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Collection

Studies on
Old World Bluestems II

by

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Margaret Hoover Brooks and K. L. Mehra

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Introduction

An intensive investigation of the old world bluestem complex was initiated at Oklahoma State University in 1952. The first bulletin of this series (Celarier and Harlan 1955) serves as an introduction to the complex, outlining most of the members of the group and differentiating the several types. This bulletin is a progress report summarizing information obtained since the first report was issued. Various phases of the research program are reported in more detail elsewhere, and for technical reports on the studies so far conducted the reader is referred to the bibliography at the end of the bulletin.

Detailed studies are necessarily confined to materials available in abundance. Since a number of forms are represented in our collection by only a few accessions and some types are lacking altogether, a complete analysis of the complex is impossible at the present time. Many new accessions have been obtained in the last two years, but in general, they have tended to confirm the treatment given in the first bulletin. Intermediate forms have been found and some have been produced artificially, but for the most part the groupings given have proved to be a reasonably reliable representation of the natural pattern of variation.

For the present, therefore, the key presented in the first bulletin is still satisfactory except for the taxon *Bothriochloa venusta* which will be discussed below. Several new types have been obtained, however, and a few accessions seem to defy classification by the system used. It is expected that when adequate information is obtained the classification and key will be revised accordingly.

Agronomic Potential

The group under most active study at the present time comprises a complex involving species of *Bothriochloa, Dichanthium,* and *Capillipedium* which are distributed from Australia westward to the Atlantic coasts of Africa and Europe. American species are not now being inten-

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[1] Cooperative investigations between the Crops Research Division, ARS, USDA and the Okla. Agric. Expt. Station.

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sively studied, and several of the Old World species are either too poorly represented in our collection or apparently too incidental to the main stream of development of the group to be of agronomic interest at this time.

In the central complex under investigation are many forms of apparent agronomic value. There are types adapted to the wet tropics with two hundred inches or more of rainfall and types adapted to deserts of 2-5 inches annual precipitation. Some are highly productive, others are miserable little plants of low apparent value. Some forms are rated very high in quality and according to literature give high animal gains; others are dry, stemmy, or pungent and presumed to be of low quality. Most of the accessions lack winter hardiness under Oklahoma conditions, but some are hardy as far north as the Dakotas. A few are susceptible to leaf diseases, but most of them are resistant to Oklahoma strains of foliar pathogens.

Ecologically, most of the forms are similar in that they appear to be best fitted to some stage of secondary succession. They do not behave as climax plants but tend rather to increase and thrive under grazing and other disturbances. They reproduce freely by seed, tending to be somewhat weedy, and as a whole are easily established in plantings. These qualities are desirable in tame forage grasses provided quality, productivity and persistence are not sacrificed to the subclimax habit.

Considering the origin and ecological behavior of these materials, it seems likely that types might be found adapted to the wide range of conditions throughout the South from Florida to California. Accordingly, preliminary adaptation trials have been started at something over twenty stations scattered across the continent. Based upon preliminary observations, it would seem likely that some forms of *Dichanthium caricosum, Bothrichloa intermedia* or *B. pertusa* would find a place along the Gulf coasts of the southeast. The Mediterranean or Senegalese forms of *D.annulatum* should fit somewhere in our dry southwest and the more productive types of *B. ischaemum* should find a place in the Southern Great Plains.

The ultimate potential of the group lies both in the utilization of selected members of the collection and in the development of altogether new combinations by plant breeding. If the vigor, producivity, and high quality of some accessions of *Dichanthium* could be combined with the winter hardiness of some *Bothriochloa* accessions, strains of great value to the Great Plains might be produced. Drouth resistance, productivity, high forage quality, winter hardiness, disease resistance, aggressive seedling establishment and other desirable qualities are all to be found in the group. No one accession possesses all of the qualities, however, and it will be necessary to combine two or more of the types by special plant breeding techniques in order to realize the ultimate potential of the group. Most of the studies reported here are directed toward these desired results.

Cytological Studies

The accessions studied to date are listed here according to the classification used previously (Celarier and Harlan, 1955).

1. *Bothriochloa decipiens* C. E. Hubb

This species is Australian, largely cleistogamous, probably sexual and as such represents an offshoot that has by passed the rest of the group. It is variable but seems to be rather isolated from other Old World *Bothriochloa* species.

2. *Bothriochloa intermedia* complex

The specific epithet is well deserved. This complex occupies a central position in the materials studied and is enormously variable. Some forms tend to grade by way of the gangetica type (see below) into the *Dichanthium annulatum* complex (Figs. 5, 6, 7, 9). Some forms of *B. intermedia* grade into the oriental type of *B. ischaemum,* and some into the common type of the latter species (Figs. 5, 9). Other types grade into *B. pertusa* and some into *Capillipedium parviflorum* (Figs. 5, 6, 9). The *B. ewartiana* of Australia appears to belong to the *B. intermedia* complex of that continent. On the whole, this seems to be a sort of central repository for much of the germ plasm of the entire group.

B. intermedia A. Camus

Tetraploids ($2n=40$) INDIA: 2554 Coimbatore; 3965 Calcutta; 5324 Indore; 4820 New Delhi; 4087 United Provinces; PHILIPPINE IS.: 4633 Quezon City; AUSTRALIA; 3726 Sydney; AMERICA (INTRODUCED): 2655 British Guiana; 2560 Texas; 1337 Texas.

Hexaploids ($2n=60$) AUSTRALIA: 4597 Gatton; 4596 Gatton.

B. intermedia gangetica type

Tetraploids ($2n=40$) INDIA: 5450 Delhi; BRITISH GUIANA (INTRODUCED): 2655; SOUTH AFRICA (PROBABLY INTRODUCED): 5168; FIJI ISLANDS (PROBABLY INTRODUCED): 5592.

B. caucasia C. E. Hubb

Tetraploids ($2n=40$) RUSSIA: 1348, 2561, 2562 and 2563. Tiflis; ENGLAND (INTRODUCED): 4006 Kew.

3. *Bothriochloa pertusa* complex

This group is too poorly sampled and inadequately studied to analyze properly. Several distinguishable types have appeared in the collection but further study is needed before much order can be made of the complex.

Tetraploids ($2n=40$) AFRICA: 5431 Senegal; 3239 Nairobi; PAKISTAN: 4635 Sargodha; INDIA: 5301 Delhi; 5406 Delhi; 4394 Dehra Dun; 6152 West Bengal; 2654 Coimbatore; CEYLON: 4021 Peradenuya; CUBA (INTRODUCED): 3185.

Hexaploids ($2n=60$) AFRICA: 5190 South Africa; 3704; Natal; 3736 Southern Rhodesia; 3681 Southern Rhodesia; 2584 Tanganyika; 3109 Kenya; 4517 Ethiopia; 4518 Ethiopia.

4. *Bothriochloa ischaemum* Keng

A number of additional accessions have been studied, but they do not change in any way the status of this species. Of particular interest, however, is the introduction of an additional pentaploid from South China.

Common type *(B. ischaemum* var. *ischaemum)*

Tetraploids ($2n=40$) SPAIN: 4439 Madrid; ITALY: 4011 Pisa; FRANCE: 3959 Grenoble; 4008 Pont de l'Arc; 4007 Strasbourg; 5730 Bas Rhin; 3794 Paris and 5731; BELGIUM: 3240 Brussels; 3701 Antwerp; 3902 Bommershaven; GERMANY: 3705 Wehrda; AUSTRIA: 3955 Vienna; CZECHOSLOVAKIA: 4251 Bohemia; 4252 Slovakia; 4250 West Kosice; HUNGARY: 4798 Budapest; 5422 Szentes; YUGOSLAVIA: 4801 Ljubljana; 4777 Ljubljana; 4803 Zemun; 4802 Belgrade; GREECE: 4776 Eastern Macedonia; TURKEY: 565 Eskisehir; 564 Eskisehir; 1366 Zonguldak; 1376 Kastamonu; 3457 Tunceli; 2553 Sinop; 3465 Kayseri; 563 Malatya; 1341 Elazig; 562 Bingol; 567 Erzincan; 1365 Trabzon; 1369 Coruh; 1358 Kars; 561 Mus; 1343 Mardin; 1360 Van; 560 Hakkari; IRAQ: 3699 Baghdad INDIA: 3057 Punjab; CHINA: 5704 Peking; and 5637.

Hexaploids ($2n=60$) TURKEY: 1359 Maras; 1368 Coruh.

Oriental type *(B. ischaemum* var. *songarica)*

Pentaploids ($2n=50$) CHINA: 726, 3503, 2559, 5635 and 5639 Amoy; 6459 Hong Kong.

Hexaploids ($2n=60$) CHINA: 1347 Triangle City; 5639 Hunan Province; and 5636.

5. *Bothriochloa venusta* A. Camus

Our material previously referred to *B. venusta* (Celarier and Harlan 1955, Celarier and Harlan, 1957) is apparently not *B. venusta*. A more careful evaluation of the published description (Hooker, 1897; Trimen, 1900) indicates that the material in our collection is an undescribed type rather than *B. venusta* and that apparently we have no valid *B. venusta* in the collection at the present time. Because of the special significance of these materials in the phylogenetic scheme, it is necessary to refer to them and in order to do this efficiently, some name must be applied. For the time being we suggest that these particular accessions be included in the *B. intermedia* complex as the gangetica type. The accessions listed there (above) are faculative apomicts intermediate between *B. intermedia* and *Dichanthium annulatum* and are probably of hybrid origin. Since the gangetica type can be crossed with both of these species, the position of the taxon is uncertain and a final disposition must await further information.

6. *Dichanthium sericeum* A. Camus

This species is primarily Australian, enormously variable, cleistogamous, sexual, diploid and probably related to a different complex than the one being described here. On morphological grounds, it seems likely that the genome of *D. sericeum* has entered into the building of several Australian species but probably is not involved in the material under discussion.

7. *Dichanthium annulatum* complex

To the three types previously described it is now necessary to add a type which was obtained from Senegal, French West Africa. It is rather similar to the Mediterranean type of *D. annulatum* except that the spikelets are nearly glabrous. Since hair patterns are rather critical in these materials, the appearance of a smooth form suggests an introgression with something we have not yet seen. There are also a number of accessions in the collection intermediate between the Mediterranean and tropical types. The distinction between these types can only be made with certainty where typical or extreme forms occur. The South African type remains readily identifiable as *D. papillosum*.

Diploids ($2n=20$) INDIA: 5396 Belatal; 3242 Calcutta; 3965b Calcutta; AMERICA (INTRODUCED): 1526b Texas.

Tetraploids ($2n=40$) AFRICA: 4391 Gabes, Tunisia; 4390 Zerkine, Tunisia; 3787 Giza, Egypt; 94 Morocco; 5429 Senegal; 5430 Senegal; 4804 Tanganyika; SAUDIA ARABIA: 4830 Al Kahrs; ISRAEL: 2565 North Gallilea; 3182 North Gallilea; IRAQ: 3093 Abu Ghraib; 1376 Baghdad; 5123 Baghdad; 5131 Baghdad; PAKISTAN: 6575 Bannu; 4636 Sargodha; 6073 Tando dam; 4099 Lahore; INDIA: 5295 Coimbatore; 2654 Coimbatore; 5797 Bombay; 5296 Dharwar; 5238 Poona; 5401 Lonavla; 5287 Sangar; 5326 Indore; 4045 Ajmer; 5398 Karnal; 5302 Karnal; 2564 Dehli; 5288 Delhi; 5411 Delhi; 5399 Rohtak; 5397 Mathura; 3713 Allahabad; 5437 Lucknow; 4600 Lucknow; 4565 Nadia; 2568 Madras; 5408 not known; CHINA: 6154; AMERICA (INTRODUCED): 4395 Cuba; 4082 Texas; 2566 Texas; 1526a Texas.

Hexaploids ($2n=60$) AFRICA: 4106 South Africa; 4080 South Africa; 4081 South Africa; 4083 South Africa; 2567 South Africa; 3716 Southern Rhodesia; AUSTRALIA (INTRODUCED?) 4788 Rodd's Bay.

8. *Dichanthium caricosum* complex

The three types suggested previously appear to be adequate at the present time. The Texas collections seem to represent a type different from other materials so far introduced.

Tetraploids ($2n=40$) AFRICA: 2661 Pretoria; South Africa; 2660 Pretoria, South Africa; 3025 Pretoria, South Africa; 4105 Transvaal, South Africa; INDIA: 5795 Bombay; 1528 Delhi; 4086 New Dehli; 5440 Poona; MALAYA: 2583; FIJI ISLANDS: 5600; AMERICA (INTRODUCED): 4084 Texas; 4291 Trinidad; 1527 Texas; 4095 California; 4097 Texas; 4096 Texas; 1529 Texas; 4098 Texas; 2571 Texas; 2570 Texas; 4094 Texas.

Embryological Studies

Early in the investigation it became apparent that apomixis was a common if not the predominant mode of reproduction in the old world bluestems, and this has recently been demonstrated (Celarier and Harlan, 1957). Embryological studies were, therefore, undertaken in order to establish the mechanism involved and to see if procedures could be developed to determine the frequency of asexual and sexual reproduction in the various accessions.

A modified Bradley squash technique (Bradley, 1948) was used which provided a rapid method for observing embryo sacs and the early stages of the developing embryo and endosperm.

Two types of sacs were observed, Figs. 1 and 2. The sexual sacs characteristic of diploids and faculative apomicts have two conspicious polar nuceli and a group of antipodal cells that stain very poorly. The asexual sacs characteristic of faculative and obligate apomicts have a single polar nucleus and no antipodal cells.

Sexual sacs have been observed in all accessions studied, but in the most strongly apomictic forms they are crowded out by one to several apomictic sacs, Figure 3. As many as seven embryo sacs have been observed in an ovule of strongly apomictic material such as Chinese hexaploid *Bothriochloa ischaemum* and King Ranch bluestem. From one to several of these sacs may contain an embryo of several dozen cells at the time of anthesis, Figure 4. Endosperm does not appear to form, however, until pollination. At present it is presumed that a sperm nucleus from the pollen fuses with the single polar nucleus and that the embryo cannot complete its development until this is accomplished. More study on this point is needed.

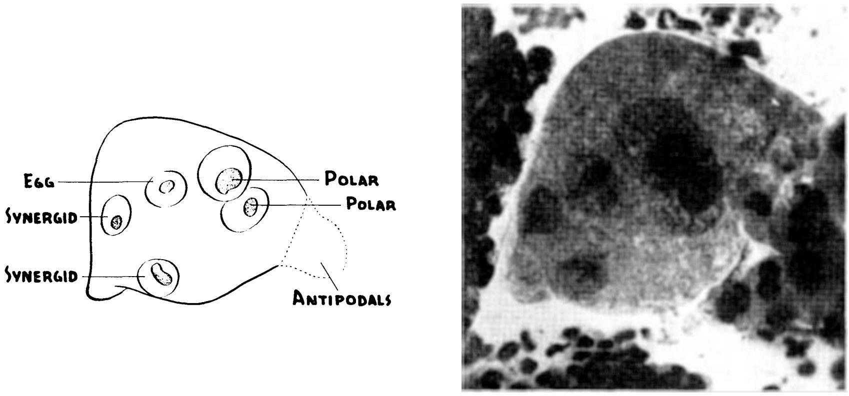

Fig. 1—Sexual embryo sac characteristic of sexual diploids and faculative apomicts, containing two polar nuclei ad several poorly straining aptipodals.

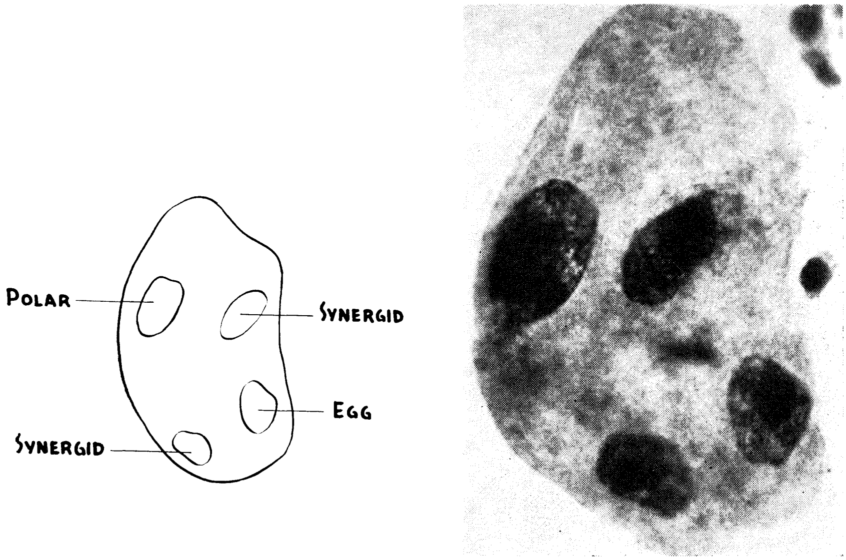

Fig. 2—Asexual embryo sac characteristic of faculative and obligate apomicts, containing a single polar nucleus and no antipodals.

A preliminary survey indicates that the complex follows the classic pattern in which the diploids are all sexual, the tetraploids largely asexual but including some facultative types and the pentaploids and hexaploids are obligate apomicts. Genetic evidence from controlled crosses agree in all particulars with the embryological data (Celarier and Harlan, 1957).

The apomictic mechanism is evidently pseudogamous apospory. The squash technique used permits a rather rapid survey of materials and it is expected that it will be an invaluable tool in determining the frequency of sexual reproduction in suspected facultative types.

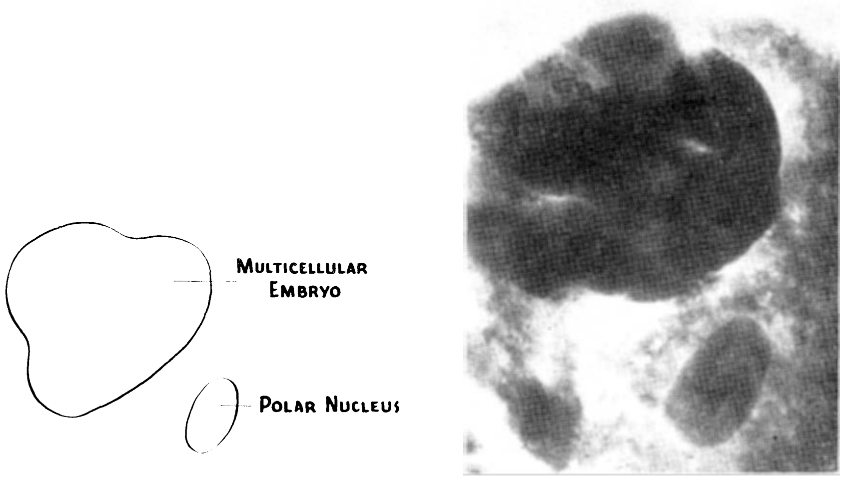

Fig. 3—Embryo sac containing a multicellular embryo and a polar nucleus before anthesis.

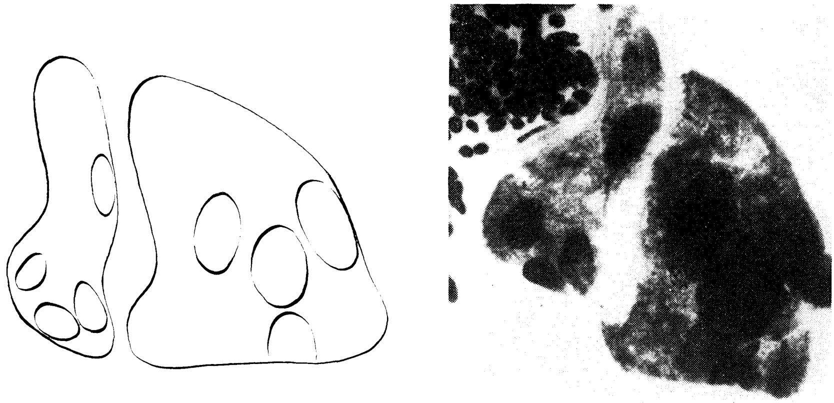

Fig. 4—Two embryo sacs in the same ovule. Both are four nucleate sacs, but note the difference in the size of both sacs and nuclei.

Crossing Studies

Several hundred hybridization attempts have been made to date by means of hand emasculations and pollinations. The technique, described elsewhere (Richardson, in press), is laborious and exacting, but the emasculation is positive and effective. A large volume of data has been assembled in these crossing studies but no attempt will be made to present it here. A brief summary of the results is presented below.

The diploid forms of *Dichanthium annulatum* are indeed sexual and cross readily with each other. Attempts to cross them with tetraploid forms, however, did not lead to much success. From over 4,000 emasculated spikelets of the diploid 3242 pollinated with pollen from tetraploid types, four seeds were obtained. Two of the four seeds germinated and one of these produced a mature plant. The plant, however, was not a triploid but a tetraploid. It evidently resulted from the development of a fertlized 2*n* egg. Morphologically, no characteristics of the male parent (5411) can be detected (however, the male and female were very similar), but the plant does not behave cytologically like an autotetraploid. Embryologically and genetically the plant appears to be largely sexual and is expected to be extremely useful in the breeding program. It resembles the mother plant in most respects, but is much larger, more robust and more vigorous and productive.

Many accessions are either obligate apomicts or reproduce sexually at such a low frequency that hybrids were not picked up. The seeds produced in the crossing attempts were stimulated by the pollen but produced only maternal plants. The most strongly apomictic types were accessions of *Bothriochloa intermedia;* tetraploid, pentaploid and hexaploid *B. ischaemum;* and the hexalpoid *D. papillosum.*

A few accessions were largely apomictic but produced occasional hybrids when suitable pollen was applied. The *D. annulatum* 3182 from Israel produced two hybrids with 4393 from India and the *D. caricosum* 2583 from Malaya produced three hybrids when crossed with *D. aristatum* 4084 from Africa. Reciprocal hybrids were also obtained. The frequency of hybrids was under 4% in all cases, the remainder of the progeny being strictly maternal.

Three accessions of the gangetica type (2655, 5450 and 5168) proved to be fairly sexual by comparison. Number 2655 has been used most, and from both genetic and embryological evidence, appears to be about 25% sexual in reproduction. As a female, it has been most interesting. Hybrids apparently have been obtained with a 6*n* *B. intermedia* from Australia, a 5n *B. ischaemum* from China (K. R. bluestem), a 6*n* *B. ischaemum* from Turkey, and a 4*n* *D. annulatum* from India. Accessions 5168 and 5450 have been crossed with a 4*n* *B. ischaemum* from China, a *B. intermedia* from India and presumptive hybrids have been found involving a 4*n* *B. pertusa* from French West Africa and a *Capillipedium parviflorum* from Australia. Hybrids between accessions of the gangetica type have also been produced.

D. annulatum 4099 from India is also more sexual than many of the others. Embyrological and genetic evidence indicate about 18% sexuality.

An analysis of the hybrids obtained revealed that many of them were derived from functional unreduced eggs. In reciprocal crosses between *D. caricosum* and *D. aristatum* the F_1 plants always resembled the mother plant more than the male. In the cross *B. intermedia* gangetica 2655 *D. annulation* 4099 a number of hybrids were obtained, about half of which had the 6*n* number of chromosomes and about half had the 4*n* number.

These results reveal clearly at least some of the evolutionary mechanisms in the group. The faculty for the production of functional unreduced female gametophytes is probably widespread in the group. Evidently even sexual diploids can on rare occasions produce gametophytes of this type resulting in highly sexual tetraploids. The occasional sexual tetraploid produced in this manner would probably cross with a variety of related materials where it occurred. Sexuality would in all probability be swamped in a few generations by such crossings with highly apomictic stocks, but an enormous amount of variability could be developed before clonal races were fixed by apomixis. The mechanism should be one of exceptional evolutionary efficiency in regions where diploids and a variety of tetraploid materials occur together.

The same phenomenon occurring at the tetraploid level results in the production of hexaploids and the very high frequency of hexaploids in our 4n x 4n crosses would indicate that this is the normal mechanism in this group for hexaploid production. A close correlation between apomixis and polyploidy has often been noted. Indeed, it has been suggested that due to the sterility of sexual polyploids, apomixis serves as a method for the preservation of hybrids that could not otherwise maintain themselves under natural conditions. The correlation is often explained on this basis. In the materials under discussion it appears more likely that polyploidy is a consequence of the tendency for faculative apomicts to produce functional unreduced eggs, and that apomixis itself is the cause of polyploidy.

TABLE 1. Proven and Presumptive Hybrids So Far Obtained

D. annulatum Mediterranean type (4*n*) x *D. annulatum* tropical type (4*n*)
D. annulatum tropical type (4*n*) x *D. annulatum* Mediterranean type (4*n*)
D. annulatum Senegalese type (4*n*) x *D. annulatum* tropical type (4*n*)
D. annulatum tropical type (4*n*) x *B. intermedia* gangetica type (4*n*)
D. caricosum (4*n*) x *D. aristatum* (4*n*)
D. artistatum (4*n*) x *D. caricosum* (4*n*)
D. caricosum (4*n*) x *D. annulatum* (4*n*)
B. intermedia gangetica type (4*n*) x *B. intermedia* (6*n*)
B. intermedia gangetica type (4*n*) x *B. ischaemum* (6*n*)
B. intermedia gangetica type (4*n*) x *B. ischaemum* (5*n*)
B. intermedia gangetica type (4*n*) x *B. ischaemum* (4*n*)
B. intermedia gangetica type (4*n*) x *D. annulatum* (4*n*)
B. intermedia gangetica type (4*n*) x *D. annulatum* (2*n*)
B. intermedia gangetica type (4*n*) x *B. pertusa* (4*n*)
B. intermedia gangetica type (4*n*) x *Capillipedium parviflorum* (4*n*)
B. intermedia (4*n*) x *B. intermedia* gangetica type (4*n*)
B. intermedia (4*n*) x *B. intermedia* (4*n*)

Only a few of the hybrids have so far been analysed, but both $2n=60$ and $2n=40$ F_1's were found in $2n=40$ x $2n=40$ crosses.

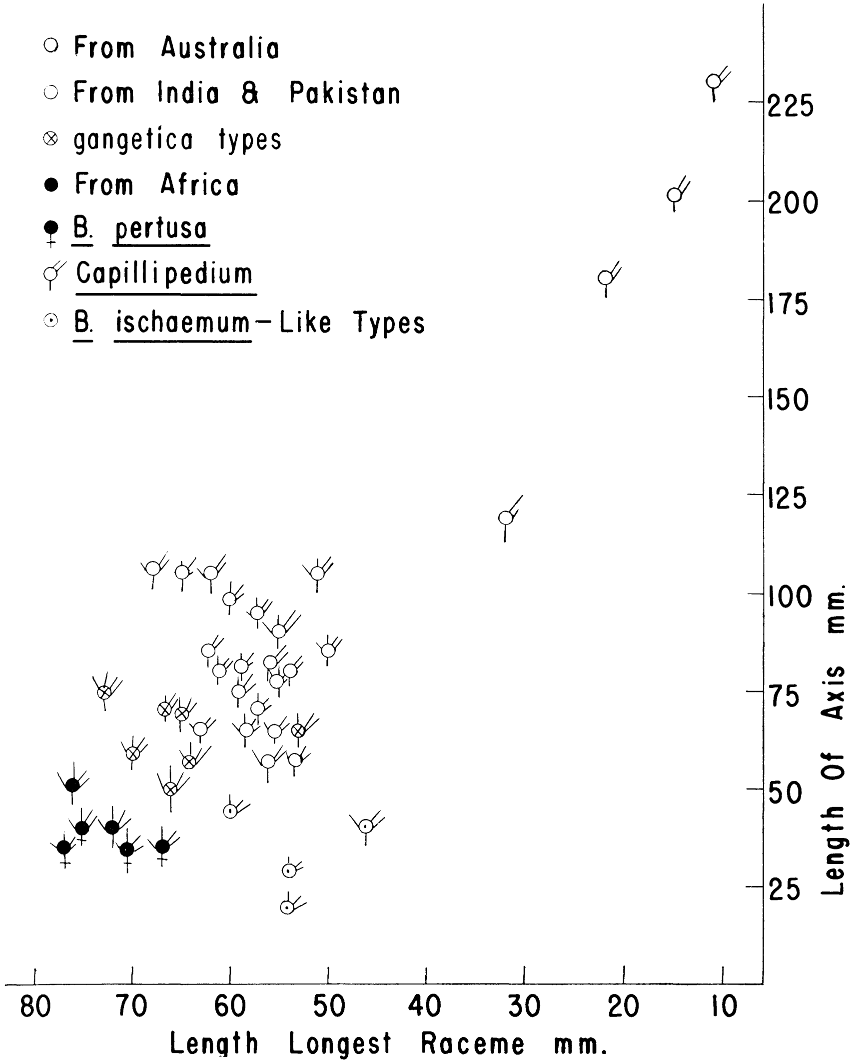

Fig. 5

Morphological Studies

The taxonomy of apomictic groups is notoriously difficult. The normal forces that tend to separate species in sexual materials are not functioning in such groups and some systematists have suggested a special terminology be used for agamic complexes (Stebbins 1950). Although the old world bluestems are largely apomictic and difficult enough from a taxonomic point of view, there still seems to be some merit in attempting to separate out the reasonably valid taxa.

A study was initiated to see if the clusters of morphological characteristics typical of the various taxa presented any consistent geographical pattern or if evidences of introgressive hybridization could be detected. The scatter diagrams of Dr. Edgar Anderson (1949) were used together with measurements of the length of the axis of the inflorescence and the length of the longest racemes. Five inflorescences were measured for each accession if the accession was uniform. If more than one type appeared in the accession, the types were measured separately.

The results of these studies are diagrammed in Figures 5, 6 and 7. A key to the whisker diagram appears below:

Hairs at node	none	○	short		long	
Number of racemes	few	○	several		many	
Breadth of racemes	broad	○	medium		slender	
Hairs on upper end of glume	none	○	medium		many	
Pits on glumes	none	○	moderate		strongly pitted	
Pungence of foliage	none	○	moderate		very strong	

The diagrams reveal rather clearly the nature of the gradation from one form into another. As indicated previously, *Bothriochloa intermedia* holds a central position in the group and grades in one way or another into *Capillipedium parviflorum, B. ischaemum, B. pertusa,* and through the gangetica type into *Dichanthium annulatum.* The latter species shows definite affinity to the *D. caricosum* complex.

Despite these morphological gradations, the bulk of the accessions fall clearly into distinct clusters and the differences between the several types are not obliterated by introgressive hybridization. It would appear that the present taxonomic treatment has some merit in defining real and natural units. These units do not merge completely because such hybridizations that do take place primarily involve genome building and the segregation expected in sexually reproducing forms is blocked by apomixis.

The fact that several species of at least three genera can be crossed artificially and probably have crossed in nature raises a question concerning the validity of the system used. In sexual material geneticists and experimental taxonomists would be inclined to at least lump such taxa

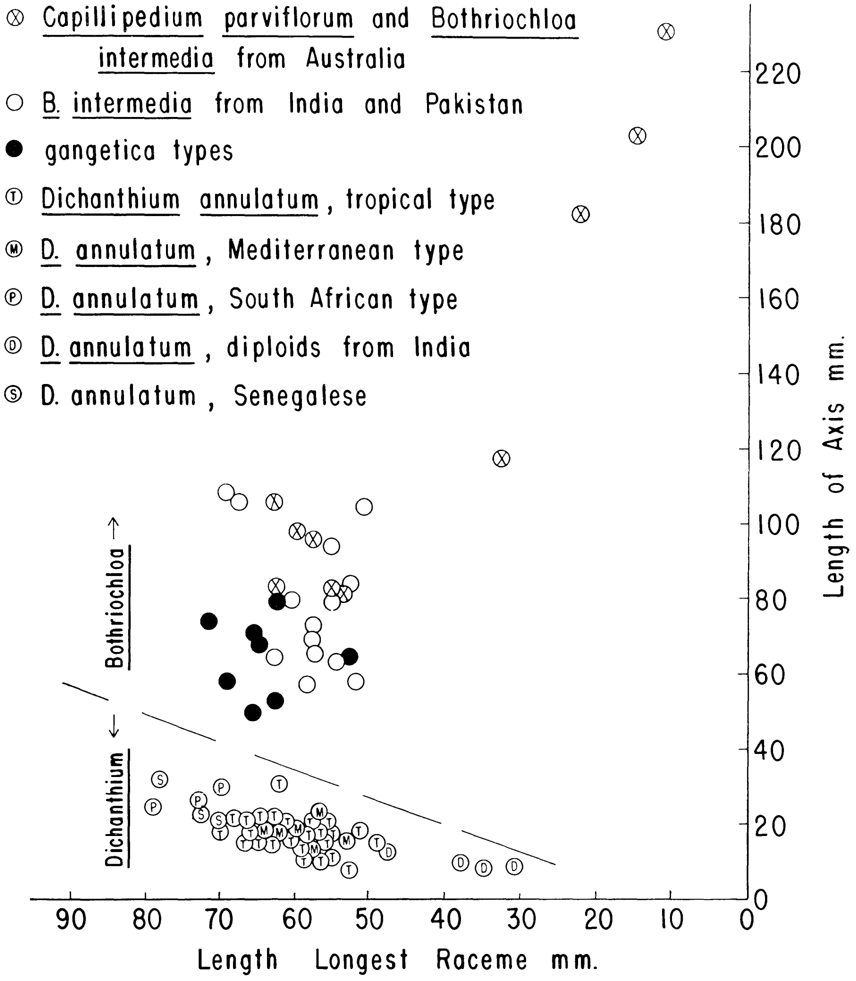

Fig. 6

into one genus if not one species. In asexual materials the situation is different, however. Many of the crosses obtained, especially those involving the widest crosses, resulted from the fertilization of unreduced eggs and a consequent increase in chromosome number. Such forms appear to be strongly apomictic and reproductively isolated. They are in effect new genomic combinations but in no way contribute to the genetic breakdown of the taxa involxed. It may be, indeed, that the three genera should be combined but such a move must await more detailed studies especially with the missing diploid forms.

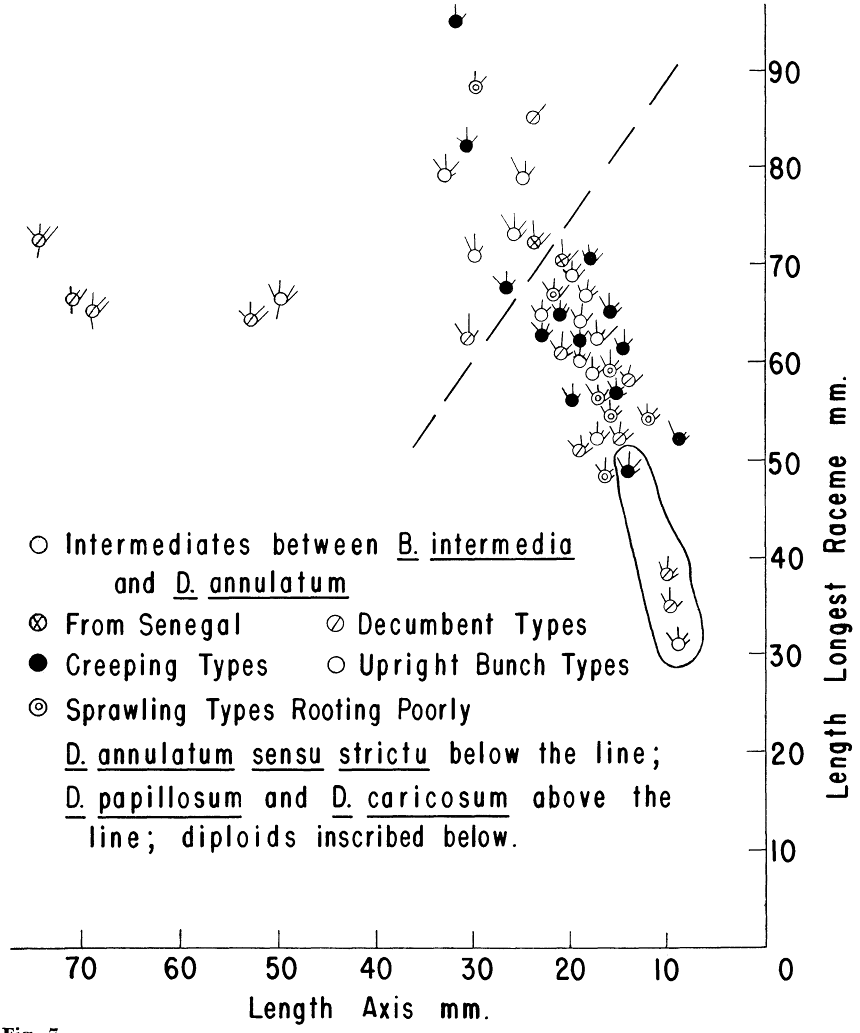

Fig. 7

Geographical Studies

Although the present collection is very incomplete and sketchy for many portions of the natural range of the old world bluestems, some geographic patterns emerge rather clearly. The common type of *B. intermedia* in the Gangetic Plain of India is the form referred to the gangetica type. Some accessions are strongly apomictic, others are somewhat sexual. The latter forms apparently cross to some extent with *D. annulatum* in the gangetic plain and with the broad leaved *B. intermedia* types of the Himalayan foothills to the north. That such crosses are possible has been demonstrated by our crossing work. That it has and is taking place is revealed in the remarkable diversity of *D. annulatum* from that region (Celarier, Mehra and Wulf, 1958), and by the studies on introgression here reported and in progress.

Furthermore, three of the four diploids in our collection came from the Gangetic Plain of India (the other as a mixture from unknown sources). It has been demonstrated that diploids occasionally produce sexual tetraploids and these can in turn be crossed readily with other tetraploids of the immediate group. Such hybrid derivatives probably lose their potential for sexual reproduction quickly but must contribute substantially to the variability of the tetraploid materials from the area. Thus, northern India is a center of exceptional evolutionary activity in both the *Dichanthium annulatum* and *Bothrichloa intermedia* complexes.

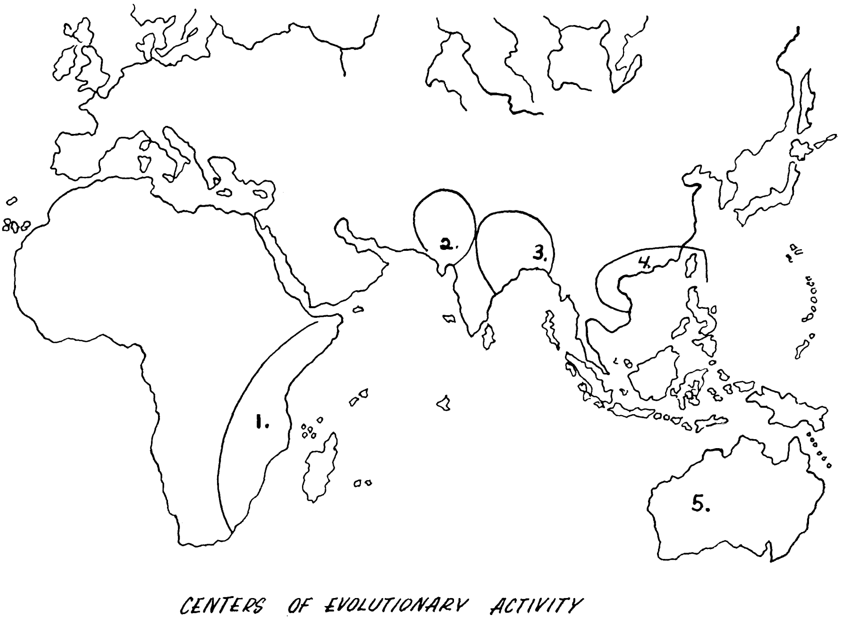

Fig. 8—Centers of evolutionary activity: (1) Bothriochloa intermedia and B. pertusa, (2) B. intermedia and B. ischaemum, (3) B. intermedia and Dichanthium annulatum, (4) B. intermedia and B. ischaemum and (5) B. intermedia and Capillipedium parviflorum.

All of the oriental forms of *B. ischaemum* have been obtained from southeast Asia, the Chinese mainland, Burma, Hong Kong and Formosa. On morphological grounds these types are evidently constructed by a genome building process involving common *B. ischaemum* and some form of the *B. intermedia* complex (Celarier, 1957b). This part of the world, then, is a center for such activity in the group.

In east Africa the *B. pertusa* complex is especially well developed including some apparently endemic forms. If the entire *B. pertusa-B. intermedia-Capillipedium* complex of our collection is considered. the occurrence of pitted glumes gives an interesting pattern. Most of the *B. intermedia* forms from Africa have pitted glumes. Those of India seem about equally divided between pitted and nonpitted forms while few of the Australian members of the complex have pits. There is good circumstantial evidence that the pitted glumes are a characteristic of a basic *B. pertusa* genome and one of its present centers of development is east Africa. Genetic exchange and genome building between *B. pertusa* and *B. intermedia is* probably most active in that part of the world.

On the other side of the Indian Ocean, other members of the *B. intermedia* complex are active in Australia. Although material in our collection is still inadequate, a rather clear step by step gradation from *Capillipedium parviflorum* to *B. intermedia* and *B. ewartiana* can be detected from the morphological data presented in Figures 5 and 6. A detailed analysis of the activity within the complex in Australia must await more material and appropriate hybridization studies.

Some other geographic patterns are less clearly apparent. In Pakistan there is some evidence for genome exchange between *B. intermedia* and common *B. ischaemum*. The two hexaploid accessions of *B. ischaemum* from Turkey appear to have been derived from unreduced eggs of a common *B. ischaemum* and reduced pollen from the same type. The result is a rather robust common *B. ischaemum* which may have appeared in the Turkish collection only because Turkey has been better sampled than most other parts of the range of this species. There are some morphological reasons to suspect that the Mediterranean type of *D. annulatum* involves genetic material from *B. ischaemum,* but no experimental evidence has yet been obtained on this point.

Phylogenetic Scheme

From the evidence now at hand it should be possible to establish the phylogenetic relationshisp of at least a portion of the complex. In order to do this it is necessary to postulate the existence of certain forms that do not occur in our collection. Prediction is one of the tests of the sci-

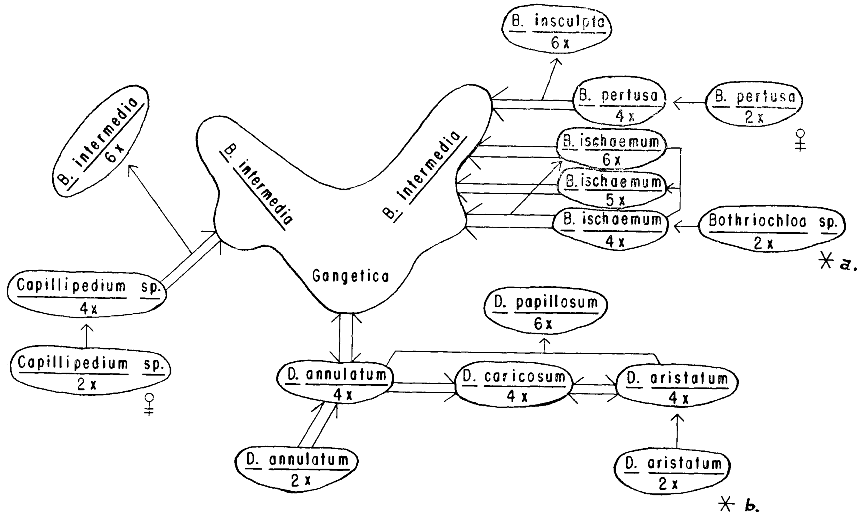

Fig. 9—A suggesed phytogenetic scheme for a portion of the Old World Bluestem comples.

✳ Not in our collection, but reported in the literature.
a. reported by Ramanthan, 1950.
b. reported by de Wet, 1954.

♀ Postulated

⇒ Double line indicates hybrids or putative hybrids have been made artificially in our laboratory; arrow indicates direction of hybridization from male to female.

→ Single line arrow indicates probably route of origin.

entific method, and we are able to predict with some confidence that these forms either exist or had existed at one time. The missing forms are diploids and the occurrence of some of them has already been reported in the literature (de Wet, 1954, Ramanathan, 1950).

A tentative proposal of a phylogenetic scheme is shown in Figure 9. The hybrids made in our laboratory give considerable support to the general relationship indicated. The fact that most hybridizations are made in only one direction is, of course, due primarily to the distribution of sexuality within the group and does not imply a greater or lesser affinity between the several members. On the other hand, natural crosses must of necessity be largely in the same direction, a situation which helps to explain the enormous diversity of the *B. intermedia* complex. Germ plasm from the entire group can move in that direction but frequently the reverse is not the case in types which are obligate or near obligate apomicts.

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