

MORPHOLOGY OF THE PACHYTENE CHROMOSOMES AND MEIOSIS IN *SORGHUM SUBGLABRESCENS*, A EU-SORGHUM

BY J. VENKATESWARLU AND V. RAMAKRISHNA REDDI

Department of Botany, Andhra University, Waltair

(Received for publication on June 15, 1956)

INTRODUCTION

OUR present knowledge of the morphology of the pachytene chromosomes in the genus *Sorghum* reveals that the pachytene chromosomes in Eu-Sorghums, which include the economically important grain Sorghums, are characterized by differential stainability and distinct centromeres, while in the rest of the Sorghums they are uniformly stained with acetocarmine with no marked accumulation of stain in any one region of the chromosome (Garber, 1947, 1950). In 1937, Longley and later Garber (1950) made some observations on the pachytene chromosomes of *Sorghum vulgare*, a Eu-Sorghum. In this, the regions immediately adjacent to the distinct centromeres were found to be heavily stained and the quality of staining decreased noticeably beyond these regions until the remainder of the chromosome was almost unstained especially at the end of each arm. More recently, Harpstead, Ross and Franzke (1954) studied the pachytene stage in *S. vulgare* during the course of their investigations on colchicine-induced variants in *Sorghum*. The photomicrographs of nuclei at the pachytene stage stained in propionocarmine presented in their paper clearly show the heavily stained proximal and the lightly stained distal regions of the chromosomes. The above authors, however, made no reference to these features in the text, their object of study of this stage being only to determine if any gross chromatin rearrangement was responsible for the origin of variant plants obtained by colchicine treatment.

So far no complete account of the morphology of pachytene chromosomes of the entire complement in any Eu-Sorghum is available. As the Eu-Sorghums form an economically important crop in the agriculture of many countries a detailed cytological study of several species belonging to them has been undertaken in this department for such a knowledge will considerably aid cytogenetical studies and will lead to a fuller understanding of the genetics of the grain Sorghums. During the course of these studies we found that *Sorghum subglabrescens* Schw. et Asch., to be very suitable for a study of the morphology of the pachytene chromosomes and it was possible to analyse the entire complement enabling the identification of all the chromosomes in each of ten nuclei analysed. The pachytene chromosomes in this species could be exceptionally well spread out using the acetocarmine squash technique

and they could be followed from one end to the other as done earlier in a few plants like *Zea mays* (McClintock, 1931; Longley, 1938, 1941; Rhoades, 1950), *Secale cereale* (Lima-de-Faria, 1950, 1952), *Lycopersicum esculentum* variety Sutton's Best of all (Brown, 1949; Barton, 1950), and *Plantago ovata* (Hyde, 1953).

Results obtained in the present study on the morphology of the pachytene chromosomes and other meiotic stages in *Sorghum subglabrescens* are presented in this paper. Some observations made on the pachytene chromosomes and meiosis in *S. roxburghii* Stapf, another Eu-Sorghum, are also included here for comparison.

MATERIALS AND METHODS

Seeds of *Sorghum subglabrescens* were obtained from the Agriculture Research Station, Nandyal, Andhra State, and cultures were raised in the Andhra University Botanical Gardens at Waltair.

For the study of pachytene chromosomes the modified acetocarmine technique developed by Lima-de-Faria (1948) for rye, was found very suitable. The young inflorescences were fixed in 1:4 acetic alcohol for 12-24 hours and then transferred to 95% alcohol overnight, after which the material was stored in 70% alcohol in a refrigerator until used for study. The preparations made according to this method showed a clear definition of the differentially stained parts of the pachytene chromosomes in almost unstained cytoplasm. The technique of iron alum mordanting prior to staining with acetocarmine originally developed for staining tomato chromosomes by Dr. Marta S. Walters, and later successfully employed by Brown (1949) and Barton (1950) was also tried but did not prove suitable as the cytoplasm was darkly stained obscuring details of the pachytene chromosomes.

All photomicrographs presented in this paper were taken from preparations when they were still fresh using a Leica camera with an attachment for photomicrographic work.

Measurements of lengths of entire chromosomes and of the heavily and lightly stained parts were made from camera lucida drawings of the pachytene chromosomes from completely analysable nuclei with the aid of a map measurer.

PACHYTENE CHROMOSOMES

The ten chromosomes of *Sorghum subglabrescens* at the pachytene stage are characterized by (i) distinct and well-defined centromeres, (ii) deeply staining segments of varying length in each arm adjacent to the centromere followed by (iii) lightly staining distal regions of different lengths (Text-Fig. 1 and Plate XIX, Figs. 1-3). The above characteristics are considered below in detail.

The centromeres are oval-shaped and seem to resemble somewhat in their structure those described in rye by Lima-de-Faria (1949). The structure of the centromere could not be made out clearly in

Sorghum subglabrescens, but in a few favourably stained preparations of *S. roxburghii* there seem to be present a pair of lightly stained chromomeres in its centromere. More intensive study, using fixatives other than those involving acetic acid which Lima-de-Faria (1950) found not suitable for study of centromere structure, is needed before definite conclusions can be reached.

The heavily stained regions of the chromosomes consist of chromomeres which stain deeply and the lightly stained distal regions show very feebly staining chromomeres, which are difficult to differentiate from the cytoplasm in which they were spread out in the squash preparations. The transition between the proximal deeply staining and the distal lightly staining segments in each arm is rather abrupt except in the case of two chromosomes of the complement in which the region of transition consists of 3 or 4 chromomeres capable of being stained noticeably and were arranged in a characteristically seriated manner. This feature proved particularly useful in individually recognising the two chromosomes from the rest of the complement. In another chromosome of the complement almost the entire short arm is constituted by the deeply stained segment. In *S. roxburghii* which has also been examined for comparison, the structure of the differentially stained chromosomes is essentially similar except that in it the deeply stained segments are more pronounced (Plate XIX, Figs. 2 and 3).

There are no knobs and no pronounced chromomeres at the ends of the chromosomes. The longest chromosome (ch. 1) of the complement is the nucleolus organising chromosome, the nucleolus organising body being situated very near to the centromere in the short arm.

PACHYTENE PAIRING

Pre-pachytene stages proved difficult to study. However, in a number of nuclei it was clearly observed that the pairing was regularly initiated in the deeply staining segments and the parts immediately adjacent to them. At this stage the pairing was not evident in the lightly stained regions. At a later stage the pairing becomes complete all along the length of the chromosomes. In late pachytene and early diplotene, the split threads fall apart earlier in the zones corresponding to the deeply staining and adjacent regions. Frequently the centromeres were found still attached to each other with a loop on either side of it.

The pairing properties of the pachytene bivalents observed in the present study show a striking similarity to the pairing behaviour of the differentially condensed pachytene chromosomes of *Agapanthus* (Darlington, 1933), in which the proximal parts are in advance....the distal parts in the process of condensation which has been ascribed to earlier assumption of spiral in the condensed parts. In *Agapanthus* (Darlington, 1933) also, as in *S. subglabrescens*, corresponding to the early synapsis of the over-condensed parts there is an earlier appearance of the secondary split in the same region accompanied by earlier falling apart of the chromosomes.

Mitotic stages from the root tip cells of *S. subglabrescens* particularly at prophase showed the middle deeply stained regions followed by lightly stained regions towards the chromosome ends. In this respect, *S. subglabrescens* resembles tomato (Brown, 1949) and *Plantago ovata* (Hyde, 1953) in which also the mitotic chromosomes show differentially stained segments. Earlier, Darlington (1933) made some observations on the mitotic chromosomes in the pollen grain division in *Agapanthus* which, however, did not show any differential regions in them, although the meiotic chromosomes are differentiated into deeply stained and lightly stained regions.

Frequent non-homologous association of the centromeres takes place during the meiotic prophase. Association of two non-homologous centromeres is common while that of three is not infrequent in both the species investigated. Plate XIX, Fig. 3, shows a case of non-homologous association of centromeres observed in *S. roxburghii*. Similar observations have been made in *Agapanthus* (Darlington, 1933) and in tomato by Brown (1949). Darlington (1933) considered the cases of non-homologous association of centromeres in *Agapanthus* as due to interlocking of the non-persistent kind. In the light of the accepted concept relating to the common forms and functions of the centromeres, it appears to us that they exert an attraction leading to fusion in a certain sense more favourably in differentially condensed chromosomes in which a lapse of repulsion exists between the deeply stained segments consequent upon the lower surface charge they are supposed to carry (Darlington, 1937, pp. 315 and 498).

DIAGNOSTIC FEATURES OF PACHYTENE CHROMOSOME COMPLEMENT

Based upon the average values of lengths obtained by complete analyses of chromosomes in ten entire nuclei, the ten pachytene chromosomes of *S. subglabrescens* have been designated in the order of their decreasing length as chromosome one to chromosome ten, chromosome one being the longest and chromosome ten being the shortest in the complement following the method of numbering originally adopted by McClintock (1929) in *Zea mays* and later by Barton (1950) in tomato. Table I shows the measurements based on the analyses of all the pachytene chromosomes in each of ten entire nuclei.

The following is a description of the individual pachytene chromosomes of the complement giving their chief diagnostic morphological features which proved particularly useful in identifying them individually.

Chromosome 1.—This is the longest of the complement, measuring on an average 80.38 microns, and has an attachment to the nucleolus very near to the centromere in the short arm. The nucleolar organising region is spherical in shape and distinctly greater in diameter than the adjoining deeply stained segments. Another characteristic feature of this chromosome is the presence of a deep staining chromomere terminating the heavily stained region in the long arm.

TABLE I

Average values of lengths in microns of the pachytene complement obtained from the complete analysis of ten cells in S. subglabrescens

Chromosome	Long arm			Short arm			Total Chromosome‡	Arm ratio S.A./L.A.
	H.S.R.*	L.S.R.†	Total arm	H.S.R.	L.S.R.	Total arm		
1	3.75	40.60	45.07	2.71	32.02	35.31	80.38 (2.35)	0.78
2	4.88	36.06	41.69	3.77	19.39	23.69	65.38 (1.66)	0.57
3	4.07	30.71	35.50	3.61	21.51	25.65	61.15 (2.77)	0.724
4	4.81	25.14	30.19	6.21	15.68	22.89	53.08 (1.67)	0.758
5	4.21	21.69	26.82	5.91	13.04	19.53	46.35 (0.95)	0.73
6	5.77	28.93	35.33	5.31	1.10	6.90	42.23 (1.13)	0.195
7	3.77	21.80	26.20	3.61	11.82	15.92	42.12 (1.34)	0.61
8	4.78	16.51	21.64	3.43	16.08	19.94	41.58 (1.07)	0.92
9	4.90	16.74	22.27	4.62	10.83	15.96	38.23 (0.97)	0.72
10	4.42	13.11	18.10	3.17	11.04	14.67	32.77 (1.04)	0.81

* Heavily stained region.

† Lightly stained region.

‡ Standard errors for entire lengths of the chromosomes are given in parentheses.

Chromosome 2.—The chief feature which proved most useful in the identification of this chromosome is that the long arm is approximately twice the length of the short arm. The heavily stained parts in both arms show an abrupt transition to the lightly stained zones. The heavily stained region in the long arm is slightly greater than that in the short arm.

Chromosome 3.—This is difficult to distinguish from the succeeding chromosome particularly in nuclei where it cannot be followed from end to end, due to the fact that both of them come close to one another in length. In some of the cells analysed it is even lesser in length than chromosome 4 while in still others it is slightly more in length than chromosome 2. However, the presence of a deep staining chromomere terminating the heavily stained part in the short arm comparable in size to that seen in chromosome 1 makes its identification certain.

Chromosome 4.—The ready identification of this chromosome on the basis of length alone is difficult for the reasons already mentioned under chromosome 3. The deeply stained chromomere terminating the heavily stained segment in the long arm and the presence of a series

of four small chromomeres in the transition region of the short arm capable of being well stained together form a reliable diagnostic basis.

Chromosome 5.—This is marked by the presence of a series of three small chromomeres in the transition region in the short arm like that described under the preceding chromosome. This chromosome measures on an average 46.35 microns.

Chromosome 6.—This is the easiest chromosome to identify in the complement due to the marked asymmetry of its arms. The long arm is about five times the length of the short arm. Also the short arm is completely stained deeply but for a small terminal part of about 1.1 microns in length. The average length of the chromosome is 42.23 microns.

Chromosome 7.—This is chiefly distinguished from the rest of the long chromosomes by the comparative short length of the lightly stained segment in the short arm. The short arm measures about half the length of the long arm (arm ratio = 0.61).

Chromosome 8.—This is readily recognised from the rest of the complement by the nearly equal length of its arms. Although in this feature chromosome 10 comes very near to it, in none of the cells analysed it comes near to this chromosome in total length there being a difference of 8.8 microns on an average.

Chromosome 9.—The quick recognition of this chromosome among the short chromosomes of the complement is facilitated by the characteristic presence of two deeply stained chromomeres terminating the heavily stained region in either arm. Its arm ratio is 0.72.

Chromosome 10.—This is the shortest chromosome of the complement measuring 32.77 microns long on an average. The arm lengths in many of the nuclei analysed have been found to be approximately equal, although on an average a difference of more than three microns was found.

Basing on the quantitative data presented in Table I the diagram of the 10 chromosomes (Text-Fig. 2) has been constructed to bring about the diagnostic features of the individual chromosomes that have been considered particularly useful in tracing their identity in the complement.

DIAKINESIS AND METAPHASE I

The differentially stained regions can be followed through diplotene to the late diakinesis stage both in *S. subglabrescens* and *S. roxburghii*.

It was possible to observe chiasmata in early and late diakinesis, metaphase I and even in early diplotene stages. Altogether 45 nuclei could be analysed in *S. subglabrescens* and 75 in *S. roxburghii* (Table II). It is clear from the data given in Table II that there is a decrease in the number of chiasmata per nucleus from diplotene to metaphase I. This is further borne out by the values of terminalisation coefficient at metaphase I given in the last column of Table II for the two species.

TABLE II

Chiasma frequencies at late-diplotene to metaphase I stages in Sorghum subglabrescens and S. roxburghii

Stage	No. of cells analysed	Bivalents with				Total Xta	Average No. of Xta per nucleus	Average No. of Xta per bivalent	Terminalisation coefficient
		4Xta	3Xta	2Xta	1Xma				
<i>S. subglabrescens</i>									
Late diplo- tene	3	7	14	8	1	87	29.0	2.9	0.15
Early diaki- nesis	14	..	54	83	3	331	23.64	2.36	0.22
Late diaki- nesis	12	116	4	236	19.66	1.97	0.45
Metaphase I	16	153	7	313	19.56	1.96	0.79
<i>S. roxburghii</i>									
Late diplo- tene	3	2	17	11	..	81	27.0	2.70	0.12
Early diaki- nesis	9	1	26	62	1	207	23.0	2.30	0.20
Late diaki- nesis	16	153	7	313	19.56	1.96	0.57
Metaphase I	47	446	24	916	19.50	1.95	0.75

It can be seen from these values that the process of the terminalisation in both the species is incomplete. In this respect the two species of Eu-Sorghum studied resemble plants like *Agapanthus*, *Avena* and *Zea mays* (Darlington, 1933 a, 1933 b and 1934) and *Lycopersicum esculentum* (Brown, 1949).

From the analyses of the nuclei at diakinesis (Table III) it was found that of the total of 260 bivalents in *S. subglabrescens* and 250 in *S. roxburghii*, 253 in the former and 242 in the latter are of the ring type.

TABLE III

Frequency of rod and ring bivalents at diakinesis and metaphase I

Species	Stage	Ring bivalents		Rod bivalents		Total bivalents
		Number	Per cent.	Number	Per cent.	
<i>S. subglabrescens</i>	Diakinesis	253	97.3	7	2.7	260
	Metaphase I	153	95.6	7	4.4	160
<i>S. roxburghii</i>	Diakinesis	242	96.8	8	3.2	250
	Metaphase I	446	94.9	24	5.1	470

Thus, in more than 90% of the nuclei at least one chiasma in either arm of each chromosome of the complement is formed irrespective of any differences in them. On the assumption that there is no localisation and that chiasma formation is at random, there should be a proportion of the chiasma in the short arm of chromosome 6 which is almost entirely constituted by its deeply stained segment, the distal light staining region measuring 1.10 microns only while the total length of the short arm is 6.90 microns on an average. On the general assumption that the number of chiasmata formed is proportional to the length of the chromosome, $6.90/35.33 \times 2.17 = 0.42$ chiasma should be formed in the short arm of chromosome 6 and $1.10/6.9 \times 0.42 = 0.07$ should be located in the light staining distal region of the arm alone, the rest being formed in the proximal dark staining region. On these considerations it may be inferred that it is very likely that there is no localisation of chiasmata in *S. subglabrescens* such as present in tomato (Brown, 1949 and Barton, 1951) and *Plantago ovata* (Hyde, 1953). Since the general inferences made by us in this respect are not directly correlated with any observations on any one of the identified bivalents on the origin and behaviour of chiasmata, a more certain evidence such as those obtained by Brown (1949) with reference to the nucleolar chromosome and by Barton (1951) on the experimental basis in tomato is necessary before establishing this point of view. Until such direct evidence as in tomato is obtained with reference to *Sorghum* it is to be considered that chiasmata are formed at random all along the length of the chromosome in *Sorghum subglabrescens*.

Other meiotic stages of divisions I and II show normal features and at the end of the two divisions the microspore nuclei show ten chromosomes in each of them.

DISCUSSION

The striking differential stainability of the pachytene chromosomes is a characteristic found in all the Eu-Sorghums so far investigated namely *Sorghum vulgare* (Longley, 1937 and Garber, 1950), *S. subglabrescens* and *S. roxburghii* (present report) and serves to distinguish them from the rest of the Sorghums studied (Garber, 1950).

As in the differentiated chromosomes of *Antirrhinum* (Ernst, 1938, 1939), tomato (Brown, 1949; Barton 1950) and *Plantago ovata* (Hyde, 1953) the pachytene chromosomes show proximal darkly staining segments followed by distal lightly staining ones in each arm. These differential regions can be followed until late diakinesis stage is reached in the meiotic cycle. In *S. subglabrescens* these regions can also be seen in mitotic chromosomes in the root tip cells. In *Plantago ovata*, Hyde (1953) was able to identify morphologically the chromosomes of mitotic prophase with those of pachytene. He concluded that this continuity suggests that the differentiation is inherent in each individual chromosome and is controlled by its submicroscopic structure.

In 1928, Heitz originally described the differentially stained regions in the chromosomes of some plants and designated the material in the

darkly staining regions as heterochromatin and that in the lightly staining regions as euchromatin. He also specifically suggested that heterochromatic segments are genetically inert and euchromatic active. Although in *Drosophila* this hypothesis with some modifications has been substantiated, in plants, however, it remains in doubt due to the fact that only a very few plants have yet been found with differentiated chromosomes in which critical cytogenetic work on the gene content of the heterochromatin is possible. So far, only in *Antirrhinum* and in tomato a detailed knowledge of the differentiated pachytene chromosomes made cytogenetic work possible. As detailed study of morphology of the pachytene chromosome complement leading to individual identification of the chromosomes has now become possible in *S. subglabrescens* and as it is possible to acquire similar knowledge in more Eu-Sorghums in the near future, it is hoped that Eu-Sorghums would prove to be very favourable material for critical cytogenetic work on the gene content of the material in the deeply staining regions which seem to be similar in certain respects to heterochromatin in plants.

Although the structure of the meiotic chromosomes of tomato resembles closely those regarded as differentiated into zones containing hetero and euchromatin, Brown (1949) used the terms 'chromatic' and 'achromatic' as the latter seem to shorten markedly without acquiring an appreciable capacity to stain deeply, unlike the typical euchromatin described by Heitz (1928) which acquires during prophase a marked capacity for deep staining and also because the various chromatic zones in tomato seemed to show a differential behaviour during the resting stage. In view of the fact that the lightly stained zones in *S. subglabrescens* do not acquire a marked capacity to stain deeply as they contract and that the differential parts show deviations from those described in tomato in their synaptic properties and in the formation of chiasmata, simple terms 'heavily stained or deeply stained' and 'lightly stained or feebly stained' have been used.

Pairing properties of the differentiated regions of the chromosomes vary in different organisms. In tomato, Brown (1949) found that pairing is initiated during late zygotene or early pachytene stages in the achromatic zones followed later by pairing in the chromatic zones. It was not possible for him to study the separation of the split sister chromosomes at the diplotene stage. In *Plantago ovata*, Hyde (1953) recorded that pairing is initiated regularly in the middle segments while separation of the divided sister chromosomes takes place, however, in the end segments during the early diplotene stage. Earlier, in his studies on the synapsis of the differentially condensed chromosomes in *Agapanthus* and *Fritillaria* Darlington (1933, 1935) showed that pairing initially takes place during pachytene in the condensed proximal regions followed by separation of the split chromosomes at diplotene in the same parts. In its pairing properties of the differentially stained regions, *S. subglabrescens* shows a close similarity to *Agapanthus* and *Fritillaria*. In *Fritillaria* the earlier pairing in proximal deeply staining regions is believed to be associated with localisation of chiasmata in the regions adjacent to the centromere. Consequently, an assumption of

a timing difference at meiosis in that the proximal parts are in advance to the distal parts with a possible relation of the former to the centromere satisfactorily explains the behaviour of heavily and lightly stained regions of the pachytene chromosomes of *S. subglabrescens*. In the Eu-Sorghums investigated during the present study, however, there does not seem to be any localisation of chiasmata as in *Fritillaria*.

It has been observed in several plants with differentiated chromosomes that the chiasmata are localised in the lightly stained regions. In 1933, Geitler found in *Agapanthus* the formation of as many as four chiasmata per bivalent, all in the euchromatic regions. Barton (1951) concluded, on the basis of experimental evidence, that chiasmata probably do not occur in the chromatic zones of tomato. More recently, Hyde (1953) made similar observations in *Plantago ovata* and concluded that chiasma formation does not take place in the deeply staining middle segments. As already pointed out in this paper, on the basis of observations on the distribution of chiasmata particularly with reference to the almost entirely deeply staining short arm of chromosome 6 in *S. subglabrescens*, there does not seem to be any apparent localisation of chiasmata in the lightly stained distal regions. Thus, in Eu-Sorghums the chromomeres of the deeply stained segments do not seem to be inherently different from those in the lightly stained regions in the capacity of the recombination of the genic material in them.

SUMMARY

S. subglabrescens Schw. et Asch., a Eu-Sorghum, is found an exceptionally favourable material for the study of pachytene chromosomes with special reference to their differential staining reaction. The differential segments can be clearly seen up to diakinesis stage in the meiotic cycle. The mitotic chromosomes in the root tip cells are also observed to show the differentially stained regions. A careful and critical study of the heavily stained proximal segments and the distal lightly stained regions, the relative lengths, arm ratios in the pachytene chromosomes proved very useful in identifying each of the ten chromosomes of the complement. Diagnostic features of each one of the pachytene chromosomes and diagram based on them are presented.

Studies on the pairing properties of the differentially stained parts show that synapsis takes place initially during early prophase in the heavily stained regions and is followed by the earlier separation of the split chromosomes in the same regions at diplotene. An assumption of timing difference at meiosis in that the proximal parts are in advance to the distal lightly stained parts is considered to be satisfactory to explain the observations as has been already done in other plants like *Agapanthus*.

Detailed studies on the distribution of chiasmata in *S. subglabrescens* and *S. roxburghii* show no apparent localisation of these in the lightly stained regions indicating thereby that the deeply and lightly stained regions show no differentiation of the chromomeres constituting them in their capacity to recombine.

ACKNOWLEDGEMENT

The writers wish to express their thanks to Shri C. Jagannadha Rao, Cotton-cum-Oil Seeds Specialist, Andhra State, for kindly supplying *Sorghum* seeds used in this investigation.

REFERENCES

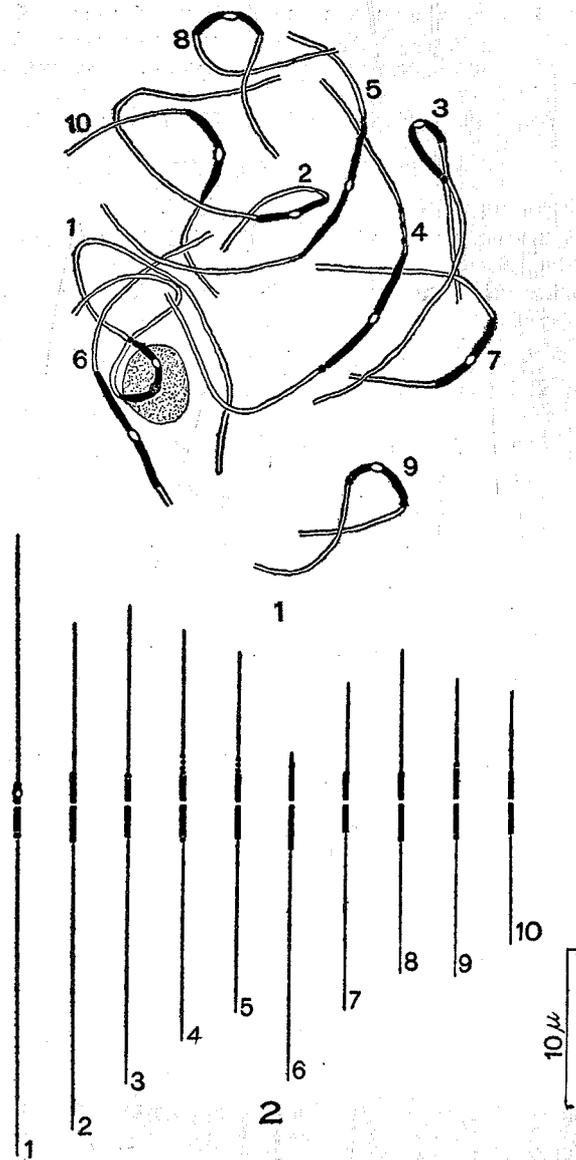
- BROWN, S. W. 1949. The structure and meiotic behaviour of the differentiated chromosomes of tomato. *Genetics*, **34**: 437-61.
- BARTON, D. W. 1950. Pachytene morphology of the tomato chromosome complement. *Amer. J. Bot.*, **37**: 639-43.
- . 1951. Localised chiasmata in the differentiated chromosomes of the tomato. *Genetics*, **36**: 374-81.
- DARLINGTON, C. D. 1933 a. Meiosis in *Agapanthus* and *Kniphofia*. *Cytologia*, **4**: 229-40.
- . 1933 b. The origin and behaviour of chiasmata, IX. Diploid and tetraploid. *Avena. Cytologia*, **5**: 128-34.
- . 1934. The origin and behaviour of chiasmata, VII. *Zea mays*. *Z.I.A.V.*, **67**: 96-114.
- . 1935. The internal mechanics of the chromosomes, III. Relational coiling and crossing-over in *Fritillaria*. *Proc. Roy. Soc. B*, **118**: 74-96.
- . 1937. *Recent Advances in Cytology*, London: J. & A. Churchill Ltd.
- ERNST, H. 1938. Meiosis und crossing over. Zytologische und genetische Untersuchungen an *Antirrhinum majus* L. *Zeitschr. Bot.*, **33**: 241-94.
- . 1939. Zytogenetische Untersuchungen an *Antirrhinum majus* L. *Zeitschr. Bot.*, **34**: 81-126.
- GARBER, E. D. 1947. The pachytene chromosomes of *Sorghum intrans*. *J. Hered.*, **38**: 251-52.
- . 1950. Cytotaxonomic studies in the genus *Sorghum*. *Univ. Calif. Publ. Bot.*, **23**: 283-362.
- HARPSTEAD, D. D., ROSS, J. G. AND FRANZKE, C. J. 1954. The nature of chromatin changes of colchicine-induced variants in *Sorghum*. *J. Hered.*, **45**: 255-58.
- HEITZ, E. 1928. Das Heterochromatin der Moose, I. *Jahrb. wiss. Bot.*, **69**: 762-818.
- HYDE, B. B. 1953. Differentiated chromosomes in *Plantago ovata*. *Amer. J. Bot.*, **44**: 809-15.
- LIMA-DE-FARIA, A. 1948. B chromosomes of rye at pachytene, *Portug. Acta Biol., Ser. A* **2**: 167-74.
- . 1949. The structure of the centromere of the chromosomes of rye. *Hereditas*, **35**: 77-85.
- . 1950. The Feulgen test applied to centromeric chromomeres. *Ibid.*, **36**: 60-74.
- . 1952. Chromomere analysis of the chromosome complement of rye. *Chromosoma*, **5**: 1-68.
- LONGLEY, A. E. 1937. Morphological characters of teosinte chromosomes. *J. agric. Res.*, **54**, 835-62.
- . 1938. Chromosomes of maize from North American Indians. *Ibid.*, **56**: 177-96.
- . 1941. Chromosome morphology in maize and its relatives. *Bot. Rev.*, **7**: 263-89.

PACHYTENE CHROMOSOMES & MEIOSIS IN SORGHUM 355

- McCLINTOCK, B. 1929. Chromosome morphology in *Zea mays*. *Science*, **69**: 629.
- , 1931. The order of the genes C, Sh, and Wx in *Zea mays* with reference to a known point in the chromosome. *Proc. nat. Acad. Sci.*, **17**: 485-91.
- RHOADES, M. M. 1950. Meiosis in maize, *J. Hered.*, **41**: 58-67.

EXPLANATION OF PLATE XIX

- FIG. 1. Pachytene in *S. subglabrescens*, \times ca. 1,500.
- FIG. 2. Pachytene in *S. roxburghii*, showing the relatively more pronounced heavily stained regions adjacent to centromeres, \times ca. 1,500.
- FIG. 3. Another cell at pachytene in *S. roxburghii*, showing a case of non-homologous association of centromeres, \times ca. 1,500.
- FIGS. 4-6. Early diakinesis, late diakinesis and metaphase I respectively in *S. subglabrescens*, showing the relative contraction of the differentially stained regions in the bivalents, \times ca. 1,000.



TEXT-FIGS. 1-2. Fig. 1. Explanatory diagram drawn from Plate XIX, Fig. 1, showing the individual chromosomes (for details of description see text). Fig. 2. Diagram of the pachytene complement in *Sorghum subglabrescens*, showing the average lengths of the chromosomes and the relative lengths of the heavily and lightly stained regions in each. The nucleolar organising region in chromosome 1 is represented by a circle, and centromeres by gaps.

