Cytology of the *Bothriochloa pertusa* Complex¹

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Received August 21, 1963

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.) Bor., 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-carmin. Each collection of a species represents an original seed sample grown in a uniform nursery as described by Celarier and Harlan (1956). Chromosome behaviour was studied in an average of twenty cells for each collection.

Chromosome number and behaviour

The cytological data are summarized in Table 1. 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 *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 a variety resembling *B. panormitana* (Parl.) Pilger with pitted and non pitted spikelets in the same raceme. Both varieties are characterized by pentaploid ($2n=50$) and hexa-

¹ Supported in part by Grants 10742 and 24952, National Science Foundation.

ploid ($2n=60$) 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 associate 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 twenty-two pairs were observed in a cell. Trivalents were rare, univalents common, and at least one tetravalent was present in most of the cells studied.

Table 1. Cytology of the *B. pertusa* complex

Name	No Collections	2n	Chromosome association			
			I	II	III	IV
<i>B. decipiens</i> var. <i>decipiens</i>	4	40	0 0	20 20	0 0	0 0
<i>B. decipiens</i> var. <i>cloncurrensis</i>	12	40	0 0	20 20	0 0	0 0
<i>B. insculpta</i> var. <i>insculpta</i>	12	50	0-16 5.0	16-22 19.8	0-2 0.2	0-3 1.2
	52	60	0-32 4.7	14-30 24.9	0-2 0.1	0-4 1.3
<i>B. insculpta</i> var.	4	50	5-8 7.3	17-22 19.7	0-1 0.3	0-1 0.6
	5	60	2-8 3.8	23-30 27.1	0 0	0-3 0.5
<i>B. longifolia</i>	3	20	0 0	10 10	0 0	0 0
<i>B. pertusa</i> var. <i>pertusa</i>	50	40	0-7 0.7	12-20 17.9	0-1 0.1	0-3 0.8
<i>B. pertusa</i> var. <i>bifoveolata</i>	20	40	0-12	12-20	0-1	0-4
	3	60	2.3	16.1	0.1	1.3
	3	60	0-4 1.2	22-25 24.8	0 0	2-3 2.3
<i>B. radicans</i> var. <i>radicans</i>	6	40	0-4 1.9	15-20 18.5	0-1 0.1	0-1 0.2
<i>B. radicans</i> var. <i>acidula</i>	8	40	0-12 2-9	12-20 17.5	0-1 0.3	0-2 0.3

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., *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 and apomicts. The chromosomes mostly 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 *Andropogon 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 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 allo-tetraploid 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 a $BBBB_2B_2B_2$ genomic constitution. Plants combining two basic genomes in three doses each should have frequent trivalent formation during meiosis. Trivalents, however, were never observed, where as two or three tetravalents were present in each cell studied. The maximum number of bivalents observed was twenty-five, 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 twenty bivalents demonstrates 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 occurring hexaploids.

The African species *B. radicans* ($2n=40$) and *B. insculpta* ($2n=50$ and $2n=60$) 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* ($2n=40$) and *B. pertusa* ($2n=40$) apparently takes place in India. Two collections, *Okla 9108* from near Delhi, and *Okla 8299* from near Poona, having $2n=60$ and $2n=40$ 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* having 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 $B_3B_3B_3B'_3$.

Hexaploids representatives of both *B. insculpta* var. *insculpta* and *B. insculpta* (atypical) 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 suggests 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. Chromosomes 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 multi-valents suggests that no or little 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:

$$\begin{aligned} B_xB_xB'_xB'_xB_3B_3 - x - B_xB_xB'_xB'_x &= B_xB_xB'_xB'_x(B_3) \\ &- x - B_3B_3B'_3B'_3 = B_xB'_xB_3B'_3(B_3) \\ B_3B_3B'_3B'_3B_xB_x - x - B_xB_xB'_xB'_x &= B_3B'_3B_xB'_x(B_x) \\ &B_3B_3B'_3B'_3 = B_3B_3B'_3B'_3(B_x) \end{aligned}$$

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

Summary

The cytology of a number of morphologically similar *Bothriochloa* species was 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

racess 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, while *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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