by de Wet and Harlan (1962) that these species represent nothing more than distinct biotypes of D. sericeum isolated from each other by means of self fertilization. Hybrids within this group are almost impossible to produce as they are cleistogamous under Oklahoma climatic conditions. The other diploid complex is confined to India, and includes species characterized by pedicellate spikelets having the lower glumes armed with marginal bulbous-based bristles. Two of these, D. maccannii Blatter and D. panchganiense Blatt. et McCann are characterized by indentations (pits) on

the lower glume of the sessile spikelets. The latter species differs from D. armatum (Hook. f.) Blatt. et McCann conspicuously only in respect to this character. Morphologically these species resemble the genus Indochloa in having, except for the lower 1-6 homogamous spikelet pairs, the remaining spikelets of each pair both heterogamous and heteromorphous. Hybridization within this group are now being attempted. Relationships with D. annulatum were demonstrated in a cross between this species and D. panchganiense.

The remaining two groups are mostly polyploid and reproduce apomictically. Celarier, Mehra, and Wulf (1958) demonstrate that D. annulatum (Forssk.) Stapf may be subdivided into a tropical and a mediterranean ecotype. Harlan et al. (1961) reconstruct the hexaploid species D. papillosum (Hochst.) Stapf almost in detail by crossing tetraploid representatives of the two D. annulatum ecotypes. The latter species is characterized by diploid as well as tetraploid races. Relationships between D. caricosum (Linn.) A. Camus and D. aristatum (Poir.) C. E. Hubbard were discussed by Celarier, de Wet, and Bakshi (1962). To this species complex also belongs D. pallidum (Hook. f.) Stapf, D. tenue (R. Br.) A. Camus, and D. theiniwinii Bor which may represent apomictic biotypes of D. caricosum. Artificial hybrids were produced between D. aristatum and D. caricosum, and morphological data presented by Celarier, de Wet, and Richardson (1961) indicate that these two species also hybridize in nature. The species D. aristatum is genetically isolated from D. annulatum but apomictically reproducing hybrids between the latter species and the other species included in this complex can be produced with relative ease. Assumed natural hybrids, as well as artificially produced hybrids between D. aristatum and

D. caricosum also cross readily with D. annulatum.

The affinities of two imperfectly known species, D. andringitrense A. Camus and D. mucronulatum Jansen, are uncertain. Morphological data suggest relationships with both D. annulatum and D. caricosum.

RELATIONSHIPS WITHIN BOTHRIOCHLOA. -- The two diploid species-complexes are confined to India. Both of these appear to be related to the widely distributed B. intermedia (R. Br.) A. Camus. The one group, includes the diploid B. compressa (Hook. f.) Henrard the tetraploid B. woodrowii (Hoof. f.) A. Camus, and the cytologically unknown species B. ensiformis (Hook. f.) Henrard. These species differ from each other mainly in degree to which the culms are compressed, and minor inflorescence characteristics.

The other diploid group includes B. concanensis (Hook. f.) Henrard, B. kuntzeana (Hack.) Henrard, and B. longifolia (Hack.) Bor. Inflorescence structure suggests affinities with B. pertusa (Linn.) A. Camus and growth habit indicates relationships with B. intermedia. Hybrids within and between these groups have as yet not been produced. Their localized distribution and morphological characteristics (Harlan et al. 1961) indicate that they may represent relics of the original basic stock which gave rise to the polyploid species of this genus. Attempts to hybridize tetraploid B. intermedia and B. longifolia, however, were not successful.

The Australian tetraploid B. decipiens (Hack.) C. E. Hubbard, the hexaploids B. ambigua S. T. Blake and B. eriantholdes (F. Meull.) C. E. Hubbard, and the cytologically unknown B. biloba S. T. Blake resemble the American

polyploid species-complex in inflorescence structure. The racemes are sessile or subsessile, and the spikelets are often almost completely covered by long silky hairs on the pedicels and rachis. Singh and de Wet (1961) indicate that sterile hybrids between members of this group and the American complex can be produced.

The remaining species could be subdivided into three large complexes. The more typical European species B. ischaemum (Linn.) Keng which extend eastward to China and adjacent islands appear to hybridize in nature with B. intermedia wherever these two species are sympatric (Harlan, 1963). Artificial hybrids between these two species can be produced with relative ease (Harlan et al. 1961), and the species B. oryzetorum (Hack.) Bor, and B. pseudoischaemum (Nees) Henrard may represent apomictic derivatives of introgressive hybridization between B. intermedia and B. ischaemum.

The widely distributed B. intermedia (R. Br.) A. Camus is extremely variable morphologically. A number of species, B. ewartiana (Domin) C. E. Hubbard, B. grahamii (Haines) Bor, B. glabra (Roxb.) A. Camus, B. haenkei (Presl.) Ohwi, and B. odorata (Lisboa) A. Camus are usually recognized (de Wet 1962). These species reproduce apomictically, can be crossed artificially in various combinations, and are so interlinked morphologically as to form a single coherent species-complex (Harlan et al. 1961).

The species-complex B. acidula (Stapf) de Wet, B. insculpta (Hochst.) A. Camus, B. panormitana (Parl.) Pilger, B. pertusa (Linn.) A. Camus, and B. radicans (Lehm.) A. Camus form a group in which the individual species are often difficult or impossible to identify with certainty. They reproduce

apomictically, and are tetraploids except for B. insculpta which is mostly hexa-ploid or pentaploid. Attempted hybrids between members within this complex were not successful. Tetraploid representatives of B. pertusa and B. intermedia, however, hybridize. Morphological data indicate that the B. insculpta may have originated from such a cross. The remaining species may represent apomicti-cally reproducing eco-biotypes of B. pertusa.

RELATIONSHIPS WITHIN CAPILLIPEDIUM. -- Only C. parviflorum (R.Br.) Stapf, and its apparently close relatives C. arachnoideum Henrard, C. caucasicum (Trin.) de Wet and C. spicigerum S. T. Blake were studied in detail. Both the latter two species may represent derivatives of introgressive hybridization between Bothriochloa intermedia and C. parviflorum (de Wet, Harlan, and Faruqi, 1963; Harlan and Chheda, 1963).

The species C. parviflorum is widely distributed, highly variable morph-ologically, and characterized by both diploid and tetraploid races. This species apparently also forms an integrated complex with C. assimile (Steud.) A. Camus widely distributed in northern India, southeast Asia, and China. These two species differ from each other mainly in growth habit (Bor, 1960). Capillipedium caucasi-cum, confined to the Caucasus region is included with the genus Bothriochloa by Henrard (1940) and Hubbard (1939). Inflorescence structure, however, places it more nearly in the genus Capillipedium. Blake (1944) described C. spicigerum from Australia to include plants intermediate in morphological characteristics between Capillipedium and Bothriochloa.

RELATIONSHIPS BETWEEN THE GENERA BOTHRIOCHLOA, CAPILLIPE-DIUM AND DICHANTHIUM. -- Conclusive evidence of intergeneric hybridization

between these three genera was presented by Harlan et al. (1961). Natural hybridization between B. intermedia and both D. annulatum and C. parviflorum was demonstrated by de Wet, Harlan, and Faruqi (1963). The genera Capillipedium and Dichanthium are genetically isolated from each other. Harlan and de Wet (1963) indicate that B. intermedia, as recognized by them, includes a hybrid complex, referred to as a compilospecies. This compilospecies (Plate V, Fig. 2) comprises a gene pool which includes genetic material of the genera Dichanthium and Capillipedium as well as B. ischaemum and probably also other species of Bothriochloa.

Over its complete range of distribution B. intermedia is sympatric with C. parviflorum and D. annulatum. On the basis of gross morphological characteristics Bor (1960) subdivides the compilospecies B. intermedia into three different species. Plants with 10-25 simple or sparsely branched racemes arranged on an elongated primary axis are referred to B. intermedia (R. Br.) A. Camus. This species is further characterized by 30 or more spikelet pairs per raceme, and the spikelets are lanceolate in outline. Particularly in Africa and Australia the majority of specimens are characterized by strongly branched racemes consisting of 15-25 spikelet pairs. These plants are usually referred to B. glabra (Roxb.) A. Camus. Artificially produced hybrids between B. intermedia and C. parviflorum (de Wet, Borgaonkar, and Chheda, 1961) indicate that plants included with B. glabra could have originated from such a cross. Introgressive hybridization may explain the range of morphological variation observed among plants in regions where these two species are sympatric. The Australian species, C. spicigerum as well as C. caucasicum confined to the

77

Plate V
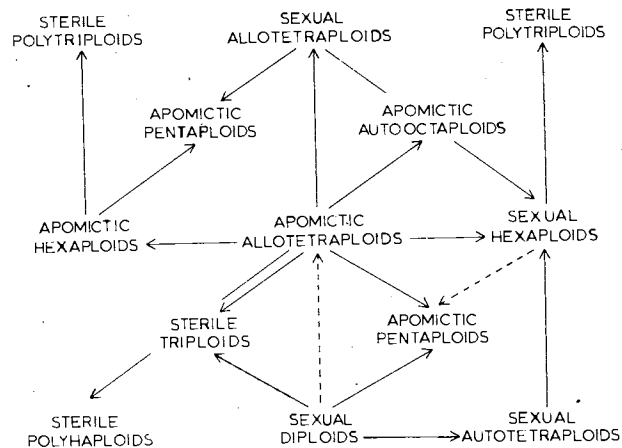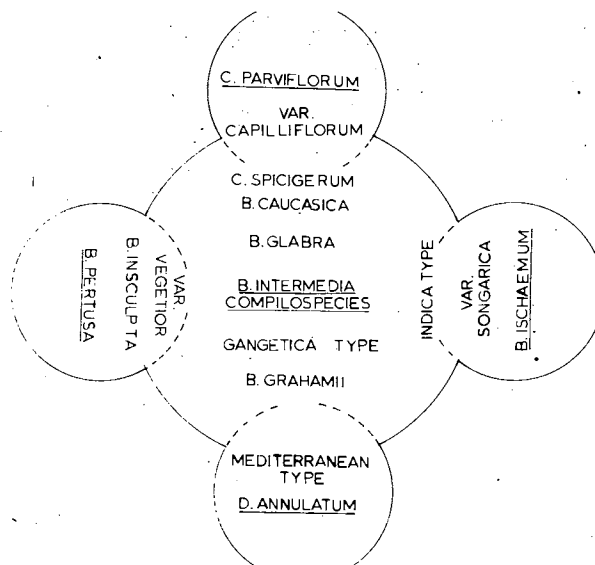
Relationships in the Bothriochloininae

Figure 1. A typical agamic complex in the Bothriochloininae.

Figure 2. Relationship between Bothriochloa, Capillipedium, and Dichanthium.

Caucasus, apparently represent well established apomictic biotypes derived from introgression with C. parviflorum.

Indian plants resembling B. intermedia, but having the racemes subequal in length to the primary axis of the inflorescence, and oblong-lanceolate spikelets, represent hybridization derivatives with D. annulatum (Harlan et al. 1961). Bor (1960) describes B. grahamii to include these plants, and Celarier and Harlan (1955) refer to them as the Gangetica race of B. intermedia. These plants resemble Dichanthium in detail, except that the lower sessile spikelets on each raceme are bisexual and awned. In contrast, Dichanthium is characterized by 1-6 male and awnless spikelets at the base of the racemes.

In western Pakistan and northern India introgressive hybridization between B. intermedia and the more typical European species B. ischaemum is obvious (Harlan, 1963). Artificial hybrids between these two species resemble these assumed natural hybrids in detail morphologically and cytologically. Celarier and Harlan (1958) suggest that B. ischaemum var. songarica may have originated through hybridization between these two species.

Morphological data suggest that B. pertusa also contributes genes to the B. intermedia compilospecies. The typically African species B. insculpta, resembles artificially produced hybrids between certain biotypes of B. intermedia and B. pertusa. This species-complex is now being studied in detail.

DISCUSSION

Evolution within each of the genera Bothriochloa, Capillipedium, and Dichanthium was probably governed, at the diploid level, and again later in the

polyploid level, by the classical forces of mutation, recombination, selection, and isolation. Each genus is characterized by sexually reproducing diploid, and essentially apomictic polyploid species. At the diploid level, at least at the present time, these three genera are genetically isolated. Morphological data suggest that not one of the polyploid species, except for the compilospecies, B. intermedia, combines genes from any two or all three of these genera. The Old World polyploids behave cytologically like segmental allopolyploids, and are extremely variable morphologically. These are mostly apomicts, but always maintain some contact with sexuality. Mutation, together with occasional hybridization consequently could give rise to a large number of distinct biotypes. The presence of sexually reproducing allopolyploids in the New World would suggest a world-wide distribution of Bothriochloa some time in the past.

Apomixis, together with genetically controlled preferential pairing in the segmental allopolyploids (Harlan and de Wet, 1963) made intergeneric as well as interspecific hybridization possible. This, however, only takes place between the compilospecies B. intermedia and various members of Capillipedium and Dichanthium. Even at the polyploid level the latter two genera are completely isolated genetically.

The original B. intermedia, which initiated this chain of interspecific and intergeneric hybridization, could not be distinguished among 300 collections studied. These represent biotypes collected over the complete range of the species, extending from southern Africa to Australia. The basic B. intermedia was probably completely swamped by an influx of genes from species of the same and the two related genera. Hybridization within this compilospecies gave rise

to a complex that defies classification.

The net result of such a genetic system, as indicated by Harlan and de Wet (1963), is a heterozygous population capable of rapid evolution. At this stage of evolutionary development, however, this system is better designed for the destruction of species, than for the production of new ones. Apomixis provides a means for rapid colonization of new habitats, and morphologically distinct biotypes can be maintained indefinitely.

Harlan and Chheda (1962) demonstrate that the genes which control preferential pairing also induce some degree of non homologous pairing. This process should eventually lead, through segmental interchange, to a cytologically balanced system. At the present time apomixis provides an escape from sterility and a genetic system in which segmental interchanges are possible when cytologically reduced gametes are produced.

This is also true of polyploid species-complexes within the genera Bothriochloa and Dichanthium (Harlan et al. 1961; de Wet and Richardson, 1962). The cytology and breeding behavior of a typical agamic complex is presented in Plate V, Fig. 1. Apomixis and a sexual potential are nicely balanced, and heterozygosity is increased through the ability of both the cytologically reduced as well as unreduced female gametes to function sexually or develop parthenogenetically. Evidently, as also demonstrated by Clausen (1961) for the genus Poa, hybridization is actually facilitated by apomixis. This wreckage of species will continue as long as the hybrids can reproduce apomictically. Sexually reproducing plants, can be obtained from crossing two facultative apomicts. Apomixis in these genera is inherited as a dominant character over sexuality. Through selection,

however, cytologically unbalanced offspring will be eliminated in the sexually reproducing biotypes. This may eventually lead to genetic isolating mechanisms, and the establishing of completely new species.

CONCLUSIONS

1. The genera Bothriochloa, Capillipedium, and Dichanthium are genetically isolated from each other at the diploid level.

2. At the polyploid level this is also true of Capillipedium and Dichanthium One species-complex, D. intermedia, on the other hand, hybridizes both in nature and under artificial conditions with representative of both the other two genera.

3. Hybridization is made possible by the maintenance of a sexual potential, genetic controlled preferential chromosome pairing,and apomixis.

4. At this stage of evolutionary development introgressive hybridization together with apomixis are breaking down species as well as generic barriers.

5. New biological species could develop from these apomictic biotypes only after new genetical isolating mechanisms become established.

6. This could take place through the establishment of a balanced cytological system by means of segmental interchange and sexual reproduction.

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