VARIATION AND SPECIES RELATIONSHIP IN THE BOTHRIOCHLOA PERTUSA COMPLEX

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PREFACE

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

The writer wishes to express her deepest gratitude to Dr. J. M. J. de Wet, Associate Professor of Botany and Plant Pathology, for his competent guidance and encouragement throughout the study. Indebtedness is also acknowledged to Dr. Walter W. Hansen, Head, Department of Botany and Plant Pathology; Dr. Eddie Basler, Associate Professor of Botany and Plant Pathology; Dr. James S. Brooks and Dr. Jack R. Harlan, Professors of Agronomy; and Dr. L. Herbert Bruneau, Associate Professor, Zoology; for their contributions as members of the advisory committee. Appreciation is expressed to Mr. Robert M. Ahring and Mr. William L. Richardson, Assistant Professors, Agronomy, for their assistance in greenhouse and field studies. Special indebtedness is due the late Dr. Robert P. Celarier, Associate Professor, Botany and Plant Pathology, whose inspiration and guidance provided the impetus for this study.

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CHAPTER I

INTRODUCTION

The taxonomic unit *Andropogon pertusus* (Linn.) Willd. was recognized by Hackel (1889) to include all plants of subgenus *Amphilopis* with subdigitately arranged racemes and pitted spikelets. Australian material was referred to *A. pertusus* var. *decipiens*; Indian representatives to *A. pertusus* var. *insculptus* subvar. *bifoveolatus*, *A. pertusus* var. *longifolius*, and *A. pertusus* var. *wightii*; plants from Africa were subdivided among *A. pertusus* var. *capensis*, *A. pertusus* var. *insculptus* subvar. *trifoveolatus*, and *A. pertusus* var. *vegetior*; while plants collected in Sicily were included in *A. pertusus* var. *panormitana*. The taxonomic problem was further complicated by Stapf (1895) who described *A. pertusus* from Africa based on a new type not resembling that of Linneaus. More recently Camus (1919) described *A. pertusus* var. *barbatus* from South-east Asia, and Maire (1928) described *A. pertusus* var. *maroccanum* from North Africa.

Members of *Andropogon* subgenus *Amphilophis* were later transferred to the genus *Bothriochloa* O. Kuntze, and the varieties of *A. pertusus* were variously classified by Camus (1931), Herter (1940), Henrad (1940, 1941), Pilger (1940), Blake (1944), Maire (1952, 1959), Parodi (1958), and Bor (1960). The species usually recognized, *B. decipiens* (Hack.) C. E. Hubb., *B. insculpta* (Hochst.) A. Camus, *B. longifolia* (Hack.) Bor, *B. panormitana* (Parl.) Pilger, *B. pertusa* (Linn.) A. Camus, and

B. radicans (Lehm.) A. Camus were studied in detail. This included cytological and biosystematic studies of collections referable to each taxonomic unit collected, as far as possible, over the complete distribution range of each species.

The Indian representatives of B. pertusa and B. insculpta extend from West Pakistan through India and southern Asia to Indonesia. The African representatives of these two species, as well as B. radicans, are widely distributed throughout the tropical and subtropical regions of this continent. Typical B. panormitana is confined to Sicily. African plants resembling this species extend from Morocco to southern Africa. Bothriochloa decipiens is widespread in Australia, where it appears to be endemic, and B. longifolia is endemic to India.

Crosses were also attempted between the various taxonomic units usually recognized. The data obtained were used in an effort to solve two major problems. First to determine the phylogenetic affinities of the members of the B. pertusa complex, and second to arrange these taxonomic units into a classification system which will express their relationships.

Taxonomy of Apomictic Groups

The chromosome number reported for Indian B. pertusa and B. insculpta is 2n = 40 (Celarier, 1956; Gould, 1956; and Harlan et al., 1958, 1961) and for the African representatives of these species, 2n = 50 and 2n = 60 were reported by de Wet and Anderson (1956), Celarier (1956), Gould (1956), de Wet (1958), and Harlan et al. (1958, 1961). The chromosome number of B. decipiens is 2n = 40, and of B. radicans is 2n = 40 (Harlan et al., 1961). Cytological, genetical, and morphological data (Harlan et al., 1961) indicated that members of the B. pertusa complex form an apomictic complex composed primarily of segmental alloploids.

Complexes in which apomixis and polyploidy exist present a taxonomic problem and have been treated in a number of ways by different systematists. Classically, each distinguishable apomictic clone could be recognized as "species". Babcock and Stebbins (1938) indicated that this method may be satisfactory only when applied to groups of obligate apomicts which are relatively few in number and are separated by relatively clear differences, as in Newfoundland representatives of Antennaria. Du Rietz (1930) defended this method on the basis that the various individuals of a clone are genotypically identical, thus making each clone a taxonomic unit of extreme homogeneity, and if the species-concept is to be based on the principle of discontinuity, each morphological distinct clone should be a species. This opinion was criticized by Muntzing, Tedin, and Turesson (1931), Fernald (1933), Turrill (1938), Babcock and Stebbins (1938), Stebbins (1941, 1950), and Gustafsson (1946, 1947 a, b) on the basis that the system is impractical. This would result in large numbers of described "species", for example, in Hieracium where over 5,000 apomictic clones are known. Some of these clones may be distinct species, but in other complexes they may be trivial variations which, under normal sexual reproduction, would quickly be lost in a common blend.

After attempting to classify apomictic complexes, especially those containing facultative apomicts, by the criteria of sexual species distinction, some systematists have come to the conclusion that sexual and asexual groups must be distinguished and divided into species by different criteria (Turesson, 1926, 1929, 1943; Du Rietz, 1930; Dobzhansky, 1941; Babcock and Stebbins, 1938; Stebbins, 1941, 1950; Camp and Gilly, 1943; Gustafsson, 1947 a, b). Dobzhansky (1941) and Babcock and Stebbins (1938) point out that the processes, polyploidy, hybridization, and apomixis which form an agamic complex blot out the differences that would be present between sexual species; thus, "the species, in the case of a sexual group, is an actuality as well as a human concept; in an agamic complex it ceases to be an actuality." As a result of this breakdown of the criteria of sexual species distinction when applied to asexual groups, a number of methods using special criteria to treat the agamic complexes systematically have been attempted.

Turesson (1926, 1929) proposed the term agamospecies for an apomictic population composed of individuals having a common origin. The forms or biotypes were denoted as forma apomicta if exclusively apomictic in reproduction, forma amphimicta if they are sexual and thus can interbreed to the largest extent with other types, and forma amphi-apomicta, if they are facultative apomicts. Turesson (1943) indicated an ecological variation occurs within each microspecies of Alchemilla vulgaris Linn. He paralleled it with ecotype formation of the sexual species, using the terms amphimict, ecotype, ecospecies, and amphimict-coenspecies for the sexual populations; and apomict, agamotype, agamospecies, apomict-coenospecies for the asexual populations.

Du Rietz (1930), dealing with strictly asexual species, divided apomicts into two types by using the terms simple and compound as proposed by Cockayne and Allan (1927). The simple asexual species consists of a single strictly asexual, biotype. This would probably include many of the apomictic species of Hieracium and Taraxacum. The compound species consists of several, practically indistinguishable, strictly asexual biotypes as in Alchemilla, and would include many of those species already divided by taxonomists on morphological characters, and should not be reclassified because of experimental data.

Agamic complexes were divided in two species groups, the apogameon and agameon by Camp and Gilly (1943). The apogameon is a species containing both apomictic and non apomictic individuals. In its simplest form it would consist of sexual forms and a single apomictic clone, each of probably wide dispersal over the same area. If these were morphologically different and different in distribution, they were differentiated as subspecies. The agameon, a species consisting of only apomictic individuals, could be of two types. It might be a segment of an apomictic complex, or of a group which is phylogenetically no longer active, with the sexual members few or absent.

In the treatment of Crepis, Babcock and Stebbins (1938) worked out a procedure which they considered to be theoretically sound and also practical. The whole of an agamic complex must be studied thoroughly. All the diploid forms must be identified and their morphological characteristics tabulated. These are then divided into species according to their morphological differences. The apomicts, which fall within the range of variation of the diploids as well as the partial allopolyploid partial apomicts are grouped, according to their degree of variation, into agamospecies. Each agamospecies contains apomicts which appear to have the same, or a similar hybridization origin, and approximately the same degree of variation between them as have the diploid species. This result is a rather polymorphic species with more or less artificial limits. After dividing the complex into species, the diploid forms are described and then, if needed, the species are further divided into subspecies and varieties on the same basis as are sexual species. The apomictic forms are not given taxonomic status comparable to subdivisions of sexual species but are divided as suggested by Turesson (1926). By this method seven sexual primitive species and two amphi-apomictic agamospecies were distinguished in Crepis and the other apomicts were attached as formae apomictae to one of these nine species.

Gustafsson (1946, 1947 a, b), who did an extensive study on apomixis, believes that each apomictic group must be treated differently according to its biological properties. To show this, he analyzed the data from thirty-five apomictic and amphi-apomictic complexes and groups of complexes, and divided them into two different series according to their complexity. In the first series, apomicts are included in one distinct complex and further divided into three parts. First, apomicts and amphimicts which are morphologically similar and which are united into a single unit, include such complexes as Lilium bulbiferum and L. croceum, Rubus idaeus, Ranunculus ficaria, Deschampsia caespitosa, and Poa bulbosa. Second, included in the apomicts which form an independent population, related to one or more sexual populations are Saxifraga foliolosa, Stellaria crassipes, Hypericum perforatum, Ochna serrulata, and Deschampsia alpina. Third, apomicts which form a closed system, unrelated to definite sexual populations include Polygonum viviparum, Cardamine bulbifera, Saxifraga cernua, Poa compressa, and Houttynia cordata.

The second series, made up of apomicts belonging to two or more different complexes which merge into one another, is also divided into three sections. First, apomictic complexes which are directly related to diploid populations but which stay distinct in nature, are *Parthenium argentatum* and *P. incanum*, *Calamagrostis epigeios*, *C. canescens*, *C. arundinacea* and *C. neglecta*, *Sorbus*, *Crepis*, *Rubus*, *Potentilla*, and *Antennaria*. Second, huge complexes which do not allow for a division into distinct microspecies, and which are not directly related to any diploid sexual populations, include *Poa nemoralis-palustris*, *Poa pratensis-arctica*. Third, *Alchemilla pentaphyllea*, *Hieracium*, *Taraxacum*, *Arnica*, and *Ranunculus auricomus* are apomictic complexes which can be split into discrete microspecies, but sexual relatives do not exist or are present as relicts.

In the taxonomic treatment of complexes in the first series, where the apomicts form part of one well-defined population, individual apomicts would rank the same as biotypes of sexual species. The large agamospermous genera, of the second series, would be given a superficial treatment by placing all the apomicts into one taxonomic unit, recognizing the primary diploids, and arranging the wide-spread polyploids as circle microspecies around them. Population can be divided and grouped around these circle microspecies. The most important forms are given the rank of tertiary microspecies, and local variations are then attached as varieties or forms. In complexes which cannot be divided into microspecies without residue, because of crossing processes going on, the distinct and widespread types still should be named. It may be possible to divide into distinct microspecies those agamospermous genera where the original sexual species are extinct or cannot be traced.

Taxonomists who studied sexual polyploid complexes have differed in their opinions as to whether or not types which are morphologically very similar to each other, but differ in chromosome number, should be recognized as separate species. Camp and Gilly (1943), Valentine (1949, 1950) and Baker (1952) suggested special categories by which diploids and polyploids that closely resemble each other in morphological characteristics are kept in the same species. Mason (1950) and Hara (1962) contended that all characters should be taken into account and that no one character is sufficient to warrant specific segregation. Löve (1943, 1951, 1954, 1960, 1962), Löve and Löve (1942, 1948, 1954, 1956), as well as Löve, Löve, and Raymond (1957) maintained that diploids and polyploids should always be placed in separate species and have pointed out that morphological differences can usually be found if a close study is made.

Bell (1943) was able to divide the diploids into morphological species in the *Sanicula crassicaulis* complex but could not attain the concept of "every polyploid level a distinct species" within the polyploid complex. Heckard (1960) made a similar treatment of the polyploid complex in *Phacelia magellanica*. This also appears to be true within the *Dichanthium-Bothriochloa-Capillipedium* complex.

CHAPTER II

SPECIES RELATIONSHIPS WITHIN THE BOTHRIOCHLOA PERTUSA COMPLEX

Classically, Hackel (1889) referred all plants belonging to Andropogon subgenus Amphilophis (Gramineae) having subdigitately arranged racemes and pitted sessile spikelets to A. pertusus (Linn.) Willd., and Camus (1931) demonstrated that members of the subgenus Amphilosphis should be transferred to Bothriochloa O. Kuntze. The varieties of A. pertusus recognized by Hackel (1889) were later variously classified as species by Stapf (1917), Camus (1931), Herter (1940), Henrard (1940, 1941), Pilger (1950), Maire (1952, 1959), Parodi (1958) and Bor (1960).

The cytology and morphology of the species usually recognized, B. decipiens (Hack.) C. E. Hubb., B. insculpta (Hochst.) A. Camus, B. longfolia (Hack.) Bor, B. panormitana (Parl.) Pilger, B. pertusa (Linn.) A. Camus, and the related B. radicans (Lehm.) A. Camus, as well as the degree of genetic isolation between them were studied in detail. The data obtained were correlated in an effort to determine the species validity, and the degree of phylogenetic affinity between the taxonomic units involved.

Material and Methods

Morphological data are based on studies of at least ten specimens from each collection. Plants studied were grown in a uniform nursery as described by Celarier and Harlan (1956). Chromosome numbers were determined from studies of microspore mother cells stained with aceto-carmine. Hybridization attempts were made following emasculation and hand pollination as described by Richardson (1958).

Results and Discussion

The species studied are highly variable morphologically, and no single character could be found that will hold absolutely for separating them. Nearly every character graded from one expression to another. Nevertheless, each taxonomic unit classically recognized is characterized by a distinctive group of character combinations (Table I).

Relative length of the racemes. -- The genus *Bothriochloa* may be subdivided, on the basis raceme length in relation to the length of the inflorescence axis, into two major species groups. In *B. intermedia* (R. Br.) A. Camus and its relatives (Harlan *et al.*, 1958) the lower racemes are shorter than the primary axis of the inflorescence. On this basis, *B. insculpta* var. *vegetior* (Hack.) C. E. Hubb. could be referred to *B. glabra* (Roxb.) A. Camus. Members of the *B. pertusa* complex are characterized by lower racemes which exceed the primary axis of the inflorescence in length.

Both raceme length and length of the primary axis are variable characters, strongly influenced by environmental factors. These two characters, however, are correlated, and the raceme length/axis length ratio was found to be relatively stable and useful in separating species. Using this ratio, the majority of specimens belonging to *B. pertusa* could be separated from the other studied species except *B. decipiens* (Plate I).

TABLE I

MORPHOLOGY*

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
B. decipiens									AUSTRALIA
3727	E	2-11 6	36-65 49	2-6 3.7	0	1	0	40	New South Wales
4598	E	5-28 13	50-70 66	4-15 7.0	0-5 0.8	1	0	40	Warwick
4611	E	4-15 8	50-60 53	3-7 4.6	0	1	0	40	Lawes
5421	E	8-20 11	58-70 66	3-5 4.2	0	1	0	40	Wagga Wagga
4789	E+	11-30 19	50-75 60	4-21 9.6	0-7 3.2	1	0	40	Queensland
6510	E+	14-28 21	50-70 68	9-19 12.6	2-5 3.5	1	0	40	Queensland
7501	E+	14-26 18	65-76 69	7-21 15.0	2-4 3.2	1	0	40	Ingbam
7548a	E+	5-22 15	50-70 63	6-16 10.1	0-6 3.9	1	0	40	Queensland

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2*n*	Origin
8134	E+	10-35 18	50-80 72	15-20 18.3	0-6 3.2	1	0	40	Ingbam
									NEW GUINEA
7545	E+	6-19 15	35-70 59	6-26 13.4	0-4 2.1	1	0	40	Brown River
8143	E+	15-25 20	60-68 63	6-18 14.4	0-6 1.8	1	0	40	Port Morsby
8144	E+	5-18 16	60-72 67	5-19 10.0	0-10 1.8	1	0	40	Brown River
B. insculpta									AFRICA
									ETHIOPIA
4517	D	24-46 36	55-70 64	7-13 10.3	0-6 2.8	1	1-2	60	Awash
4407	D	20-57 33	65-91 73	12-15 13.0	0-9 2.4	1	1	60	Asmara
9408	D	32-38 34	68-71 69	11-13 12.0	5-8 6.7	1	2-3	60	Alemaya
9409	D	21-26 23	53-55 54	8-9 8.7	0	1	0-2	60	Alemaya

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
									KENYA
3239	D	14-21 18	60-72 66	6-7 6.3	0-1 0.3	1	1-2	60	Nairobi
3109	D	15-30 20	55-73 67	8-15 10.5	0-2 0.5	1	1-2	60	Kitale
5469	D	14-25 22	55-75 68	6-12 8.3	0	1	1-4	60	Kitale
7546	D	18-35 30	60-75 70	10-15 12.5	1-2 1.2	1	1-4	60	Nairobi
2584	D	12-21 16	60-65 63	4-7 5.5	0	1	1-2	60	TANGANYIKA
									CONGO
3667	D	28-39 35	73-82 79	9-18 11.8	3-26 9.5	1	1-2	60	Yangambi
									MOZAMBIQUE
9586	D	30-47 41	81-90 84	10-13 11.7	4-11 7.0	1	1-2	50	Namaacha
9587		23-45 36	69-79 73	8-11 9.2	1-8 5.9	1	0-1	60	Namaacha

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
									SWAZILAND
9588	D	35-45 41	65-76 72	9-12 10.7	3-7 5.3	1	0-1	60	Goba
9589	E	60-70 65	70-85 75	8-15 12.5	0-2 0.4	1	1-4		Stegi
9590	D	30-34 32	60-75 70	9-12 10.4	0-2 0.6	1	1-2	50	Bremersdorp
									RHODESIA
3736	D	24-50 38	50-70 63	10-15 12.3	0-6 2.5	1	1-3	60	Salisbury
4624	D	12-20 16	42-50 46	7-9 7.7	0-1 0.3	1	2-3	60	Salisbury
4625	D	15.20 18	40-53 47	5-11 8.0	2-7 4.5	1	2-3	60	Salisbury
4626	D	13-21 17	46-48 47	7-9 8.3	1-2 1.7	1	2-4	60	Salisbury
4627	D	24-49 34	74-77 75	8-17 11.7	0-50 17.0	1	1-2	60	Salisbury

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits		2n	Origin
						S	P		
4628	D	18–22 20	59–65 62	8–10 9.3	5–6 5.3	1	2–4	60	Salisbury
9437	E	22–30 27	58–62 60	9–15 9.5	2–5 2.5	1	1–2	60	Salisbury
9438	D	50–65 55	70–85 75	12–15 12.5	15–20 18.2	1	1–3		Banket
9439	E	40–65 45	60–85 65	10–12 10.5	0	1	1–3		Banket
9441	E	40–60 45	55–85 65	10–14 12.5	0	1	1–3		Mazabuka
9443	D	48–58 53	84–100 90	17–21 18.7	27–47 34.7	1	2–3		Zimba
9444	E	50–65 55	60–85 65	14–19 15.5	0	1	1–3		Wankie
9448	D	20–25 22	62–63 63	9–11 9.8	1–5 2.5	1	1–2	50	Chilimanzi
9449	D	24–30 27	63–68 66	9–10 9.5	2–3 2.5	1	1–2	60	Enkeldoorn

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits		2n	Origin
						S	P		
									SOUTH AFRICA
3681	D	15-40 28	60-90 71	4-10 5.6	0	1	1-2	60	Pietermaritzburg
3704	E	28-57 41	62-75 71	19-28 22.6	0-35 11.3	1	1-2	60	Pietermaritzburg
4090	D	16-25 20	61-75 68	6-9 7.6	0-1 0.6	1	1-2	50	Pietermaritzburg
4091	D	38-54 48	61-95 83	10-15 11.8	3-10 6.2	1	1-3	60	Pietermaritzburg
4905	D	35-55 43	67-85 76	10-15 12.0	1-42 12.5	1	1-2	50	Pretoria
4906	D	30-55 42	68-88 80	10-14 12.7	0-25 3.9	1	0-2	60	Pretoria
4907	D	20-57 33	65-91 73	12-15 13.0	0-9 2.4	1	1-4	60	Rietondale
5152	D	14-36 26	47-69 60	7-15 11.7	0-12 4.3	1	1-3	60	Rietondale
5168	D	22-35 28	54-70 63	9-11 10.3	0-1 0.3	1	0-1	60	Rietondale

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	ST	Pits		2$\underline{n}$	Origin
						S	P		
5190	D	46-51 48	75-92 81	19-22 21.0	4-23 16.3	1	1-3	60	Rietondale
5191	D	40-55 47	65-85 75	15-21 19.2	3-10 8.8	1	1-3	60	Rietondale
5192	D	33-37 34	73-82 77	12-19 14.7	4-30 18.0	1	1-3	60	Rietondale
5194	D	22-33 29	61-82 69	9-14 11.4	0-6 3.0	1	1-3	60	Rietondale
6902	D	31-49 40	74-90 82	9-12 10.9	0-19 10.4	1	1-2	50	Rietondale
7473	D	36-52 42	57-77 70	9-13 10.8	2-9 5.0	1	1-2	60	Barberton
8587	D	26-41 34	72-87 77	8-15 11.0	0-7 3.3	1	1-4	60	Pretoria
8588	D	30-46 36	81-96 90	8-10 8.8	0-2 0.8	1	1-3	60	Pretoria
9567	D	10-26 20	64-71 68	5-11 8.0	0-2 0.8	1	1-2	60	Onderstepoort
9568	D	20-40 30	45-65 50	5-8 7.5	0	1	1-3		Onderstepoort

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
9569	D	19-25 22	60-73 65	8-9 8.3	0-2 0.7	1	2-3	60	Pretoria
9570	D	18-23 20	68-75 71	7-8 7.3	1-2 1.3	1	2-3	50	Swartspruit
9571	D	20-40 35	60-75 65	8-10 9.5	0	1	1-3	60	Swartspruit
9572	D	35-56 48	88-90 89	9-13 11.0	5-22 10.3	1	1-2	50	Brits
9573	D	33-38 36	84-90 88	10-12 11.5	0-5 1.5	1	2-3	60	Brits
9574	D	30-40 25	50-75 55	4-8 6.5	0	1	1-3		Machadodorp
9575	D	29.30 30	65-69 67	8-9 8.5	4-5 4.5	1	1	60	Machadodorp
9576a	D	25-34 30	61-66 64	9-11 9.7	1-2 1.3	1	1-2	60	Machadodorp
9577	D	26-37 30	68-74 71	10-12 10.5	0-2 0.7	1	1	60	Lydenburg
9578	D	40-60 45	70-90 85	10-15 12.5	2-4 3.0	1	1-3		Graskop

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits		2n	Origin
						S	P		
9579	D	35-40 36	64-71 68	9-12 9.5	1-2 1.5	1	1-2	50	Graskop
9580	D	32-55 43	69-88 78	11-14 12.3	0-11 5.8	1	1	50	Graskop
9581	D	45-60 50	65-85 75	10-12 10.5	0-2 0.5	1	1-3		Nelspruit
9582	D	30-50 35	60-85 65	7-10 8.5	0	1	1-3		Barberton
9583	D	31-39 35	76-90 85	9-12 10.0	0-6 3.5	1	1		Barberton
9584a	D	30-43 34	64-78 72	9-11 10.0	0-16 4.0	1	1	60	Komatipoort
9585	D	28-45 34	68-78 73	9-12 10.5	0-1 0.3	1	1	50	Komatipoort
9592	D	37-57 45	66-75 72	10-18 13.0	12-14 12.3	1	1-2		Groblersdal
9593	D	42-45 43	61-65 62	10-11 10.5	0-2 1.0	1	1-2	60	Groblersdal
9594	D	28-56 39	73-83 78	10-13 11.8	1-16 5.5	1	1-2	50	Marble Hall

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits		2n	Origin
						S	P		
9595	E	40-59 50	71-101 87	11-16 14.3	0-4 1.0	1	2-3	60	Marble Hall
9596	D	34-44 38	67-75 69	11-12 11.2	4-12 8.0	1	0-1	50	Nylstroom
9597	D	19-34 26	62-64 63	7-10 8.3	0-2 0.7	1	0-3	60	Roedtan
9599	D	39-41 40	73-89 84	14-17 15.7	2-15 7.0	1	0-1		Potgieters
9600a	D	35-45 40	79-89 84	17-19 17.7	2-27 11.3	1	1-2	60	Naboomspruit
9600b	D	26-32 30	69-84 76	8-10 9.0	0-7 4.3	1	1-2	60	Naboomspruit
9601	D	38-47 43	73-87 82	14-19 16.3	25-32 28.7	1	1-2	60	Radium
9602	D	21-39 33	66-74 72	9-12 11.0	1-4 2.3	1	0-1	60	New Castle
9603	D	42-47 45	78-80 79	19-24 21.5	4-19 11.5	1	1-3	60	Stanger
9604	D	40-60 45	60-75 65	8-10 9.5	2-5 4.1	1	1-3		Umhlanga

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
9605	D	38-50 43	69-83 76	12-13 12.7	0-6 3.0	1	0-2	60	Oribi
9606	D	38-50 43	60-75 65	10-15 13.5	5-10 8.5	1	1-3		Izingolweni
9607	D	42-48 46	79-86 83	6-20 18.0	3-16 9.7	1	1-2	60	Kokstad
9608	D	50-65 55	65-95 75	10-15 14.0	3-6 4.2	1	1-2		Umzimkulu
9609	D	50-65 55	65-80 70	10-15 12.5	4-8 6.5	1	1-2		Ixopo
9610a	D	31-42 37	56-65 61	8-12 10.0	0	1	1	60	Richmond
9610b	D	25-31 28	65-72 69	9-12 10.6	0-2 0.7	1	1-2	60	Richmond
9610c	D	36-43 40	71-85 79	17-20 18.3	5-9 4.3	1	1-2	60	Richmond
9611	D	35-55 40	60-70 65	10-11 10.5	0-1 0.1	1	1-2		Machadodorp
9612	D	30-50 36	50-75 55	8-12 9.6	0	1	1-2		Roodeplaat

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
9613	D	28–35 30	60–70 65	8–10 9.2	0–3 0.5	1	1–3		Pretoria
9614	D	22–30 25	50–65 55	8–10 8.9	0–3 0.5	1	1–3		Koster
									INDIA
9093	P	6–12 9	46–56 51	3–5 4.0	0	1	1–3	60	Poona
9095	P	6–20 14	55–65 60	3–8 5.4	0–2 0.8	1	0–1	60	Panchgani
9097	P	19–23 21	58–59 59	7–8 7.7	0	1	0–2	60	Mt. Abu
2654	P	7–9 8	43–50 46	4–5 4.3	0	1	1–2	40	Coimbatore
4394b	P	16–23 20	54–65 60	7–9 7.8	0	1	1–2	40	Dehra Dun
5396	P	27–65 33	52–65 57	9–14 11.0	0–10 7.4	1	0–1	40	Belatal
8280	P	33–58 42	54–68 58	13–22 15.8	0–3 0.8	1	0–3	40	Lonavla

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
8283	P	6-11 8	40-47 44	4-5 4.3	0	1	1-2	40	Rajkot
8285	P	10-18 14	46-54 51	5-7 6.0	0	1	0-1	40	Rajkot
8285-3b	P	19-35 26	67-100 89	6-9 7.5	0	1	0-2	40	Rajkot
8287	P	13-20 17	48-61 55	5-6 5.5	0	1	0-3	40	Mulshi
8299	P	39-40 40	50-53 52	11-13 12	0	1	1-2	40	Malavli
8308	P	9-13 11	47-50 49	5-6 5.2	0	1	0-1	40	Saurashtra
8981a	P	22-36 30	47-73 60	7-14 9.9	0-8 2.7	1	0-4	40	Jammu
8985b	P	10-17 12	52-55 53	4-8 6.0	0	1	1-2	40	Dalhousie
8987b	P	10-17 13	51-60 56	4-5 4.7	0	1	1-2	40	Mandi
9090b	P	10-19 16	49-66 58	4-7 5.8	0	1	0-1	40	Delhi

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
9096	P	9-32 23	65-83 74	5-9 6.6	0-8 1.6	1	0-3	40	Mt. Abu
9098	P	15-27 21	62-77 68	5-10 7.3	0	1	0-2	40	Baroda
B. longifolia									INDIA
8300	E	30-40 36	35-55 52	10-16 14	0	1	0	20	Poona
8301	E	35-50 42	50-70 65	20-40 32.0	0-8 1.0	1	0	20	Poona
B. panormitana									AFRICA
									ETHIOPIA
4518	D	31-49 37	68-92 76	10-16 13.1	0-22 5.0	+	+	60	Awash
									MOROCCO
5402	D	42-60 53	61-66 63	10-18 14.2	1-3 2.3	1	0	60	Tamanor
									RHODESIA
9447	D	18-35 25	62-67 65	7-12 9.2	0-3 2.0	1	+	50	Balla Balla

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
9487	D	20-34 25	48-65 55	7-10 8.5	0-1 0.4	+	+		Bulawayo
9497	D	20-40 35	60-85 70	10-15 11.5	2-4 1.5	+	+		Wankie
									SOUTH AFRICA
9598	D	28-39 33	71-78 74	13-17 15.1	0-7 4.3	1	+		Roedtan
9676	D	22-26 24	60-69 65	8-10 9.2	0	1	+		Machadodorp
9683	D	40-65 50	65-85 70	10-12 11.5	0-3 1.5	+	0		Marble Hall
9684	D	38-46 42	70-86 79	12-14 13.2	3-6 4.5	+	0	50	Nylstroom
9685	D	30-36 34	80-86 82	11-12 11.5	2-4 2.5	+	0	50	Marble Hall
B. pertusa									INDIA
4806	P	8-23 16	49-55 51	6-8 7.0	0-2 0.5	1	-	40	Hyderabad

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
5301	P	10-20 16	45-55 49	6-9 7.5	0-1 0.3	1	0	40	Delhi
5309	P	5-12 9	36-45 41	3-5 4.3	0	1	0	40	Dehra Dun
5403	P	15-24 19	55-65 57	5-9 7.0	0	1	0	40	Mathura
5406	P	7-14 11	45-55 50	4-6 5.0	0	1	0	40	Delhi
5408b	P	7-8 7	43-45 44	4-6 5.0	0	1	0	40	Bareilly
6152	P	10-16 15	42-50 49	5-9 6.3	0	1	0	40	W. Bengal
8279	P	11-23 17	45-56 51	6-7 6.5	0-1 0.5	1	0	40	Bombay
8281	P	14-17 15	43-61 54	5-7 6.3	0	1	0	40	Nasrapur
8282a	P	8-10 9	40-43 42	4-6 5.0	0	1	0	40	Sangamner
8282b	P	10-24 18	56-63 60	5-8 6.7	0	1	0	40	Sangamner

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
8284	P	11-22 18	66-77 71	5-8 7.1	0	1	0	40	Rajkot
8285-3a	P	11-18 14	46-57 48	5-7 5.8	0	1	0	40	Rajkot
8286	P	9-18 14	35-46 42	5-8 6.6	0	1	0	40	Mulshi
8288a	P	6-15 12	41-50 47	4-7 5.5	0	1	0	40	Purundai
8289a	P	8-20 16	47-52 49	4-7 5.7	0-1 0.5	1	0	40	Kandalah
8289b	P	9-21 14	38-46 43	5-11 7.0	0-8 2.7	1	0	40	Kandalah
8290	P	6-9 8	38-53 47	3-4 3.7	0	1	0	40	Panchgani
8292	P	8-13 11	41-50 46	6-8 6.8	0	1	0	40	Kotharud
8886a	P	5-19 14	59-71 66	4-8 6.5	0	1	0	40	Ajmer
8962	P	34-48 40	65-80 74	9-12 11.0	6-23 10.2	1	0	40	Kangra

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
8977a	P	27-30 29	63-67 65	10-11 10.5	0-4 2.0	1	0	40	Dehra Dun
8980	P	12-29 21	48-69 59	5-11 8.8	0-10 3.8	1	0	40	Jullundur
8981b	P	8-22 16	51-67 57	4-8 5.0	0	1	0	40	Jammu
8982	P	8-30 17	51-66 58	4-9 6.9	0-3 0.6	1	0	40	Pathankot
8984a	P	12-24 17	53-59 56	6-8 6.8	0-2 0.5	1	0	40	Pathankot
8985a	P	8-27 16	48-60 55	4-8 5.6	0-4 1.0	1	0	40	Dalhousie
8986	P	14-25 18	45-58 50	6-8 6.6	0-1 0.2	1	0	40	Kangra
8987a	P	16-30 22	55-61 59	5-9 7.3	0	1	0	40	Mandi
8988a	P	16-45 25	48-75 61	8-12 9.9	0-12 5.1	1	0	40	Nahan
8988b	P	7-20 15	53-66 60	4-6 5.3	0-1 0.3	1	0	40	Nahan

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
8988c	P	17-19 18	53-66 57	6-7 6.3	0	1	0	40	Nahan
8989	P	21-36 27	54-62 58	8-13 11.0	1-7 4.0	1	0	40	Alwar
9090a	P	11-25 19	41-62 56	5-9 7.7	0	1	0	40	Delhi
9091	P	13-22 16	55-67 62	6-7 6.3	0	1	0	40	Delhi
9092	P	4-14 8	40-50 45	5-7 6.2	0	1	0	40	Poona
									PAKISTAN
4635II	P	31-35 33	57-62 60	8-9 8.7	0-2 1.0	1	0	40	Sargodha
									CEYLON
4021	P	13-23 17	45-64 51	5-8 7.0	0-1 0.3	1	0	40	Peradeniya
									CHINA
6154	P	8-12 9	38-40 39	4-5 4.7	0	1	0	40	Yunnan

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
									AFRICA
									SENEGAL
5431	D+	16-23 19	52-64 58	7-9 8.1	0-2 0.8	1	+	40	Dakar
									KENYA
5467	D+	9-20 16	47-61 56	6-9 8.1	0-1 0.3	1	+	40	Kitale
									RHODESIA
9479	D+	36-48 41	60-65 63	12-14 13.2	0	1	+	40	Kafue
9480	D+	18-26 23	44-53 50	8-11 9.2	0	1	+	40	Zimba
9481	D+	23-28 25	50-52 51	11-13 11.5	0	1	+	40	Lupani
9482	D+	17-24 22	46-52 50	7-10 9.2	0	1	+	40	Shabisi

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits S	Pits P	2n	Origin
									SOUTH AFRICA
9680	D+	30-45 35	45-60 55	5-10 7.5	0	1	+	40	Lydenburg
B. radicans									AFRICA
									KENYA
3055	D+	25-35 30	45-65 55	5-10 8.4	0	0	0		Nairobi
5468	D+	40-45 42	55-65 58	5-15 10.2	0-1 0.5	0	0	40	Nairobi
									RHODESIA
9440	E	40-65 55	60-75 65	10-15 12.2	0	0	0	40	Salisbury
9488	E	41-56 49	70-86 77	14-19 18.1	8-17 15.0	0	0	40	Balla Balla
9489	E	30-40 35	60-75 65	10-18 14.4	3-8 5.6	0	0	40	Filabusi

TABLE I (Continued)

Name and No.	GH	LPA	LLR	PR	SR	Pits		2n	Origin
						S	P		
									SOUTH AFRICA
9682	D+	20-41 35	59-69 63	7-14 12.2	2-15 9	0	0	40	Pretoria

*For each collection, the first line lists range and the second mean in respect to the characters studied.

GH.--Growth habit: E-erect; E+-erect and robust; D-decumbent; D+-culms becoming erect from a short creeping base; P-prostrate.

LPA.--Length primary axis of inflorescence in millimeters.

LLR.--Length longest raceme in millimeters.

PR.--Number of primary racemes.

SR.--Number of secondary and tertiary racemes.

S.--Sessile spikelets.

P.--Pedicellate spikelets.

Pits.--+-trace; 0, 1, 2, 3, 4-number of pits present on lower glume.

LEGEND TO PLATE I

Scatter diagram indicating morphological affinities.

● : *Bothriochloa pertusa* (Indian)

◒ : *Bothriochloa pertusa* (African)

○ : *Bothriochloa insculpta* (African)

◕ : *Bothriochloa insculpta* (Indian)

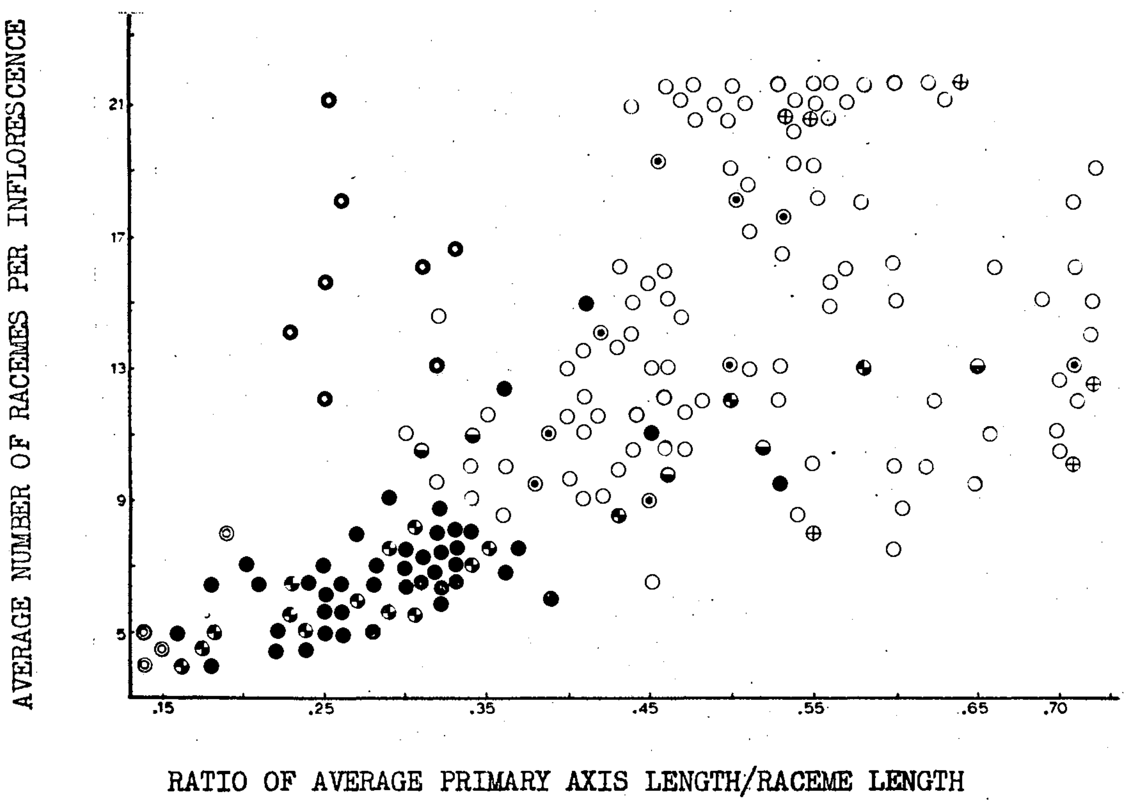
⊙ : *Bothriochloa panormitana* (African)

◉ : *Bothriochloa decipiens* (Australian)

◎ : *Bothriochloa decipiens* (Australian)

⊕ : *Bothriochloa radicans* (African)

PLATE I


AVERAGE NUMBER OF RACEMES PER INFLORESCENCE
21
17
13
9
5
.15
.25
.35
.45
.55
.65
.70
RATIO OF AVERAGE PRIMARY AXIS LENGTH/RACEME LENGTH

Raceme number and order of branching. -- Raceme number per inflorescence varies within a species. The range, characteristic of a species, is usually present within a single plant. For this reason, average number of racemes per inflorescence is a relatively stable characteristic. The two varieties of B. decipiens (Plate I) differ conspicuously from each other in this respect. Similarly, B. pertusa is mostly characterized by fewer racemes per inflorescence than are the other species studied.

The racemes are subdigitately arranged in whorls on two or more nodes of the primary axis, or else more or less opposite, or alternating. Node number is usually correlated with raceme number, but is a less reliable character than the latter. The racemes are simple or divided. The lower ones are usually divided into secondary and tertiary branches in specimens referable to B. decipiens var. cloncurrensis, B. insculpta, B. longifolia and B. panormitana. Simple racemes usually characterize B. pertusa, B. radicans, and typical representatives of B. decipiens.

Pits on the glumes. -- This character usually forms the basis for separating B. insculpta, B. pertusa and B. radicans from each other. Typically, B. pertusa is characterized by pitted sessile and non-pitted pedicellate spikelets. On this basis Maire (1952, 1959) recognized B. pertusa var. panormitana to include the Sicilian B. panormitana, and B. pertusa var. maroccana to include African plants resembling those from Sicily. The variety B. pertusa var. tunetana A. Camus was recognized by Maire (1959) to include African plants differing from B. pertusa var. maroccana mainly in their reduced size. Growth habit, inflorescence structure and cytogenetical data indicate that B. panormitana and B. pertusa var. maroccana are more closely related to B. insculpta. Similarly, B. pertusa var. tunetana resembles B. radicans except for pit characters. The Indian representatives of B. insculpta, as recognized by Bor (1960), have pitted sessile and pedicellate spikelets that are characteristic of this species, but they resemble B. pertusa in most other morphological features. Numerous African plants resembling B. insculpta in growth habit, inflorescence structure and cytology, have only the lower sessile spikelets on each raceme pitted, and the pedicellate ones are either faintly pitted or not pitted at all.

Glume pubescence. -- The lower glume of sessile spikelets are usually pilose below the middle, but in most Indian specimens of B. insculpta the sessile spikelets are glabrous. Degree of pubescence is variable in all the species studied. The lower glume of pedicellate spikelets is essentially glabrous below the middle in all the species studied. Above the middle the lower glumes of both sessile and pedicellate spikelets are often shortly ciliate along the margins.

Hairs on the culm-nodes. -- The nodes may be glabrous, bearded all over, or the hairs may form a distinct ring below each node. Glabrous nodes characterize B. decipiens and most of the African specimens referable to B. pertusa. Indian representatives of B. pertusa and the African B. radicans usually have a ring of short or long hairs at the base of the nodes. More rarely the nodes are completely glabrous or woolly all over. Woolly nodes were often encountered in B. panormitana and B. insculpta. The lower nodes on a culm are sometimes more or less woolly all over while the hairs are arranged in a ring on the upper nodes. Very rarely the nodes were found to be glabrous in members of B. insculpta.

Growth habit. -- The species were found to be quite consistent in respect to this character. An erect growth habit characterizes *B. decipiens* and *B. longifolia*, while members of *B. pertusa* and Indian representatives of *B. insculpta* are typically prostrate plants. Rambling culms, which often grow erect at first and then bend over to become erect again at flowering time, are characteristic of African *B. insculpta*, *B. panormitana* and *B. pertusa* var. *maroccana*. The flowering culms of *B. radicans* and *B. pertusa* var. *tunetana* arise from a short creeping base which is often strongly branched at the lower nodes.

Leaf shape. -- The leaves are more or less linear-lanceolate and extremely variable in length. They are mostly basal, but often also cauline. In Indian representatives of *B. pertusa* the basal leaves are shorter and more lanceolate than the cauline ones. Extremely long, linear leaves characterize *B. longifolia*. In general African representatives of *B. insculpta* have broader and longer leaves than Indian specimens.

Long, bulbous-based hairs are often present on the upper surface of the leaves. These are usually more prominent and frequent in members of *B. radicans*.

Cytogeography. -- Chromosome numbers encountered are $2n = 20$, 40, 50 and 60. The only diploid ($2n = 20$) is *B. longifolia* endemic to southern India. Typical representatives of *B. pertusa* are tetraploid and extend from West Pakistan through India and southern Asia to Indonesia. African representatives of this species are tetraploid, pentaploid or hexaploid. Both *B. pertusa* var. *tunetana* ($2n = 40$) and *B. pertusa* var. *maroccana* ($2n = 50$, 60) appear to be widely distributed in Africa. The African representatives of *B. insculpta* are pentaploid or hexaploid, and widely distributed throughout the tropical and subtropical regions of this continent. The Indian representatives of B. insculpta are confined to the more tropical regions, and these plants are either tetraploid or hexaploid.

Typically B. panormitana is confined to Sicily. African plants resembling this species in detail (B. pertusa var. maroccana) extend from Morocco to southern Africa. Plants from Sicily were not available for cytological study. North African plants that should be referred to B. panormitana are hexaploid.

Crossing data. -- Attempts at crossing the various species and varieties are indicated in Table II. Celarier and Harlan (1956) demonstrated that diploid ($2n = 20$) representatives of Bothriochloa reproduce sexually, while polyploids are usually apomicts. The diploid sexual species B. longifolia was not used as a parent in hybridization experiments. Emasculation of the apomictic polyploid species followed by pollination with a morphologically distantly related species usually provided no seedset at all, while attempted crosses between morphologically similar species generally produce some seedset, although usually no hybrids. Harlan et al. (1948, 1961) demonstrated that these polyploids are pseudogamous gametophytic apomicts and always require pollination for parthenogenetic development of the cytologically unreduced female gamete. Apparently only pollen from closely related species, as was demonstrated by de Wet and Richardson (1963), can induce parthenogenetic development of the gametes. On this basis, the species usually recognized appears to be well isolated genetically. Some degree of affinity can be demonstrated between B. radicans and tetraploid African representatives of B. pertusa, while the Indian representatives appear

TABLE II

ATTEMPTED HYBRIDS

Parents	Origin	No. Emasculations	% Seedset	No. Hybrids
B. insculpta (2n = 60)	Africa			
x B. decipiens (2n = 40)	Australia	40	0	0
x B. ewartiana (2n = 40)	Australia	40	0	0
x B. glabra (2n = 40)	Africa	3500	6	0
x B. grahamii (2n = 40)	India	495	0	0
x B. insculpta (2n = 40)	India	80	0	0
x B. insculpta (2n = 50)	Africa	240	4	0
x B. pertusa (2n = 40)	India	1070	3	0
x B. pertusa (2n = 40)	Africa	260	3	0
x B. radicans (2n = 40)	Africa	180	0	0
B. insculpta (2n = 50)	Africa			
x B. glabra (2n = 50)	Africa	760	2	0
x B. grahamii (2n = 40)	India	80	0	0
x B. insculpta (2n = 60)	Africa	178	6	0
x B. pertusa (2n = 40)	India	120	10	0
B. pertusa (2n = 40)	India			
x B. ewartiana (2n = 60)	Australia	195	0	0
x B. glabra (2n = 40)	Africa	730	2	0
x B. grahamii (2n = 40)	India	280	0	0
x B. insculpta (2n = 50)	Africa	80	0	0
x B. insculpta (2n = 60)	Africa	650	10	0
x B. ischaemum (2n = 40)	Europe	190	0	0
x B. radicans (2n = 40)	Africa	480	0	0
x B. panormitana (2n = 60)	Africa	40	10	0
x B. pertusa (2n = 40)	Africa	280	10	0
B. pertusa (2n = 40)	Africa			
x B. glabra (2n = 40)	Africa	568	0	0
x B. grahamii (2n = 40)	India	40	0	0
x B. insculpta (2n = 50)	Africa	80	6	0
x B. insculpta (2n = 60)	Africa	89	2	0
x B. pertusa (2n = 40)	India	80	10	0
B. panormitana (2n = 60)	Africa			
x B. insculpta (2n = 50)	Africa	40	2	0
x B. insculpta (2n = 60)	Africa	320	6	0

TABLE II (Continued)

Parents	Origin	No. Emasculations	% Seedset	No. Hybrids
B. radicans (2n = 40)	Africa			
x B. glabra (2n = 40)	Africa	390	4	0
x B. grahamii (2n = 40)	India	580	5	0
x B. insculpta (2n = 60)	Africa	170	2	0
x B. pertusa (2n = 40)	India	280	0	0
x B. pertusa (2n = 40)	Africa	190	10	0
B. decipiens (2n = 40)	Australia			
x B. pertusa (2n = 40)	India	180	0	0
x B. radicans (2n = 40)	Africa	210	0	0
B. ewartiana (2n = 60)	Australia			
x B. insculpta (2n = 60)	Africa	390	0	0
B. ischaemum (2n = 40)	Europe			
x B. pertusa (2n = 40)	India	190	0	0
B. glabra (2n = 40)	Africa			
x B. insculpta (2n = 50)	Africa	140	1	0
x B. insculpta (2n = 60)	Africa	620	10	0
x B. panormitana (2n = 60)	Africa	320	2	0
x B. pertusa (2n = 40)	India	700	1	0
x B. pertusa (2n = 40)	Africa	390	5	0
x B. radicans (2n = 40)	Africa	390	2	0
B. grahamii (2n = 40)	India			
x B. insculpta (2n = 50)	Africa	280	1	0
x B. insculpta (2n = 60)	Africa	1600	2	0
x B. panormitana (2n = 60)	Africa	280	2	0
x B. pertusa (2n = 40)	India	580	2	0
x B. pertusa (2n = 40)	Africa	620	15	4
x B. radicans (2n = 40)	Africa	300	12	0

to be only distantly related to this strictly African species. Morphologically B. insculpta appears to be related to B. panormitana, and pollen of either one induced seedset in the other. Morphological relationships between hexaploid B. insculpta and tetraploid B. glabra was pointed out earlier, and this is further indicated by seedset percentage.

The only hybrids obtained were from a cross between a facultative apomictic plant of B. grahamii (Haines) Bor and B. pertusa (4n) collected in Senegal. This particular plant induced 10 per cent seed set in B. radicans, and the latter species induced 12 per cent seed set in B. grahamii. Hybrids, however, between B. radicans and B. grahamii were not obtained. Indian representatives of B. pertusa induced only 2 per cent seed set in B. grahamii. The latter species apparently combine genes of various other species of Bothriochloa as well as of the related Dichanthium annulatum (Forssk.) Stapf (Harlan, Chheda and Richardson, 1962). This apparently enables it to hybridize rather easily with various other species. Morphological data suggest that B. insculpta represents a cross between B. glabra and some African representative of B. pertusa. Harlan et al. (1958) demonstrated that both the cytologically reduced, as well as unreduced female gametes of these facultative apomicts, may function sexually. The hexaploid may combine four basic genomes of B. glabra and two of African B. pertusa. Pentaploid representatives of B. insculpta may represent hybrids between hexaploid and tetraploid African plants. Cytologically these polyploids behave like segmental allopolyploids as defined by Stebbins (1947). Chheda and Harlan (1963), however, demonstrated that in Bothriochloa hybrids, chromosome pairing takes place preferentially between genomes, and that genetically controlled non-homologous pairing often takes place.

From a biosystematic point of view, the species B. decipiens, B. insculpta, B. longifolia, B. pertusa, B. panormitana, and B. radicans are distinct taxonomic units. The Indian representatives of B. insculpta could more naturally be treated as a variety of B. pertusa. The African plants usually referred to B. pertusa are of two distinct morphological types. The tetraploid B. pertusa var. tunetana appears to be identical with B. intermedia var. acidula (Stapf) C. E. Hubbard. Morphological and genetical data suggest that these plants are closely related to B. radicans. The hexaploid and pentaploid plants usually referred to B. pertusa var. maroccana are morphologically identical to the Sicilian hexaploid B. panormitana. These plants appear to be related to B. insculpta (5n, 6n). A detailed taxonomic treatment of these species will be presented elsewhere.

Conclusions

1. Morphological and cytogenetical data indicated that the species B. decipiens (Hack.) C. E. Hubb., B. insculpta (Hochst.) A. Camus, B. longifolia (Hack.) Bor, B. panormitana (Parl.) Pilger, B. pertusa (Linn.) A Camus, and B. radicans (Lehm.) A. Camus are variable, but distinct taxonomic units.

2. From a biosystematic point of view glume characteristics, on which the classification of these species were usually based, appeared to be unreliable.

3. Indian representatives of the more commonly African B. insculpta could more naturally be transferred to the Asiatic B. pertusa as a

variety.

4. The African B. pertusa var. maroccana Maire could not consistently be separated from the Sicilian B. panormitana, and this species could be treated as a variety of B. insculpta.

5. The recently described B. pertusa var. tunetana A. Camus from Tunesia was found to be identical to B. intermedia var. acidula (Stapf) C. E. Hubbard. Cytogenetical and morphological data suggested that these plants should be regarded as a variety of B. radicans.

CHAPTER III

BIOSYSTEMATICS OF BOTHRIOCHLOA PERTUSA

The most extensive taxonomic study of *B. pertusa* (Linn.) A. Camus (Gramineae) was by Hackel (1889) who included this species in *Andropogon* subgenus *Amphilophis*. Nash (1903) raised this subgenus to generic rank, and Camus (1931) demonstrated that the species included in *Amphilophis* Nash should be referred to *Bothriochloa* O. Kuntze.

The species *A. pertusus* (Linn.) Willd. as recognized by Hackel (1889) is polymorphic and widely distributed. On the basis of gross morphological characters numerous varieties and subvarieties were recognized, many of which were later raised to specific rank. More recently Blatter and McCann (1935) indicated that *Amphilophis pertusus* (Linn.) Stapf, even in the restricted sense as recognized by them, is extremely variable.

The present study deals primarily with Indian and South-east Asian representatives of the *B. pertusa* complex. Morphological and cytological data were studied in an effort to resolve the taxonomic status of this species.

Material and Methods

Seed collected in nature were germinated, and the plants grown in a uniform nursery as suggested by Celarier and Harlan (1956). Morphological data are based on a study of these plants as well as investigations at the Herbarium of the Royal Botanic Gardens at Kew, England (K), and the Rijksherbarium at Leiden, Holland (L). Specimens studied cytologically are filed with the Oklahoma State University at Stillwater. Chromosome numbers were determined from developing microsporocytes stained with aceto-carmine.

Synonymy

The species _Holcus pertusus_ Linn., on which _Andropogon pertusus_ (Linn.) Willd. was based, refers to a plant collected in the East Indies (Mant. Alt. 301. 1771). Typically this species is a creeper, rooting at the nodes where it forms tufts of short leaves with longer cauline leaves on the geniculately ascending flowering culms. The 3-11 racemes are digitately arranged on a short primary axis; the rachis, joints, and pedicels are densely ciliate, giving the racemes a silky appearance. Sessile spikelets are oblong-lanceolate; the lower glume is subchartaceous, more or less hairy below the middle, with a deep pit (indentation) above the middle; the upper glume is lanceolate, membraneous and glabrous. The lemma of the lower floret is awnless and empty; the lemma of the upper floret forms the base of an awn and includes a flower. Pedicellate spikelets resemble the sessile ones, but they are usually narrower, neither pitted nor awned, and male or neuter.

The varieties recognized by Hackel (1889) were variously classified into species by modern taxonomists (Table III). Hubbard (1934) gave the Australian _A. pertusus_ var. _decipiens_ Hack. specific rank. Blake (1944) demonstrated conclusively that this Australian species, first identified by Brown (1810) with _A. pertusus_, differs from the latter in the larger, more lanceolate sessile spikelets with a solitary stamen, and the

TABLE III

CLASSIFICATION OF ANDROPOGON PERTUSUS

Andropogon Linn.	Bothriochloa O. Ktze
A. pertusus var. barbatus A. Camus, Anam, Phan-rung, Chevalier 30541 et 30546 (P).	B. pertusa (Linn.) A. Camus, Ann. Soc. Linn. Lyon 1930, 76: 164. 1931.
A. pertusus var. capensis Hack. Africa, Key River, Drége 4325.	B. insculpta (Hochst.) A. Camus, loc. cit.: 165.
A. pertusus var. decipiens Hack. Australia, Queensland, O'Shannon s.n. (BRI).	B. decipiens (Hack.) C. E. Hubbard, Kew Bull. 1934: 444. 1934.
A. pertusus var. insculptus (Hochst.) Hack. Africa, Abyssinia, Schimper s.n. ex Herb. Hook. (K).	B. insculpta (Hochst.) A. Camus, loc. cit.
A. pertusus var. insculptus subvar. biofoveolatus (Steud.) Hack. India, Wight Herb. Andropogon No. 156 (K).	B. insculpta (Hochst.) A. Camus, loc. cit. according to Bor (1960); B. pertusa var. bifoveolata (Steud.) de Wet et Higgins comb. nov.
A. pertusus var. insculptus subvar. trifoveolatus Hack. Africa, Abyssinia, Schimper 80 (K).	B. insculpta (Hochst.) A. Camus, loc. cit.
A. pertusus var. longifolius Hack. India, Madras, Wallich 8803 ex Herb. Wight (K).	B. longifolia (Hack.) Bor, Grasses Burma, Ceyl. Ind. Pakist.: 108, 1960.
A. pertusus var. maroccanum Maire. Africa, Morocco, Maire et Wilczek s.n. (Herb. Univ. Algeriensis).	B. pertusa var. maroccana Maire, Bull. Soc. Hist. Nat. Afr. Nord 31: 45. 1940.
A. pertusus var. panormitanus (Parl.) Hack. Sicily, Palermo, Herb. Parlatore.	B. panormitana (Parl.) Pilger in Engl. et Prantl, Nat. Pflanzenfam. 14e: 161. 1940.
A. pertusus var. vegetior Hack. Africa, Sudan, Schweinfurth 1027 (K).	B. insculpta var. vegetior (Hack.) C. E. Hubbard, Kew Bull. 1934: 109. 1934.
A. pertusus var. wightii Hack. India, Wight 1696 (K).	B. pertusa (Linn.) A. Camus, loc. cit.

greatly reduced pedicellate spikelets.

Camus (1931) raised the African A. pertusus var. insculptus subvar. trifoveolatus Hack. to specific rank. This species, B. insculpta (Hochst.) A. Camus, differs very conspicuously from typical A. pertusus. The type of A. insculptus Hochst., Schimper No. 80 (K) from Abyssinia, is a robust plant with mostly cauline leaves, decumbent culms, and the pedicellate spikelets are 1-3 pitted. Stapf (1917) demonstrated that A. pertusus var. capensis Hack. (Drege 4325, Key River, So. Africa) should be included in A. insculptus. Bor (1960) referred the Indian A. pertusus var. insculptus subvar. bifoveolatus (Steud.) Hack., and A. subunifoveolatus Steud. to B. insculpta. These Indian plants differ from each other primarily in pit characteristics. The type of A. bifoveolatus Steud., Wight Herb. No. 156 (K), resembles A. insculptus in respect to pit characteristics, but the plant is more slender, and the lower glume of the sessile spikelets is completely glabrous. Some Indian specimens have only some of the sessile spikelets distinctly pitted and the pedicellate spikelets may be pitted or not pitted in the same raceme. These characteristics describe the type of A. subunifoveolatus, Herb. Hohenacker 918 (K), in detail.

The Indian A. pertusus var. longifolius Hack. was given specific rank by Bor (1960) who demonstrated that it undoubtedly represents a good species. The type, Wallich 8803 (K) collected at Madras, represents an erect, tufted plant with 30-40 centimeters long linear leaves. The sessile spikelets are distinctly pitted, and as is characteristic of A. pertusus, the pedicellate spikelets are unpitted.

The Indian varieties A. pertusus var. wightii Hack. (Wight Cat. No. 1696) with villous sheaths and the more common A. pertusus var. genuinus

Hack. with more or less glabrous sheaths, should be included in typical A. pertusus as suggested by Hooker (1897). Both of these varieties are characterized by unpitted pedicellate spikelets.

Hackel (1889) regarded A. panormitanus Parl., distributed in Sicily and Northwestern Africa, as a variety of A. pertusus. Pilger (1940) transferred this variety to Bothriochloa and gave it specific rank. A specimen collected at the type locality Palermo, Ball s.n. ex Herb. Parlatoreanum (K), was studied. This specimen differs from typical representatives of A. pertusus in being a robust plant with decumbent culms and the lower primary racemes are strongly divided.

The African A. pertusus var. vegetior Hack. was transferred to B. insculpta as a variety by Hubbard (1934). The type, Schweinfurth 1027 (K) from the Sudan, resembles B. insculpta in spikelet morphology, but the primary axis of the inflorescence is elongated, exceeding the lower racemes in length. As indicated by Hubbard (1934) this variety definitely does not belong with B. pertusa.

Camus (1919) described A. pertusus var. barbatus from Anam (Chevalier 30541 et 30546), but recognized no varieties when this species was transferred to Bothriochloa (Camus, 1931). This variety could evidently be included in typical B. pertusa.

Maire (1940) described B. pertusa var. maroccana, and Maire (1941) demonstrated the presence of B. pertusa var. maroccana forma emasculata. This variety resembles B. panormitana (Parl.) Pilger in growth habit and gross morphological characters (Maire, 1952) and definitely does not belong with B. pertusa. Similarly B. pertusa var. tunetana from Tunesia, described by Camus (1957), could more naturally be excluded from B. pertusa. Maire (1959) pointed out that B. pertusa var. tunetana differs from B. pertusa var. maroccana in having glabrous nodes, from B. panormitana by its scabrous leaves, and from both by its small size.

Morphology

Bor (1960), although recognizing B. pertusa in its restricted sense, pointed out that this species extends eastward from Arabia to South-east Asia, and that it is also present in tropical Africa. Chippindall (1955) and Sturgeon (1956) demonstrated that B. pertusa is not present in southern Africa. The present study indicated that typical representatives of B. pertusa are absent from the natural flora of Africa, but that it was introduced from India and became established to a limited extent in some tropical regions.

The Indian representatives of A. pertusus as recognized by Hackel (1889) were subdivided by Bor (1960) among B. insculpta (Hochst.) A. Camus, B. longifolia (Hack.) Bor and B. pertusa (Linn.) A. Camus. These, and morphologically similar Indian species, may be distinguished, the one from the other, by the following key characteristics:

1. Lower glume of sessile spikelets hairy below the middle.
    2. Lower glume of sessile spikelets with one, rarely two circular pits.
        3. Racemes mostly 9-15 in number, up to 8 centimeters long; plants decumbent or erect ... B. kuntzeana
        3. Racemes mostly 2-12 in number, up to 5 centimeters long; plants prostrate, flowering culms decumbent ... B. pertusa
    2. Lower glume of sessile spikelets with a slit-like depression; plants decumbent or erect ... B. kuntzeana
1. Lower glume of sessile spikelets glabrous below the middle, or

essentially so.

4. Lower glume of sessile spikelet not pitted.

  5. Lower glume of pedicellate spikelet with a slit-like depression on the back — B. kuntzeana

  5. Lower glume of pedicellate spikelets rounded on the back, never pitted.

    6. Pedicel of pedicellate spikelets grooved — B. foulkesii

    6. Pedicel of pedicellate spikelets solid — B. concanensis

4. Lower glume of sessile spikelets pitted.

  7. Lower glume of pedicellate spikelets with 1-4 circular pits — B. insculpta

  7. Lower glume of pedicellate spikelets not pitted, or with a slit-like depression.

    8. Lower glume of sessile spikelets coriaceous; pedicellate spikelets not pitted — B. longifolia

    8. Lower glume of sessile spikelets membraneous to chartaceous; pedicellate spikelets usually with a slit-like depression — B. kuntzeana

The species, as recognized by Bor (1960), are quite distinct. Herbarium studies, however, revealed that the Indian representatives of B. insculpta differ conspicuously from African material included in this species. Typical representatives of B. pertusa extend throughout India to Ceylon and eastward to Indonesia. These are prostrate plants with decumbent flowering culms; 2-12 racemes per inflorescence with only the lower ones sometimes divided; the lower glume of sessile spikelets pilose below the middle and distinctly pitted, and the lower glume of pedicellate spikelets essentially glabrous and never pitted.

Plants with the sessile spikelets distinctly pitted and the pedicellate ones 1-4 pitted, which Bor (1960) included in B. insculpta, similarly extend from India to Indonesia. They differ from African representatives of B. insculpta in the following salient morphological features. The Indian plants are less robust, with the culms geniculately ascending from a creeping base; the lower glume of sessile spikelets is more obtuse, and completely glabrous on the back. From B. pertusa these specimens differ mainly in respect to the presence of pits on the pedicellate spikelets, and the tufts of leaves at the lower nodes of the culms are longer and more linear. Some specimens resemble B. pertusa more closely in having the pedicellate spikelets only faintly pitted, or only some pedicellate spikelets in a raceme distinctly pitted. Many of these specimens are often difficult to distinguish from B. kuntzeana (Hack.) Henr. on the basis of spikelet morphology. In the latter species, the lower glume of sessile spikelets often has a distinct slit-like pit, and the lower glume of pedicellate spikelets may be rounded on the back, have a slit-like depression, or else pitted and non-pitted pedicellate spikelets may be present in the same inflorescence. This species differs from B. pertusa and the Indian B. insculpta very distinctly in growth habit and inflorescence morphology. Hooker (1897) and Blatter and McCann (1935) demonstrated that Andropogon kuntzeanus Hack. is characterized by tall, erect culms; the racemes are densely fascicled and the rachis and pedicels are plumosely ciliate with long hairs.

Blatter and McCann (1935) suggested that, only from genetical tests could we expect to get an insight into the natural variation of B. pertusa. Attempted crosses between various biotypes of B. pertusa, as well as between this and other species were unsuccessful. Celarier and Harlan (1958) demonstrated that B. pertusa and B. insculpta reproduce by means of gametophytic apomixis. Harlan et al. (1958, 1961) indicated that diploid representatives of Bothriochloa reproduce sexually, tetraploids are mostly facultative apomicts and higher polyploids are essentially obligate apomicts. Harlan (1963) reported that B. kuntzeana and B. longifolia are diploids ($2n = 20$). Typical representatives of B. pertusa are all tetraploids ($2n = 40$), African representatives of B. insculpta are pentaploid ($2n = 50$) or hexaploid ($2n = 60$), and Indian representatives of the latter species are tetraploid or hexaploid. Hybrid data presented by de Wet, Borgaonkar, and Richardson (1963) indicated that tetraploid, pentaploid and hexaploid collections of B. pertusa and B. insculpta are essentially obligate apomicts.

From a taxonomic point of view the diploid B. kuntzeana is a distinct species. With the Indian representatives removed from B. insculpta, the African representatives form a more or less natural group. These Indian plants with pitted pedicellate spikelets could be regarded as apomictic biotypes of B. pertusa. Babcock and Stebbins (1938), Gustafsson (1946, 1947 a, b) and Stebbins (1950) demonstrated that agamospecies are often highly variable. Variation in chromosome number is probably due to hybridization. Clausen (1954, 1961) indicated apomixis may actually facilitate occasional hybridization. In apomicts the cytologically reduced or unreduced female gamete may function sexually, giving rise to hexaploids among a hybrid progeny of tetraploid parents.

Taxonomy

The species B. pertusa as recognized in this study may be characterized as follows:

BOTHRIOCHLOA PERTUSA (Linn.) A Camus, Ann. Soc. Linn. Lyon 1930, 76: 164. 1931. Based on Holcus pertusus Linn.

Holcus pertusus Linn., Mant. Alt. 301. 1771. Type not seen.

Andropogon pertusus (Linn.) Wild., Sp. Pl. 4: 922. 1806. Not of Stapf 1895.

A. pertusus var. barbatus A. Camus, Bull. Mus. Hist. Nat. Paris 25: 370. 1919. Annam, Chevalier 30541, 30546.

A. pertusus var. wightii Hack. in D. C. Monogr. Phan. 6: 481. 1889. India, Wight 1696.

A. pertusus var. insculptus subvar. bifoveolatus (Steud.) Hack. in DC., loc. cit. 483. Based on A. subunifoveolatus Steud. et A. bifoveolatus Steudel.

A. bifoveolatus Steud., Syn. Pl. Glum. 1: 380, 1854. India, Wight Herb. Andropogon No. 156 (K).

A. subunifoveolatus Steud., loc. cit. 380. India, Herb. Hohenacker No. 918 (K).

A. angustifolius Parl., Fl. Palerm. 1: 369. 1845. Not of Sibth. et Sm. 1806, misapplied by Parlatore.

Lepeocercis pertusa (Linn.) Hassk., Pl. Jav. Rar. 52. 1848.

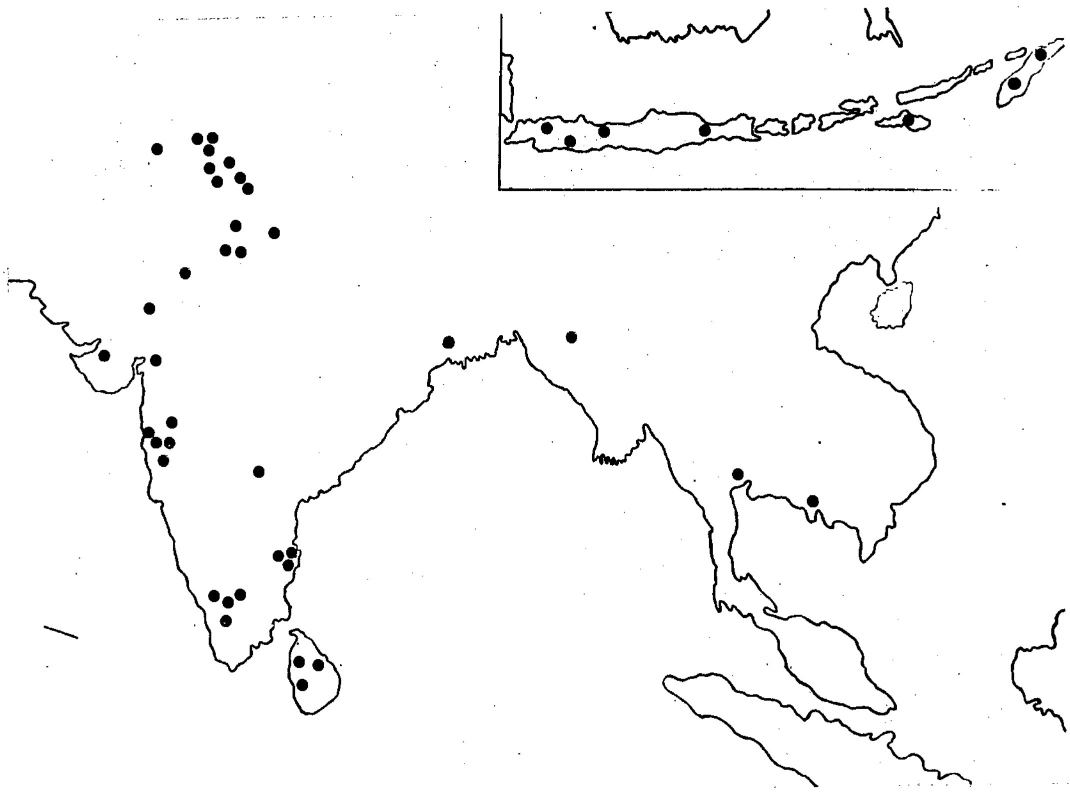
Amphilophis pertusa (Linn.) Hash ex Stapf in Agric. News W. Ind. 15: 179, 1916.

Distribution: Extends from Pakistan to Ceylon and Indonesia. Introduced into tropical and subtropical regions of both the Old and New World (Plate II).

LEGEND TO PLATE II

Distribution of *Bothriochloa pertusa*.

PLATE II



Cytology: Segmental allopolyploids characterized by $2\underline{n} = 40$ and 60 chromosomes. At meiosis, during microsporogenesis, the chromosomes mostly form bivalents, although some chromosomes may fail to pair or associate into multivalents.

Description: Perennial, prostrate or rambling, flowering culms geniculately ascending, rooting at the lower nodes; nodes bearded to glabrous. Leaves 5-20 centimeters long, linear, the lower often short and crowded at the base of the stem, glabrous, pubescent or sparingly pilose, margins often scabrid; sheaths terete or slightly compressed, shorter than the internodes, often sparingly pilose; ligule a ciliate membrane.

Racemes 2-15, subdigitately arranged on a short primary axis exceeded in length by the lower racemes; rachis and pedicels slender, densely ciliate. Sessile spikelets bisexual, rarely, the lowest on a raceme, male, 3-4 millimeters long, oblong-lanceolate, callus bearded. Lower glume with a deep pit above the middle, sometimes with a trace of a second pit also present, glabrous or more frequently hairy below the middle, 5-9-nerved, margins narrowly incurved; upper glume lanceolate, acuminate, 3-5-nerved, often slightly longer than the lower glume, usually glabrous, rarely ciliolate at the apex. Lemma of empty lower floret linear-oblong, nerveless, glabrous; lemma of bisexual upper floret forming the base of a well developed awn, palea absent. Pedicellate spikelets like the sessile, but narrower, awnless, male or neuter. Lower glume usually not pitted, 7-13-nerved, glabrous or ciliate, rarely 1-4-pitted; upper glume 3-5-nerved, glabrous; lemma of lower floret linear-oblong, of upper floret small or absent.

Two varieties (Plate III) are recognized on the basis of pittedness

LEGEND TO PLATE III

Extremes of morphological variation in leaf and inflorescence characteristics.

Figure 1. Typical *Bothriochloa pertusa* var. *pertusa*

Figure 2. *Bothriochloa pertusa* var. *bifoveolata*

PLATE III

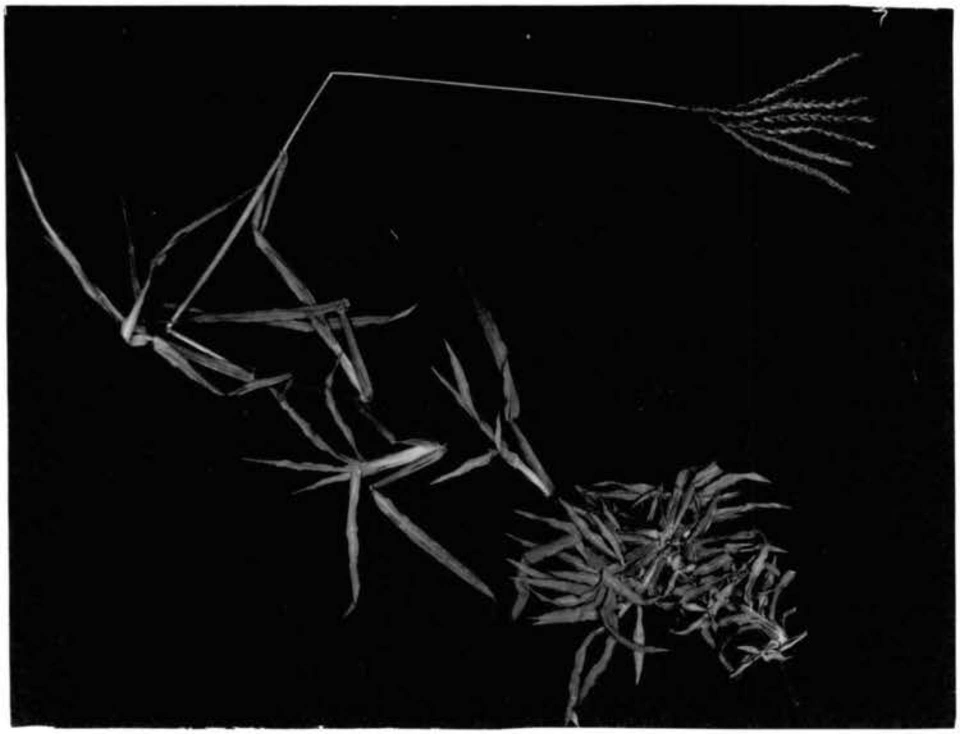


Fig. 1

Fig. 2

of the pedicellate spikelets (Plate IV).

Bothriochloa pertusa var. pertusa. Based on Holcus pertusus Linn. loc. cit.

Characterized by pitted sessile, and non pitted pedicellate spikelets. The lowest pedicellate spikelet on a raceme may occasionally be pitted. Plant studied cytologically are tetraploid (2n = 40).

Specimens studied: PAKISTAN: Sargodha, Okla 4635-2. INDIA: Wight 1696; Ajmere, Okla 8886a; Kangra, Okla 8962, 8986; Dehra Dun, Okla 5309, 8977a; Jullundur, Okla 8980; Jammu, Okla 8981b; Pathankot, Okla 8982, 8984a; Dalhousie, Okla 8985a; Mandi, Okla 8987a; Nahan, Okla 8988 a, b; Alwar, Okla 8989; New Delhi, Okla 5406, 6840, 9090a, 9091; Mathura, Okla 5403; West Bengal, Okla 6152; Bangalore, Okla 8251; Coimbatore, Okla 5408b; Hyberabad, Okla 4806a; Madras, Gamble 10830, 12740 (K); Mysore, Meebold 10576 (K); Poona, Okla 9092; Khandala, Okla 8279, 8289; Sangamner, Okla 8282a; Rajkot, Okla 8284, 8285-3b; Mulshi, Okla 8286, 8287; Panchgani, Okla 8290, 8291; Kotharud, Okla 8292. CEYLON: Uva, Ballard 1128 (K); Okla 4021, 7500. BURMA: Kyaukpyu, Wallace 9041 (K). CHINA: Southern, Okla 6154. INDONESIA: Java, van Oostroom 12645 (L), van Stennis 17450, 17473 (L), Backer 37558 (L); Timor, van Stennis 17978 (L).

Bothriochloa pertusa var. bifoveolatus (Steud.) de Wet et Higgins comb. nov. Based on Andropogon bifoveolatus Steud. loc. cit., Wight Herb. Andropogon No. 156 (K).

Characterized by having both the sessile and pedicellate spikelets pitted, the latter often with 2-4 pits. Pitted and not pitted pedicellate spikelets are sometimes present in the same raceme or inflorescence. Plants studied cytologically are tetraploid (2n = 40) or hexaploid

LEGEND TO PLATE IV

Spikelet morphology.

Figure 1. *Bothriochloa pertusa* var. *pertusa*

Figure 2 and 3. *Bothriochloa pertusa* var. *bifoveolata*

PLATE IV

Fig. 1

Fig. 2

Fig. 3

($2n = 60$).

Specimens studied: INDIA: Dalhousie, Okla 8984, 8985b; Mandi, Okla 8987b; New Delhi, Okla 5301, 9094, 9095; Dehra Dun, Okla 4394b; Belatal, Okla 5396; Jammu, Okla 8981a; Coimbatore, Fischer 1407 (K), Narayanaswamy 3188 (K), Okla 2654; Panchgani, Okla 9094, 9095; Mt. Abu, Okla 9096, 9097, 9098; Khandala, Okla 8283, 8299; Lonavla, Okla 8280; Jammu, Okla 8281, 8281a; Sangamner, Okla 8282; Rajkot Okla 8285-1, 8285-3b; Mulshi, Okla 8287; Saurastra, Okla 8308; Nilgiris, Schmidt s.n. (K), Perrottet 1311, 1314 (K), Gamble 15321, 20720 (K), Wight 3394 (K); Pulneys, Bourne 1027, 1028, 1340 (K); Silver Falls, Bourne 1943 (K). INDONESIA: Java, Okla 5585; Sumba, de Froideville 1621, 1982 (L), Hoekstra 19 (L).

Conclusions

1. Typically *B. insculpta* (Hochst.) Stapf is confined to Africa and *B. pertusa* extends from West Pakistan eastward.

2. When these two species are separated on the basis of spikelet structure some African specimens are usually included in *B. pertusa* and some Asiatic specimens in *B. insculpta*.

3. It was suggested that the African plants be excluded from *B. pertusa*.

4. The Indian plants usually classified with *B. insculpta* could more naturally be included in *B. pertusa*.

5. Indian representatives of *B. insculpta* differ from *B. pertusa* mainly in the presence of indentations on the lower glume of pedicellate spikelet, and resemble African *B. insculpta* mainly in respect to this characteristic.

6. The new combination *B. pertusa* var. *bifoveolatus* (Steud.) de Wet et Higgins was proposed to include Indian plants usually classified with *B. insculpta*.

CHAPTER IV

BIOSYSTEMATICS OF BOTHRIOCHLOA INSCULPTA AND B. RADICANS

Stapf (1917) indicated that B. insculpta (Hochst.) A. Camus (Gramineae) is a polymorphic species, widely distributed throughout the tropical and subtropical regions of Africa. Bor (1960) pointed out that this species extends into India, but de Wet and Higgins (1963) demonstrated that the Indian representatives could more naturally be included in B. pertusa (Linn.) A. Camus.

The African representatives of Bothriochloa O. Kuntze are usually subdivided, on the basis of inflorescence structure, into two major groups. First, the extremely variable B. glabra (Roxb.) A. Camus which is characterized by numerous, more or less divided racemes arranged along an elongated primary axis. Second, a group of species characterized by relatively few racemes subdigitately arranged along a short primary axis. The latter group was studied in an effort to determine the taxonomic status of the various species usually recognized.

Material and Methods

Morphological data are based on studies at the herbarium of the Royal Botanic Garden at Kew, England; the Rijksherbarium at Leiden, Holland; the Jardin Botanique de l'Etat at Brussels, Belgium; as well as on studies of plants grown in a uniform nursery at Stillwater, Oklahoma. Herbarium specimens of plants studied morphologically and cytologically are filed with the Oklahoma State University. Chromosome numbers were determined from developing microsporcytes stained with aceto-carmine.

Morphology and Discussion

African representatives of *Bothriochloa* were variously subdivided into species and varieties by Stapf (1917), Camus (1931), Maire (1952, 1959), and Jacques-Felix (1962).

The species and varieties usually recognized may be distinguished, the one from the other, by the following key characteristics:

1. Racemes arranged on an elongated primary axis, exceeding the lower racemes in length.
    2. Sessile spikelets pitted or not pitted; pedicellate spikelets rarely pitted; often only some spikelets in a raceme pitted ..... *B. glabra*
    2. Sessile spikelets pitted; pedicellate spikelets consistently 1-4 pitted ..... *B. insculpta* var. *vegetior*
1. Racemes subdigitately arranged on a short primary axis, usually distinctly shorter than the lower racemes.
    3. Spikelets never pitted.
        4. Plants erect, tufted; culms not excessively branched ..... *B. ischaemum*
        4. Plants strongly branched from a slightly decumbent base ..... *B. radicans*
    3. Sessile spikelets usually distinctly pitted; pedicellate spikelets pitted or not pitted.
        5. Pedicellate spikelets consistently 1-4 pitted ..... *B. insculpta* var. *insculpta*

5. Pedicellate spikelets pitted or not pitted in the same inflorescence, rarely consistently non-pitted.

 6. Plants small, slender, forming dense tufts from a decumbent base.

  7. Sessile spikelets linear to lanceolate-oblong; pits small, often absent or present in the same inflorescence ... B. intermedia var. acidula

  7. Sessile spikelets oblong; pits conspicuous ... B. pertusa var. tunetana

 6. Plants more robust, rambling, with the flowering culms geniculately ascending.

  8. Upper glume of sessile spikelets mucrorate; lower glume of pedicellate spikelets involute ... B. panormitana

  8. Upper glume of sessile spikelets acute; lower glume of pedicellate spikelets two-keeled ... B. pertusa var. maroccana

Celarier and Harlan (1958) indicated that B. ischaemum (Linn.) Keng extends across southern Europe, and along the mountainous regions of Asia to the China coast. Maire (1959) pointed out that this species is also present in the Atlas mountain region of North Africa. These African representatives are typical representatives of the species and easy to distinguish on the basis of growth habit from the widely distributed African B. radicans (Lehm.) A. Camus.

Hackel (1889) treated Andropogon radicans Lehm. as a variety of A. ischaemum Linn., and Stapf (1907) described A. ischaemum var. somalensis to include a plant collected in Somaliland (Appleton s.n., K).

Both of these varieties were cited by Stapf (1917) as synonyms for Amphilophis radicans which was later transferred to Bothriochloa by Camus (1931). Plants with slender, erect or slightly decumbent culms, linear leaves which are often pilose and few-15 racemes with non-pitted spikelets typically characterize B. radicans. Plants referable to B. intermedia var. acidula (Stapf) C. E. Hubbard, and to B. pertusa var. tunetana A. Camus differ from B. radicans mainly in respect to the presence or absence of pits on the spikelets.

Stapf (1917) tentatively described Amphilophis intermedia var. acidula to include a variable group of plants from Africa and the West Indies. The West Indian material at Kew were subdivided by Stapf (The Agric. News W. Indies 15, No. 368: 179. 1916) into three groups. First, plants resembling Andropogon ischaemum var. americanus Hack. which were included in a new species A. feracidulus. Second, plants with glabrous culm nodes and pitted sessile spikelets which resemble A. panormitanus Parlatore. Third, a variable group of plants representing a hybrid complex involving various Old World species.

The African material is quite distinct from the West Indian plants. The type, Johnson 1017 from the Gold Coast (K) represents a small semi-erect plant with glabrous nodes; racemes arranged along a short primary axis, with the lower racemes divided; sessile spikelets pitted and the pedicellate spikelets not pitted. It is almost impossible to distinguish between this plant, and specimens included by Camus (1957) in B. pertusa var. tunetana. From a taxonomic point of view B. intermedia var. acidula and B. pertusa var. tunetana should be united into a single taxonomic unit. The specific name B. intermedia can not be accepted. The type for B. intermedia, Brown 6184 from Keppel Bay, Australia (BM), is characterized by an inflorescence with numerous racemes arranged along an elongated primary axis which exceed the lower racemes in length. The specific name B. pertusa is commonly accepted for African plants with pitted sessile spikelets on subdigitately arranged racemes (Jacques-Felix, 1962; Maire, 1959; Bor, 1960). Typically, B. pertusa is confined to India and South-east Asia. The morphology of this species was fully discussed by de Wet and Higgins (1963) who demonstrated that the African representatives differ from more typical members of B. pertusa in growth habit. These African plants resemble B. radicans in detail, except for the pitted sessile, and occasionally pitted pedicellate spikelets. For these reasons they could more naturally be included as a variety of B. radicans.

Maire (1952) included the Sicilian species B. panormitana (Parl.) Pilger as a variety of B. pertusa, and pointed out that it resembles B. pertusa var. maroccana very closely. The latter variety differs from B. panormitana mainly in having the pedicellate spikelets never pitted. Typical representatives of B. panormitana have the pedicellate spikelets often faintly pitted. Gross morphological characters are so similar that B. pertusa var. panormitana (Parl.) Maire et Weiller and B. pertusa var. maroccana should be combined into a single taxonomic unit. These plants differ conspicuously from B. pertusa (Linn.) A. Camus in growth habit. These African plants are robust, with erect culms from a rambling base. Typically B. pertusa is a small creeper with tufts of short leaves at the lower nodes, and longer more linear cauline leaves on the ascending flowering culms. In growth habit B. panormitana resembles B. insculpta in detail.

The most common African species is B. insculpta, characterized by pitted sessile and pedicellate spikelets, the latter usually with 2-4 distinct indentations. These are mostly robust plants erect or ascending from a decumbent base. Extremely robust, suberect plants with numerous, often strongly divided racemes are usually hexaploid (2n = 60). Smaller plants with the flowering culms ascending from a decumbent base, and with few-15 racemes are mostly pentaploid (2n = 50). The characteristics of the pentaploids describe the type, Schimper s.n. from Abyssinia (K), in detail. These morphological and cytological differences, however, are not sufficiently distinct to allow for the recognition of different varieties. Some specimens, resembling the pentaploid representatives of B. insculpta, differ from this species in pittedness of the spikelets. The pedicellate spikelets are either non-pitted or only faintly pitted, and the sessile spikelets may be pitted, or only the lower ones on a raceme may be pitted. Except that they are distributed in tropical and subtropical Africa, rather than North Africa and Sicily, these specimens resemble B. panormitana in detail. The latter species is typically a hexaploid, and the tropical African plants resembling B. panormitana are either pentaploid or hexaploid. Morphological and cytological data suggest that B. panormitana is widely distributed in Africa, and could more naturally be classified as a variety of B. insculpta.

The variety B. insculpta var. vegetior (Hack.) Hubbard, based on Schweinfurth 1027 (K), collected in the Sudan, more naturally belongs with B. glabra (Roxb.) A. Camus. It resembles B. insculpta only in having the pedicellate spikelets 2-4-pitted. Pittedness of the spikelets is a variable character, and African representatives of B. glabra are often characterized by pitted or non-pitted spikelets in the same raceme.

Plants studied cytologically are tetraploid with 2n = 40 chromosomes rather than pentaploid or hexaploid as characteristic of B. insculpta.

Cytologically the African representatives of Bothriochloa behave like segmental allopolyploids as defined by Stebbins (1947). The species B. radicans, B. intermedia var. acidula, B. glabra, and B. insculpta var. vegetior are tetraploid while B. panormitana and B. insculpta var. insculpta are characterized by pentaploid and hexaploid races. Harlan et al. (1961), and de Wet, Borgaonkar and Richardson (1963) demonstrated that these polyploids are facultative apomicts. Natural hybridization apparently takes place occasionally between B. radicans with non-pitted spikelets, and B. intermedia var. acidula with pitted sessile spikelets. This could explain the origin of plants with indistinct pits on the lower glumes, as well as those with only some sessile apikelets distinctly pitted.

Morphologically, hexaploid B. insculpta appears to represent a hybrid between a plant resembling the pentaploid race of B. insculpta, and tetraploid B. glabra. Harlan et al. (1958) demonstrated experimentally that in Bothriochloa, the cytologically unreduced female gamete of facultative apomictic tetraploids may function sexually to produce hexaploid hybrids. A tetraploid race of B. insculpta, however, appears to be absent. Tetraploid B. radicans or B. intermedia var. acidula may be the one parent, and could have crossed with B. glabra to produce the hexaploid B. insculpta. Similarly, these tetraploid species may have crossed with the hexaploid, giving rise to the pentaploid race. Attempted hybrids, in various combinations, between these species have so far failed. Cytologically it would not appear as if B. insculpta represents an interspecific hybrid of the type discussed above. The chromosomes mostly associate into pairs although univalents and/or multivalents were occasionally observed. Chheda and Harlan (1963) demonstrated, however, that in artificially produced hybrids among species of *Bothriochloa* chromosome pairing takes place preferentially and bivalent formation is the rule.

Taxonomy

The taxonomy of *B. ischaemum* was fully discussed by Celarier and Harlan (1957). In Africa this species is apparently confined to the Atlas Mountains of North Africa. Genetically *B. ischaemum* appears to be only distantly related to the more typically African representatives of *Bothriochloa*. The widely distributed (Africa to Australia) *B. glabra* was not studied in detail, and will not be included in the present taxonomic treatment. Morphological data, however, suggested that this species may have contributed towards the origin of *B. insculpta*. The remaining African species and varieties will be described in detail.

BOTHRIOCHLOA RADICANS (Lehm.) A. Camus, Ann. Soc. Linn. Lyon 1930, 76: 164. 1931. Based on *Andropogon radicans* Lehm.

Andropogon radicans Lehm., Ind. Sen. Hort. Hamb. 1828. Type not seen.

A. ischaemum var. *radicans* Hack. in DC., Monogr. Phan. 6: 476. 1889. Based on *A. radicans* Lehm.

A. ischaemum var. *somalensis* Stapf, Kew Bull. 1907: 210. 1907. Somaliland, *Appleton s.n.* (K).

Amphilophis radicans (Lehm.) Stapf in Prain, Fl. Trop. Afr. 9: 172. 1917. Based on *A. radicans* Lehm.

Andropogon pertusus Stapf, Kew Bull. 1895: 209. 1895. Not of Willd. 1806; also of Stapf in Prain, loc. cit: 175, excluding synonyms.

Amphilophis intermedia var. acidula Stapf in Prain, loc. cit.: 174.

Gold Coast, Christiansborg, Johnson 1017 (K).

Bothriochloa intermedia var. acidula (Stapf) C. E. Hubb., Kew Bull. 1934: 109. 1934.

B. pertusa var. tunetana A. Camus in Dubuis et Faurel, Bull. Soc. Hist. Nat. Afr. Nord 48: 478. 1957. Tunisia, Serres s.n. (Type in Herb. L. Faurel).

Distribution: Widespread in Africa (Plate V).

Cytology: Segmental allotetraploid; $2n = 40$ chromosomes mostly forming bivalents during microsporogenesis. Univalents and/or multivalents were occasionally observed.

Description: Perennial, slender, culms up to 50 centimeters tall, erect, or ascending from a short creeping base, with tufts of leaves and shoots, often rooting at the nodes; if erect, sparingly branched. Leaf-sheaths glabrous or bearded at the nodes; ligule truncate and ciliate; leaf-blades linear up to 10 centimeters long, sparingly hairy or pilose, rarely glabrous.

Racemes few-15, subdigitately arranged, longer than the primary axis of the inflorescence, mostly undivided, rarely the lowest raceme branched. Sessile spikelets linear - oblong, 2-3 millimeters long, bisexual; callus bearded. Glumes equal in size; lower glume hairy towards the base and along the margins near the apex, pitted or not pitted, often with pitted and not pitted spikelets in the same raceme; upper glume lanceolate, ciliate upwards. Lemma of empty lower floret hyaline; lemma of bisexual upper floret forming the base of a well-developed awn. Pedicellate spikelets male or neuter, as long as, or slightly shorter than, the sessile spikelets, glabrous, rarely faintly

LEGEND TO PLATE V

Distribution of *Bothriochloa* *insculpta* and *Bothriochloa* *radicans*.

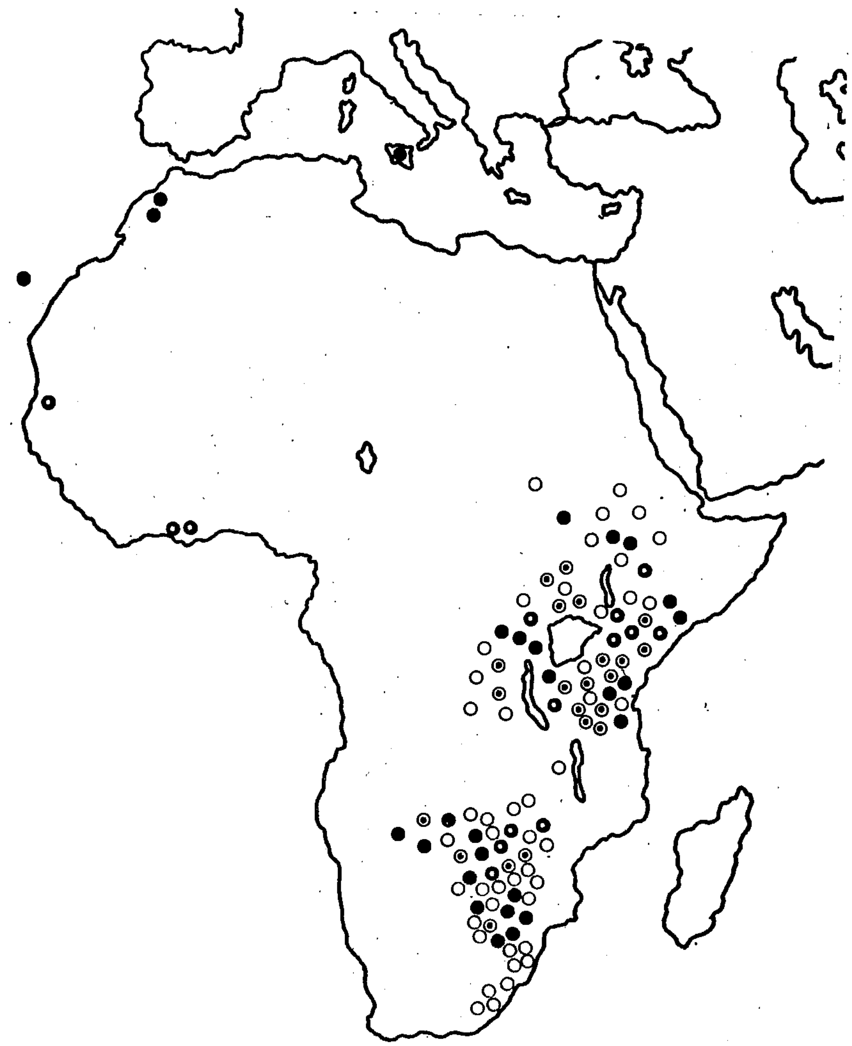
○ : *Bothriochloa* *insculpta* var. *insculpta*

● : *Bothriochloa* *insculpta* var. *panormitana*

◎ : *Bothriochloa* *radicans* var. *radicans*

◉ : *Bothriochloa* *radicans* var. *acidula*

PLATE V



pitted.

Two varieties are recognized on the basis of pit characteristics.

B. radicans var. radicans. Based on A. radicans Lehm., with neither the sessile nor the pedicellate spikelets ever pitted (Plate VI).

Specimens studied: SOMALILAND: Hasuslawe, Glover and Gilliland 985 (K); Hargeisa, Glover and Gilliland 14 (K). SUDAN: Kapoeta, Myers 13991 (K); Equatoria, Jackson 823 (K). UGANDA: Moholuya, Thomas 3949 (K); Karamoja, Thomas 3184 (K). TANGANYIKA: Tarangire River, Lamprey 280 (K); Manyara, Fitzgerald 2126 (K); Moshi, Webster T. 265 (K). KENYA: Makipenzi, Bally 9737 (K); Moyale, Gillett 12853 (K); Athi River Bogdan 1575 (K); Suk Reserve, Bogdan 2998 (K); Okla 3055, Okla 5468. CONGO: Albert National Park, Germain 2983 (K), Lebrun 9248 (K). ANGOLA: Gossenweiller 8409 (K). BECHUANALAND: Drummond and Seagrief 5240 (K). RHODESIA: Banket, Okla 9440; Balla Balla, Okla 9488; Filabusi, Okla 9489. SOUTH AFRICA: Pretoria, Okla 9682.

B. radicans var. acidula (Stapf) de Wet et Higgins comb. nov. Based on Amphilophis intermedia var. acidula Stapf. Also included in this variety are African plants referred to B. pertusa by Stapf (1917) and B. pertusa var. tunetana A. Camus (Plate VII).

Differs from typical representatives of the species in having at least some sessile spikelets in an inflorescence pitted, and the pedicellate spikelets occasionally faintly pitted.

Specimens studied: SENEGAL: Dakar, Okla 5431; Baldwin 5721 (K). GHANA: Apam, Hall 1775 (K); Christiansborg, Johnson 1017 (Type, K). SOMALILAND: Boroma, Hemming 1282 (K). ETHIOPIA: Messanona, Mooney 7050 (K). UGANDA: Serere, Harker 227 (K). TANGANYIKA: Eanong, Fitzgerald 2230 (K). KENYA: Kibwezi, Webster 135 (K); Kitale,

LEGEND TO PLATE VI

Bothriochloa radicans var. *acidula*.

Figure 1. Decumbent plant

Figure 2. Plant with erect culms from a short prostrate base

PLATE VI

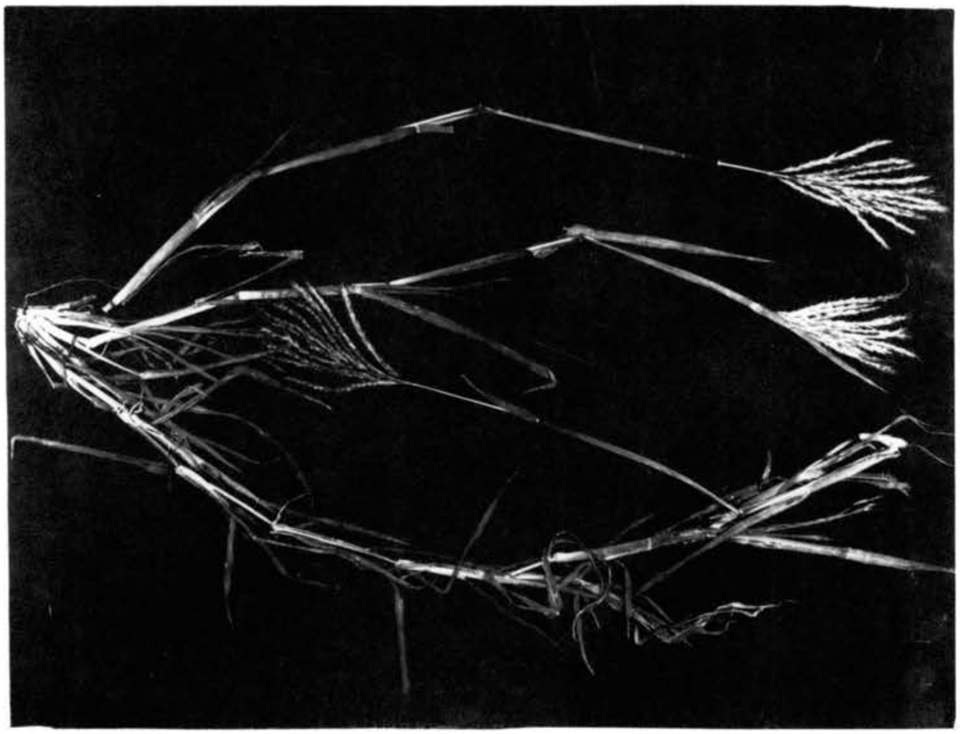


Fig. 1

Fig. 2

LEGEND TO PLATE VII

Bothriochloa radicans var. *radicans*.

Figure 1. Erect plant

Figure 2. Decumbent plant

PLATE VII

Fig. 1

Fig. 2

Okla 5467. RHODESIA: Mazabuka, Okla 9479; Zimba, Okla 9480; Lupani, Okla 9481; Shabisi, Okla 9482.

BOTHRIOCHLOA INSCULPTA (Hochst.) A. Camus, Ann. Soc. Linn. Lyon 1930, 76: 165. 1931. Based on Andropogon insculptus Hochst.

Andropogon insculptus Hochst. ex. Rich., Tent. Fl. Abyss. 2: 458. 1851. Africa, Abyssinia, Schimper s.n. ex Herb. Hook. (K).

A. pertusus var. insculptus (Hochst.) Hack. in DC., Monogr. Phan. 6: 483. 1889. Based on A. insculptus Hochst.

A. pertusus var. insculptus subvar. trifoveolatus Hack. in DC., loc. cit. 483. Africa, Abyssinia, Schimper 80 (K).

A. pertusus var. maroccanum Maire, Bull. Soc. Hist. Nat. Afr. Nord 19: 65. 1928. Africa, Morocco, Maire et Wilczek (Herb Univ. Algeriensis).

Amphilophis insculpta (Hochst.) Stapf in Prain, Fl. Trop. Afr. 9: 176. 1917. Based on A. insculptus Hochst.

Bothriochloa panormitana (Parl.) Pilger in Engl. et Prantl, Nat. Pflanzenfam. 14e: 161. 1940. Based on A. panormitanus Parl.

Andropogan panormitanus Parl., Fl. Ital. 1: 140. 1848. Palermo, Monte Pellegro, Sicily.

Bothriochloa pertusa var. maroccana Maire, Bull. Soc. Hist. Nat. Afr. Nord. 31: 45. 1940. Based on A. pertusus var. maroccanum Maire.

B. pertusa var. panormitana (Parl.) Maire et Weiller in Maire, Fl. Afr. Nord 1: 279. 1952. Based on B. panormitana (Parl.) Pilger.

Distribution: Widespread in tropical and subtropical Africa; also in Morocco, Sicily, Canary Islands, and introduced to the New World (Plate V).

Cytology: Segmental allohexaploid and allopentaploids; 2n = 50 and

$2n = 60$ chromosomes mostly associate into bivalents during microsporogenesis. Multivalents and univalents were often observed.

Description: Perennial, robust, tufted, culms up to 120 centimeters tall, often rather slender and rambling, usually decumbent to suberect; nodes pilose. Leaf-sheaths glabrous or hairy, shorter than the internodes; ligule short and scarious; leaf-blades linear, contracted at the base up to 25 centimeters long, rarely pubescent.

Racemes few to many, subdigitately arranged on a primary axis exceeded by the lower racemes in length. Sessile spikelets bisexual, linear-oblong 3-4.5 millimeters long. Lower glume sparingly hairy or pilose below the middle, 7-9-nerved, usually pitted, rarely only the lower sessile spikelets in a raceme with distinct pits; upper glume lanceolate with ciliate margins. Lemma of empty lower floret oblong, hyaline; lemma of bisexual upper floret forming the hyaline base of a well developed awn. Palea absent. Pedicellate spikelets male or neuter, well developed, linear-oblong. Lower glume glabrous, pitted or rarely not pitted, usually with 2-4-pits arranged in a row along the back, sometimes with only some pedicellate spikelets in a raceme or inflorescence pitted; upper glume as long as the lower, acute.

This is an extremely variable species, and is subdivided into two varieties.

B. insculpta var. *insculpta*. Based on *Andropogon insculptus* Hochst. loc. cit. from Abyssinia, *Schimper s.n. ex Herb. Hook.* (K). (Plate VIII).

Characterized by having both the sessile and pedicellate spikelets distinctly pitted, the latter usually with 2-4 pits arranged in a row along the back of the lower glume. In respect to growth habit, two

LEGEND TO PLATE VIII

Bothriochloa insculpta var. *insculpta*.

Figure 1. Robust, suberect plant with $2\underline{n} = 60$

Figure 2. Slender plant with rambling culms and $2\underline{n} = 50$

PLATE VIII

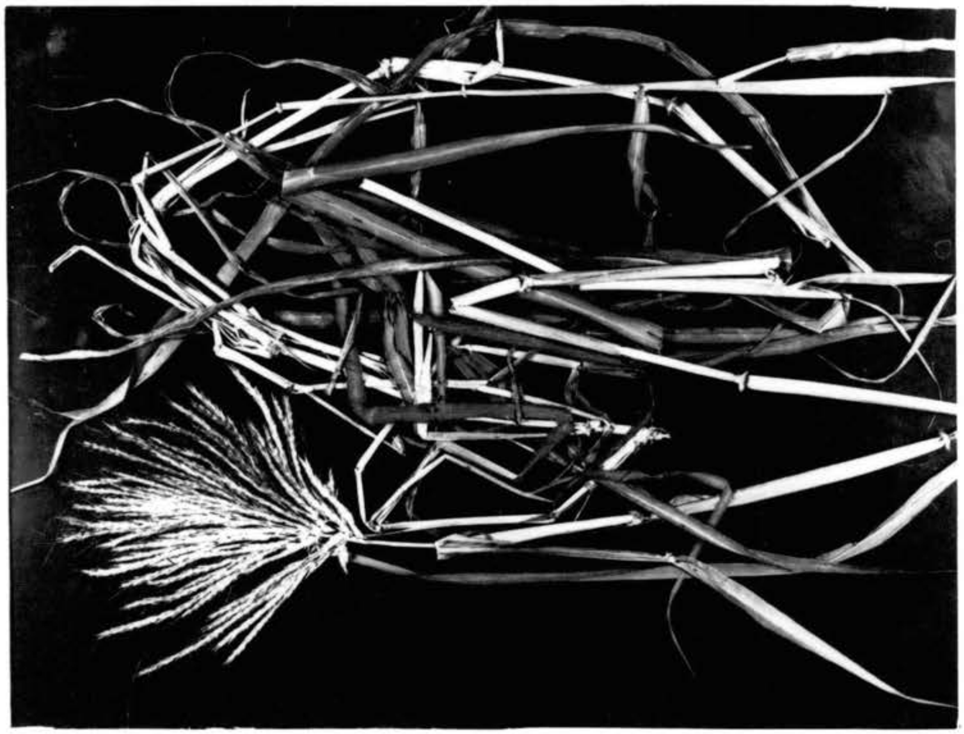


Fig. 1

Fig. 2

races may be recognized: extremely robust plants which are suberect, with numerous racemes per inflorescence, and more slender plants with rambling culms having fewer racemes per inflorescence. The more slender plants are usually pentaploid, while the robust specimens are hexaploid.

Specimens studied: SUDAN: Equatoria, Myers 9221. ETHIOPIA: Jimma, Mooney 6260 (K), Okla 4517, 9407, 9408, 9409. NYASILAND: Zomba, Wiehe N509 (K). UGANDA: Karamaja, Hudson 266 (K); Masaka, Michelmore 1337 (K). TANGANYIKA: Missenya, Okla 2584; N'gong, van Someren 9552 (K); Kabete, Edwards 2493 (K). KENYA: Kitale, Okla 3109; Nairobi, Okla 3239; Yatta plains, Edwards 81 (K). CONGO: Yangambi, Okla 3667; Kasonsero, Bequaert 5038 (BRLU); Kabare, Bequart 5329 (BRLU). RUANDA: Troupin 5789 (BRLU). NO. RHODESIA: Livingston, Okla 9443; Kafue, Okla 9441; Zimba, Okla 9456a. SO. RHODESIA: Rusape, Fitt 69 (K); Banket, Okla 9438, 9439; Choma, Okla 9442; Wankie, Okla 9444; Chilimanzi, Okla 9448; Enkeldoorn, Okla 9449; Lupani, Okla 9504a. SOUTH AFRICA: TRANSVAAL: Pretoria, Okla 8588, 9567, 9568; Hercules, Okla 9569; Swartspruit, Okla 9570, 9571; Brits, Okla 9572, 9573; Lydenburg, Okla 9574, 9575, 9577; Graskop, Okla 9578; Pilgrims Rest, Okla 9579; Witrevier, Okla 9580; Nelspruit, Okla 9581; Barberton, Okla 9582, 9583; Komatipoort, Okla 9584; Middelburg, Okla 9591; Groblersdal, Okla 9592, 9593, 9594; Marble Hall, Okla 9595; Nylstroom, Okla 9596; Roedtan, Okla 9597, 9599; Naboomspruit, Okla 9600; Warmbaths, Okla 9601. NATAL: New Castle, Okla 9602; Stanger, Okla 9603; Umhlanga, Okla 9604; Port Shepstone, Okla 9605; Harding, Okla 9606; Ixopo, Okla 9608; Richmond, Okla 9609, 9610. SWAZILAND: Goba, Okla 9588; Stegi, Okla 9589; Bremersdorp, Okla 9590.

B. insculpta var. panormitana (Parl.) de Wet et Higgins comb. nov.

Based on Andropogon panormitanus Parl. loc. cit. from Sicily, Palermo, Herb. Parlatore (Plate IX).

This variety is recognized to include plants referred to Bothriochloa panormitana (Parl.) Pilger. This species is usually recognized to include only plants from southern Italy and Sicily. Maire (1952) referred this species to B. pertusa (Linn.) A. Camus as a variety, and included the North African material resembling plants from Sicily in B. pertusa var. maroccana.

These two varieties, as recognized by Maire (1952), resemble typical Indian representatives of B. pertusa mainly in having the sessile spikelets pitted, and the pedicellate ones usually not pitted. Growth habit, however, is typically B. insculpta. The plants are relatively robust ramblers rather than small creepers, with longer leaves than those characteristic of B. pertusa.

Plants included in B. insculpta var. panormitana differ from typical representatives of B. insculpta primarily in pittedness of the spikelets. Pit characters are variable. The sessile spikelets are usually distinctly pitted, but pits are sometimes absent from the upper spikelets of each raceme. The pedicellate spikelets may be faintly pitted, or some spikelets in a raceme may be distinctly 1-4-pitted. Plants studied cytologically are pentaploid or hexaploid.

Specimens studied: EUROPE: Sicily, Palermo, Ross 293 (K), Schultz 644 (G). CANARY ISLANDS: Las Palmas, Gelert, s.n. (K). MOROCCO: Adadir, F.A.O. Rome No. 3442 comp. with type (K); Tamanor, Okla 5402. SUDAN: Mahaitabal, Andrews 3954 (K); SOMALILAND: Buramo, Farquharson 46 (K); Medisha, Glover and Gilliland 939 (K). ETHIOPIA: Jimma, Okla 4518;

LEGEND TO PLATE IX

Bothriochloa *insculpta* var. *panormitana*.

Figure 1. Slender plant with rambling culms and $2n = 50$

Figure 2. Robust, decumbent plant with $2n = 60$

PLATE IX

Fig. 1

Fig. 2

Alamata Ghat, Mooney 8597 (K). UGANDA: Karamaja, Thomas 2964 (K); Katwe, Thomas 4153 (K). KENYA: Machakos, Bogdan 1300 (K); Moyale, Grillett 14153 (K). TANGANYIKA: Lake Proviace, Greenway 7416 (K); Kilimanjaro, Greenway 6709 (K). CONGO: Nyakosi, Lebrun 9248 (BRLU); Albert Park, Troupin 8976 (BRLU); Ruzizi, Taton 1021 (BRLU). RHODESIA: Balla Balla, Okla 9447; Bulawayo, Okla 9487; Wankie, Okla 9497. SOUTH AFRICA: Roedtan, Okla 9598, 9685; Machadodorp, Okla 9676; Bronkhorstspruit, Okla 9679; Marble Hall, Okla 9683; Nylstroom, Okla 9684.

Conclusions

1. On the basis of pit characteristics, two varieties of B. radicans are recognized. They are B. radicans var. radicans, and B. radicans var. acidula (Stapf) de Wet et Higgins comb. nov., based on Amphilophis intermedia var. acidula Stapf.

2. Bothriochloa insculpta is an extremely variable species and is subdivided into two varieties. These are B. insculpta var. insculpta, and B. insculpta var. panormitana (Parl.) de Wet et Higgins comb. nov. based on Andropogon panormitanus Parlatore.

CHAPTER V

CYTOLOGY OF THE BOTHRIOCHLOA PERTUSA COMPLEX

The taxonomy of *Andropogon pertusus* (Linn.) Willd. was fully discussed by Hackel (1889). This large and morphologically variable species was later transferred to *Bothriochloa* O. Kuntze by Camus (1931), and subdivided into *B. decipiens* (Hack.) C. E. Hubb., *B. insculpta* (Hochst.) A. Camus, *B. longifolia* (Hack.) Bar, and *B. pertusa* (Linn.) A Camus. The cytology of these species as well as the related *B. radicans* (Lehm.) A. Camus was studied. The data will be discussed in relation to the origin of the complex as a whole.

Material and Methods

Cytological studies were made from developing microspore mother cells stained with aceto-carmine. Each collection of a species represents an original seed sample grown in a uniform nursery as described by Celarier and Harlan (1956). Chromosome behavior was studied in an average of 20 cells for each collection.

Chromosome Number and Behavior

The cytological data are summarized in Table IV and Plate X. The chromosome number of *B. decipiens* ($2n = 40$) was previously reported by Harlan *et al.* (1961). This species is characterized by two distinct morphological types (Blake, 1944); robust plants referred to as

TABLE IV

CYTOLOGY OF BOTHRIOCHLOA PERTUSA COMPLEX

Name	No. Collections	2n	Chromosome Association* I	II	III	IV
B. decipiens var. decipiens	4	40	0	20	0	0
			0	20	0	0
B. decipiens var. cloncurrensis	12	40	0	20	0	0
			0	20	0	0
B. insculpta var. insculpta	12	50	0-16	16-22	0-2	0-3
			5.0	19.8	0.2	1.2
	52	60	0-32	14-30	0-2	0-4
			4.7	24.9	0.1	1.3
B. insculpta var. panormitana	4	50	5-8	17-22	0-1	0-1
			7.3	19.7	0.3	0.6
	5	60	2-8	23-30	0	0-3
			3.8	27.1	0	0.5
B. longifolia	3	20	0	10	0	0
			0	10	0	0
B. pertusa var. pertusa	50	40	0-7	12-20	0-1	0-3
			0.7	17.9	0.1	0.8
B. pertusa var. bifoveolata	20	40	0-12	12-20	0-1	0-4
			2.3	16.1	0.1	1.3
	3	60	0-4	22-25	0	2-3
			1.2	24.8	0	2.3
B. radicans var. radicans	6	40	0-4	15-20	0-1	0-1
			1.9	18.5	0.1	0.2
B. radicans var. acidula	8	40	0-12	12-20	0-1	0-2
			2.9	17.5	0.3	0.3

*Both range and average number of chromosome configurations are indicated.

LEGEND TO PLATE X

Chromosome configurations.

Figure 1. Metaphase I ($2\underline{n} = 20$)

Figure 2. Anaphase I ($2\underline{n} = 40$)

Figure 3. Anaphase I ($2\underline{n} = 50$)

Figure 4. Anaphase I ($2\underline{n} = 60$)

Figure 5. Metaphase I ($2\underline{n} = 40$) showing univalents, bivalents, trivalents and quadrivalents

Figure 6. Telophase I ($2\underline{n} = 60$) showing bridges, fragments and laggards

PLATE X

Fig. 1

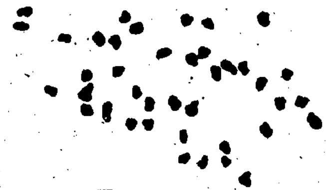


Fig. 2

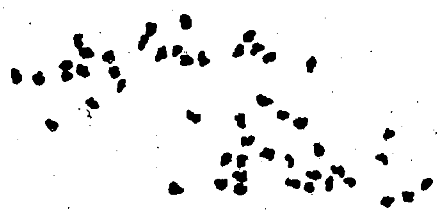


Fig. 3

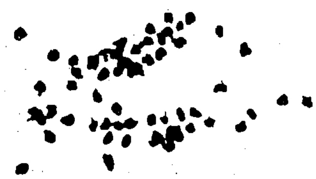


Fig. 4

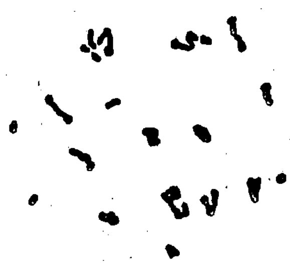


Fig. 5

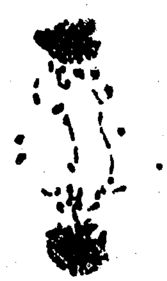


Fig. 6

B. decipiens var. cloncurrensis (Domin) C. E. Hubb., and smaller plants included in B. decipiens var. decipiens (Hack.) C. E. Hubbard. Both varieties are tetraploid (2n = 40) and the chromosomes associate strictly into bivalents during meiosis of microsporogenesis. This species reproduces strictly by sexual means (de Wet, Borgaonkar and Richardson, 1963).

Chromosome numbers of 2n = 50 and 2n = 60 were reported in the morphologically variable B. insculpta by de Wet and Anderson (1956), Celarier and Harlan (1957), de Wet (1958) and Harlan et al. (1958). Two varieties are recognized, B. insculpta var. insculpta (Hochst.) A. Camus with both the sessile and pedicellate spikelets pitted, and B. insculpta var. panormitana (Parl.) de Wet et Higgins with pitted and non-pitted spikelets in the same raceme. Both varieties are characterized by pentaploid (2n = 50) and hexaploid (2n = 60) races, and reproduce by means of gametophytic apomixis. They behave cytologically like segmental allopolyploids as defined by Stebbins (1947). The chromosomes of the hexaploids often associated strictly into bivalents, but univalents, trivalents and tetravalents were commonly encountered. The different collections studied behave essentially alike cytologically. The pentaploids are cytologically more irregular than the hexaploids. The chromosomes never associate strictly into bivalents, and never more than 22 pairs were observed in a cell. Trivalents were rare, univalents common, and at least one tetravalent was present in most of the cells studied.

The Indian B. longifolia is a diploid (2n = 20). Harlan (1963) and de Wet, Borgaonkar and Richardson (1963) demonstrated that a number of other Indian endemics, B. compressa (Hook.f.) Henr., B. concanensis (Hook.f.) Henr., B. foulkesii (Hook.f.) Henr., and B. kuntzeana (Hack.)

Henr., are diploids. These diploid species reproduce sexually, and their chromosomes associate strictly into bivalents during meiosis.

Typical representatives of B. pertusa are tetraploid apomicts. The chromosomes generally associate into bivalents, with univalents and multivalents only occasionally present. Plants referred to B. pertusa var. bifoveolata (Steud.) de Wet et Higgins were included in B. insculpta by Bor (1960). This variety is Indian rather than African in distribution, and resembles B. pertusa rather than B. insculpta in morphological characters, except for pitted pedicellate spikelets. Members of B. pertusa var. bifoveolata are tetraploid or hexaploid apomicts. Cytology of the tetraploids is comparatively regular. The hexaploids are characterized by the presence of two or three tetravalents in each cell studied.

The African B. radicans with non-pitted spikelets never formed a part of Andropogan pertusus as recognized by Hackel (1889). Atypical specimens with pitted sessile spikelets, included in B. radicans var. acidula (Stapf) de Wet et Higgins, were often confused with the Indian B. pertusa (Stapf, 1917). Both varieties are apomictic tetraploids. The chromosomes usually form bivalents during meiosis, but some chromosomes may fail to pair, or associate into multivalents.

Discussion

The sexually reproducing B. decipiens from Australia does not seem to be closely related to the Indian B. longifolia and B. pertusa, or the African B. insculpta and B. radicans. Blake (1944) demonstrated affinities between B. decipiens ($2n = 40$) and the hexaploid Australian species B. ambigua S. T. Blake. Their resemblance to B. pertusa is only in respect to the occasionally pitted sessile spikelets.

The apomictic B. pertusa is widely distributed in the tropical and subtropical regions extending from West Pakistan to Indonesia. The diploid Indian species B. foulkesii, B. longifolia and B. kuntzeana resemble B. pertusa in respect to inflorescence structure. These diploids, however, are robust, erect or decumbent grasses while B. pertusa is a slender prostrate plant with geniculately ascending flowering culms. They apparently did not contribute directly towards the origin of tetraploid B. pertusa.

Cytological data presented suggest that B. pertusa is a segmental allotetraploid to which the genomes BBB_2B_2 were assigned by Harlan et al. (1961). The B and B_2 genomes are sufficiently different to allow strict bivalent formation, but closely enough related for occasional multivalents to be produced during meiosis. Celarier and Harlan (1957) demonstrated that both the cytologically reduced as well as unreduced female gamete of facultative apomictic Bothriochloa species can function sexually. Hexaploid plants of B. pertusa var. bifoveolata could have originated from the fertilization of a cytologically unreduced female gamete. Apparently typical B. pertusa (with non-pitted pedicellate spikelets) and B. pertusa var. bifoveolata often hybridize in nature. This could explain the presence of both tetraploid and hexaploid plants with only some of the pedicellate spikelets pitted, or all of them faintly pitted.

Hexaploids that originated from hybridization between tetraploid members of B. pertusa must be assigned an $BBBB_2B_2B_2$ genomic constitution. Plants combining two basic genomes in three doses each should be characterized by frequent trivalent formation during meiosis.

Trivalents, however, were never observed, whereas two or three tetravalents were present in each cell studied. The maximum number of bivalents observed was 25, and univalents were usually present. Chheda and Harlan (1963) demonstrated experimentally that in *Bothriochloa* hybrids of this nature chromosome pairing takes place preferentially. The 40 chromosomes (BBB_2B_2) derived from the one parent pair preferentially among each other. The presence of more than 20 bivalents demonstrate some degree of homology between the remaining B and B_2 basic genomes. This mode of chromosome association will give rise to the formation of tetravalents rather than trivalents, as was observed in the naturally occuring hexaploids.

The African species *B. radicans* (2*n* = 40) and *B. insculpta* (2*n* = 50 and 2*n* = 60) are morphologically allied. Harlan *et al.* (1961) suggested that hexaploid *B. insculpta* represents a hybrid between the segmental allotetraploid *B. intermedia* ($B_xB_xB'_xB'_x$) and *B. pertusa* (BBB_2B_2), which includes the complete chromosome complement of the last mentioned species. These authors, however, did not study *B. radicans*, and the available morphological data suggest that this species rather than *B. pertusa* may represent one of the parents of *B. insculpta*. The absence of *B. pertusa* from the natural flora of Africa, and the sympatric distribution of *B. radicans* and *B. intermedia* on this continent, further suggest that *B. insculpta* could have originated from hybridization between them.

Natural hybridization between *B. intermedia* (2*n* = 40) and *B. pertusa* (2*n* = 40) apparently takes place in India. Two collections, *Okla 9108* from near Delhi, and *Okla 8299* from near Poona, having 2*n* = 60 and 2*n* = 40 chromosomes respectively, may represent products of such a cross.

Typically *B. intermedia* is a robust, erect grass with the lower racemes of the inflorescence far exceeded by the primary axis in length. In contrast, *B. pertusa* is a slender creeper with subdigitately arranged racemes. These hybrids are robust plants with decumbent culms and the racemes are arranged on the slightly elongated primary axis of the inflorescence.

African plants of *Bothriochloa* with open false panicles are usually referred to *B. glabra* (Chippindall, 1955). Bor (1960) indicated that this species, with its strongly divided racemes, is closely allied to *B. intermedia* which has mostly simple racemes. African plants with simple and divided racemes were commonly encountered. Similarly members of *B. insculpta* are characterized by strongly branched or simple racemes. African plants will be referred to as *B. glabra* and the genome constitution $B_xB_xB'_xB'_x$ is assigned to these segmental allotetraploids. Typical representatives of *B. radicans* are erect, and tufted plants characterized by non-pitted spikelets, while *B. radicans* var. *acidula* has erect culms which arise from a short prostrate base, and the sessile spikelets are usually pitted. This segmental allotetraploid species is assigned the genome constitution $B_3B_3B'_3B'_3$.

Hexaploid representatives of both *B. insculpta* var. *insculpta* and *B. insculpta* var. *panormitana* are of two morphological types; extremely robust, suberect plants, and more slender decumbent plants. Although artificial hybrids between *B. radicans* and *B. glabra* could not be produced, morphological data suggest that the suberect plants combine the complete chromosome complement of *B. glabra* and the haploid genomes of *B. radicans* var. *acidula*. Similarly, the more slender, decumbent hexaploids may combine the complete chromosome complement of *B. radicans* var. acidula and the haploid genomes of B. glabra.

Cytologically these two morphological types ($B_xB_xB'_xB'_xB_3B'_3$ and $B_3B_3B'_3B'_3B_xB'_x$) behave essentially alike. The chromosomes often associate strictly into bivalents, although tetravalents were encountered in some cells. Chromosome pairing apparently takes place preferentially between chromosomes derived from the cytologically unreduced gamete. Some degree of homology between the chromosomes of the B_3 and B'_3, as well as between the B_x and B'_x basic genomes allows for the formation of additional bivalents. The low frequency of multivalents suggests that little or no homology exists between the basic genomes of B. glabra and B. radicans.

Pentaploid representatives of B. insculpta may represent backcross populations to either of the two parents. They are extremely variable morphologically. Cytologically, following preferential chromosome pairing in the hexaploids, these pentaploids may be of four basic genome combinations as follows:

$B_xB_xB'_xB'_xB_3B_3$ -x- $B_xB_xB'_xB'_x$ = $B_xB_xB'_xB'_x(B_3)$

-x- $B_3B_3B'_3B'_3$ = $B_xB'_xB_3B_3(B'_3)$

$B_3B_3B'_3B'_3B_xB_x$ -x- $B_xB_xB'_xB'_x$ = $B_3B'_3B_xB_x(B'_x)$

-x- $B_3B_3B'_3B'_3$ = $B_3B_3B'_3B'_3(B_x)$

Preferential chromosome pairing between homologous chromosomes, and pairing between partially homologous chromosomes when their close homologous are absent, apparently gave rise to an average of 20 bivalents, as was observed in these pentaploids. The 10 chromosomes of the additional basic genome were often present as univalents, or they contributed towards the formation of trivalents and tetravalents.

Conclusions

1. The Australian *B. decipiens* (2*n* = 40) and *B. ambigua* (2*n* = 60) are morphologically allied, sexually reproducing allopolyploids based on *n* = 10.

2. The Indian endemic *B. longifolia* is a sexually reproducing diploid.

3. The remaining species studied are gametophytic apomicts, and behave cytologically like segmental allopolyploids.

4. Tetraploid and hexaploid races characterize *B. pertusa*.

5. Cytological and morphological data indicated that the hexaploids originated from the fertilization of a cytologically unreduced gamete.

6. *Bothriochloa radicans* and *B. glabra* are tetraploids, while *B. insculpta* is characterized by pentaploid and hexaploid races.

7. Morphological data indicated that hexaploid *B. insculpta* could have originated from a cross between plants resembling *B. radicans* and *B. glabra*.

8. These hexaploids are of two morphological types, and it was proposed that the one combines the complete chromosome complement of *B. glabra* and the haploid complement of *B. radicans*, while the other originated from fertilization of the cytologically unreduced gamete of *B. radicans*.

9. Pentaploids apparently represent backcross populations to either parent.

CHAPTER VI

SUMMARY

The morphological characters of species and varieties recognized as valid taxonomic units are summarized in Table V.

The species B. decipiens (Hack.) C. E. Hubb., B. insculpta (Hochst.) A. Camus, B. longifolia (Hack.) Bor, B. panormitana (Parl.) Pilger, B. pertusa (Linn.) A. Camus, and B. radicans (Lehm.) A. Camus were classically treated as varieties of Andropogon pertusus (Linn.) Willd. Morphological and cytogenetical data indicated that these are variable, but distinct taxonomic units. From a biosystematic point of view, glume characteristics of which the classification of these species were usually based, appeared to be unreliable. Indian representatives of the more commonly African B. insculpta could more naturally be transferred to the Asiatic B. pertusa as a variety. The African B. pertusa var. maroccana Maire could not consistently be separated from the Sicilian B. panormitana, and this species should be treated as a variety of B. insculpta. The recently described B. pertusa var. tunetana A. Camus from Tunesia was found to be identical to B. intermedia var. acidula (Stapf) C. E. Hubbard. Cytogenetical and morphological data suggested that these plants should be regarded as a variety of B. radicans.

Typically B. insculpta is confined to Africa and B. pertusa extends from West Pakistan eastward. When these two species are separated on

TABLE V

MORPHOLOGY OF THE BOTHRIOCHLOA PERTUSA COMPLEX

Name	2n	Glumes Pitted		Pedicel	Raceme No.		Ratio*	Growth	Distribution
		Ses.	Ped.	Groove	Prim.	Sec.	L.P.A./L.L.R.	Habit	
B. concanensis	20 50	−	−	−	3−10	0−3	0.37	Erect Robust	India; Western Ghats
B. decipiens									
var. *decipiens*	40	±	−	+	2−7	0	0.14	Erect Slender	Australia
var. *cloncurrensis*	40	±	−	+	4−26	0−10	0.28	Erect Robust	Australia
B. foulkesii	20	−	−	+	3−10	0−4	0.38	Erect Robust	India; Nilgiris
B. insculpta									
var. *insculpta*	50 60	+	+	+	4−28	0−21	0.43	Decumbent Robust	Africa
var. *panormitana*	50 60	±	±	+	7−18	0−22	0.49	Decumbent Robust	Africa; Sicily
B. kuntzeana	20	±	±	+	10−25	0−5	0.79	Erect Robust	India; southern
B. longifolia	20	±	−	+	5−18	0−2	0.68	Erect Robust	India; southeastern
B. pertusa									
var. *pertusa*	40	+	−	+	3−13	0−7	0.29	Prostrate Slender	India to Indonesia
var. *bifoveolata*	40 60	+	±	+	3−28	0−10	0.27	Prostrate Slender	India to Indonesia
B. radicans									
var. *radicans*	40	−	−	+	5−19	0−17	0.57	Decumbent Slender	Africa
var. *acidula*	40	±	−	+	8−14	0−1	0.48	Decumbent Slender	Africa

*Length of primary axis / Length of longest raceme the basis of spikelet structure some African specimens are usually included in B. pertusa and some Asiatic specimens in B. insculpta. It was suggested that the African plants be excluded from B. pertusa. They differ from this species mainly in the presence of indentations on the lower glume of pedicellate spikelets, and resemble B. insculpta mainly in respect to this characteristic. The new combination B. pertusa var. bifoveolatus (Steud.) de Wet et Higgins was proposed to include Indian plants usually classified with B. insculpta. Bothriochloa radicans is strictly African in its distribution. On the basis of pit characteristics, two varieties, B. radicans var. radicans and B. radicans var. acidula (Stapf) de Wet et Higgins comb. nov. (based on Amphilophis intermedia var. acidula Stapf), were recognized. Bothriochloa insculpta is an extremely variable species and is subdivided into two varieties. These are B. insculpta var. insculpta and B. insculpta var. panormitana (Parl.) de Wet et Higgins comb. nov. based on Andropogon panormitanus Parlatore.

The cytology of a number of morphologically similar Bothriochloa species were studied. The Australian B. decipiens ($2n = 40$) and B. ambigua ($2n = 60$) are morphologically allied, sexually reproducing allopolyploids based on $n = 10$. The Indian endemic B. longifolia is a sexually reproducing diploid. The remaining species studied are gametophytic apomicts, and behave cytologically like segmental allopolyploids. Tetraploid and hexaploid races characterize B. pertusa. Cytological and morphological data indicated that the hexaploids originated from the fertilization of a cytologically unreduced gamete. Bothriochloa radicans and B. glabra are tetraploids, whereas B. insculpta is characterized by pentaploid and hexaploid races. Morphological data indicated that hexaploid B. *insculpta* could have originated from a cross between plants resembling B. *radicans* and B. *glabra*. These hexaploids are of two morphological types and it was proposed that the one combines the complete chromosome complement of B. *glabra* and the haploid complement of B. radicans, while the other originated from fertilization of the cytologically unreduced gamete of B. *radicans*. Pentaploids apparently represent backcross populations to either parent.

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