

THE ORIGIN OF CULTIVATED SORGHUM

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PREFACE

Each chapter of this thesis is written, with minor modifications, in the form and style of the biological journal to which it will be presented for publication. The taxa of Snowden are not recognized as species for the purpose of this thesis; consequently they are not underlined in the usual manner. It is believed that this method of presentation will allow for more accurate and comprehensive interpretation of the material.

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CHAPTER I

INTRODUCTION

In the genus Sorghum Moench the cultivated forms are among the most widely domesticated crops of the world, ranking a strong fourth to wheat, rice, and maize in the order of total world acreage. It is one of the world's oldest cereals, having come under domestication probably no less than 5000 years ago (Doggett, 1965).

In terms of utilization, sorghum presents a very diverse picture. As with all cereals, the grain is the most widely used, serving as a grain for popping, parching, and making porridges and tortilla-like cakes for human consumption (Burkill, 1936; Snowden, 1936). The grain of kafir corn is also used for the production of beer in various parts of Africa south of the Sahara with other forms serving this same purpose in Ethiopia and northern Africa. The vegetative parts of the plant, along with the grain, are used as feed for domestic animals. The stalks are also used for fencing and building materials in the same manner as bamboo. Sweet forms are grown for the making of sugar and syrup. The long floral branches of *S. dochna* var. *technicum* are used extensively as broom straw. In the areas where sorghum is grown, no single variety may possess all of the

qualities desired by man; consequently he has selected his sorghums according to his needs and has grown them side by side. This procedure, practiced by generations of men, has complicated the history of the crop considerably.

Sorghum, as any plant that has been closely allied with man for any period of time, has evolved rapidly into a diversity of types; and at least three fairly distinct categories can be recognized at the present time, the wild species, the cultivated forms, and the companion weeds of the cultivated forms. In contrast to the early theory that the companion weed is the progenitor of the cultivated plant, investigations by Heiser (1955) with Helianthus, Zohary (1962) with Hordeum, and others have shown that many of the companion weeds represent hybrids between the cultivated and wild species.

The recognized wild prototypes of all the domesticated sorghums are limited to Africa south of the Sahara and range far down into the temperate zone of South Africa. This fact alone is a strong indication that the African continent was the site of the first stages in the domestication of the crop.

The most comprehensive taxonomic study of the genus is that of Snowden (1936, 1955) who recognized some fifty-two species as belonging to the section Eusorghum. These included thirty-one cultivated species of the subsection Arundinacea series Sativa, seventeen wild fodder species of the subsection Arundinacea series Spontanea, and four naturally

occurring rhizomatous species belonging to the subsection Halepensia. Recently two more rhizomatous species, *S. randolphianum* Parodi and *S. alnum* Parodi, were described to include hybrids between grain sorghums and a rhizomatous species.

It is generally agreed that both the cultivated and wild species of *Eusorghum* have strongly influenced each other in their development and evolution. All of the cultivated forms are interfertile, and genetic barriers between the series *Sativa* and *Spontanea* of Snowden are quite weak if they exist at all (Laubscher, 1945). Between the subsections *Arundinacea* and *Halepensia*, barriers to crossing may be somewhat stronger, but numerous instances of hybridization between the two indicate that interfertility still exists.

If this is the case, then the common gene pool shared by the wild, cultivated, and weedy forms would maintain a high degree of variation which can, in fact, be observed throughout the group. It will be the purpose of this study to examine the extent of this variation and to present lines of evidence for consolidating the species of *Eusorghum* into a single taxonomic unit.

Taxonomy of Sorghum Moench

Prior to the seventeenth century, the references to Sorghum in the literature are scarce, and there is some question as to the accuracy of these citations since the

names used could have referred to Sorghum, Setaria, Panicum, Pennisetum, or those plants to which the name millet has been applied (Snowden, 1936). Linnaeus originally classified Sorghum under the genus Holcus, and Moench later established it as a separate genus (Doggett, 1965). The species were assembled into the subgenus Sorghum of the genus Andropogon by Hackel (1889). The subgenus Sorghum was given generic rank by Stapf (1917), who recognized two sections, Eusorghum and Sorghastrum. These were distinguished by the type of panicle branching and the status of the pedicelled spikelets.

Snowden (1936) kept Sorghastrum as a distinct genus, suggesting that by excluding Sorghastrum from Sorghum a more uniform genus would be maintained. The genus as recognized by Snowden was subdivided into Eusorghum and Parasorghum. Parasorghum has bearded nodes and simple panicle branches while Eusorghum has glabrous or finely pubescent nodes with subdivisions of the primary branches of the panicle, the lateral, and the terminal racemes. The characters used by Snowden to distinguish the species within the genus are: the size, shape, and density of the panicle; the position of the branches in relation to the axis; the shape and size of the spikelets; the size of the glumes in relation to seed size; the grain color; the absence or presence of awns; the size and shape of the leaves; the growth habit of the plant; and the habitat.

Garber (1950), using cytological and taxonomic studies

as well as some hybridization experiments, reorganized the classification of the genus. Using the group name, Sorghastreae, he retained in it two main genera, Sorghum and Cleistachne. He split the genus Sorghum into six subgenera, Eusorghum (the same as Snowden's section Eusorghum), Chaetosorghum, Heterosorghum, Sorghastrum, Parasorghum, and Stiposorghum. Celarier (1958b) was not in agreement with Garber on all points of his classification and felt that extensive modifications of the pedicellate spikelet and specific vegetative characters of Sorghastrum, along with a lack of experimental evidence bearing on the relationship between the two, were sufficient grounds to exclude Sorghastrum from the genus Sorghum.

More detailed reviews of the taxonomic literature of Sorghum can be found in Snowden (1936) and Vinall, Stephens, and Martin (1936).

Hybridization in Sorghum

The ability or inability of taxonomic units to cross and produce fertile offspring is quite often used as a tool in determining relationships between groups of organisms. Although the success or failure of hybrid formation does not necessarily unite or separate species, it does give the biosystematist a strong foundation upon which to construct further theories of relationship with regard to the taxa.

In the literature of Sorghum, numerous references to hybrids between the taxa can be found. A summary of the

hybrids reported is found in Table I. The hybrids listed in Table I illustrate the point that if we consider crossing as an indication of the breakdown of genetic barriers between taxa, then the barriers to crossing in sorghum are almost nonexistent. These crosses represent bridges between several of Snowden's species and, on the larger scale, between his subseries within the series *Sativa*, between series *Sativa* and *Spontanea*, and the subsection *Arundinacea* and *Halepensi*.

In practically all cases recorded, the degree of crossing ranged from good to fair. Pritchard (1965) reported in his crosses between *S. alnum* and *S. halepense* that there was a maximum natural crossing of 57% but that the mean was only 20%. He interpreted this as showing that some *S. alnum* plants exhibit a degree of genetic isolation from *S. halepense* when the two species are grown together under natural conditions. If this degree of genetic isolation between these species occurs generally, it is possible that the incidence of hybrids occurring naturally between them would be relatively low.

Harlan (1965), discussing the role that weed races play in the evolution of cultivated plants, pointed out that weed-cultigen hybrids are not abundant in nature. These may suddenly arise as hybrid swarms which quickly subside within a few generations with selection toward weediness or cultigen acting on the products of introgression. If this is so, the same process could occur among the weeds and between

TABLE I
SUMMARY OF REPORTED SORGHUM HYBRIDS

HYBRIDS	AUTHOR
S. aethiopicum -x- S. vulgare	Thangam (1963)
S. alnum -x- S. propinquum	Magoon and Shambulingappa (1962a)
S. alnum -x- S. halepense	Endrizzi (1957)
S. ankolib -x- S. nitens	Shambulingappa and Magoon (1953)
S. arundinaceum -x- S. caffrorum	Shambulingappa and Magoon (1953)
S. bicolor -x- S. virgatum	Bhatti (1963)
S. caffrorum -x- S. alnum	Endrizzi (1957)
S. caffrorum -x- S. ankolib	Shambulingappa and Magoon (1953)
S. caffrorum -x- S. arundinaceum	Magoon and Shambulingappa (1962b)
S. caffrorum -x- S. drummondii	Endrizzi (1957)
S. caffrorum -x- S. durra	Magoon and Shambulingappa (1962b)
S. caffrorum -x- S. halepense	Endrizzi (1957)
S. caffrorum -x- S. melaleucum	Shambulingappa and Magoon (1953)
S. caffrorum -x- S. saccharatum	Magoon and Shambulingappa (1962b)

TABLE I (Continued)

HYBRIDS	AUTHOR
S. caffrorum -x- S. sudanense	Magoon and Shambulingappa (1962b)
S. caffrorum -x- S. verticilliflorum	Magoon and Shambulingappa (1962b)
S. caudatum -x- S. sudanense	Shambulingappa and Magoon (1953)
S. cernuum -x- S. technicum	Kadamov (1959)
S. dochna -x- S. subglabrescens	Thangam et al. (1964)
S. dochna -x- S. sudanense	Sethupathy et al. (1964)
S. dochna -x- S. verticilliflorum	Endrizzi (1957)
S. durra -x- S. virgatum	Kidd (1956)
S. halepense -x- S. durra	Thangam et al. (1964)
S. halepense -x- S. roxburghii	Krishnaswamy et al. (1956)
S. halepense -x- S. subglabrescens	Raman et al. (1965)
S. halepense -x- S. sudanense	Durra and Stebbins (1952)
S. nervosum -x- S. dochna	Shambulingappa and Magoon (1953)
S. nervosum -x- S. halepense	Ananthasayana et al. (1964)
S. nervosum -x- S. stapfii	Ananthasayana et al. (1964)
S. nervosum -x- S. sudanense	Ananthasayana et al. (1964)
S. nitens -x- S. ankolib	Shambulingappa and Magoon (1953)

TABLE I (Continued)

HYBRIDS	AUTHOR
S. nigricans -x- S. vulgare	Shambulingappa and Magoon (1953)
S. subglabrescens -x- S. roxburghii	Satish Rao et al. (1964)
S. sudanense -x- S. halepense	Sethupathy et al. (1964)
S. vulgare -x- S. alnum	Pritchard (1965)
S. vulgare -x- S. arundinaceum	Endrizzi (1957)

the weed and truly wild forms. Processes of this sort appear to be indicative of the differentiation-hybridization cycles, discussed by Ehrendorfer (1959), which represent the two major forces in biotype formation.

Thangam (1963) crossed *S. aethiopicum* (subseries Spontanea), which Snowden considered as one of the wild progenitors of the cultivated sorghums, with a cultivated sorghum (subseries Sativa). He reported that single plants, having morphological characteristics of each type except *S. nervosa*, could be selected from the progeny. From his results, he drew the conclusion that the Spontanea types have played an important role in the evolution of cultivated sorghum races and that the absence of the Nervosa types indicated a separate origin for these. Only the abstract of this paper has been read, and no further interpretation can be made.

In several of the crosses listed involving *S. vulgare* no mention is made of the variety. Generally the cultivated sorghums are grouped under *Sorghum vulgare* Pers., and then referred to by common or varietal names such as milo, kafir, durra, or hegari. Doggett (1965) has pointed out that this is a very practical system, but that the name *S. vulgare* Pers. is illegitimate and should be replaced by the proper term *S. bicolor* (Linn.) Moench (Clayton, 1961).

Cytology of Sorghum and Sorghum Hybrids

Within the section *Sorghum*, the subsection *Halepensis* is characterized by a chromosome number of $2n=40$, with the

exception of *S. propinquum* which has a diploid number of 20. All of the subsection *Arundinacea* are considered as diploids with 20 chromosomes.

The basic chromosome number in *Sorghum* appears to be 5 (Garber, 1950; Celarier, 1956; Doggett, 1965). Endrizzi and Morgan (1955), from a study of haploids, suggested that the diploid *Sorghums* with a chromosome number of 20 are ancient tetraploids. This would make the 40 chromosome *Halepensis* octoploid (Bennett and Merwine, 1966).

Root tip studies by Sharma and Bhattacharjee (1957) on eighteen "species" of *Sorghum* were used to construct idiograms based on the position of primary and secondary constrictions and the relative size of the chromosomes. The amount of variation in chromosome morphology was not excessive; ten major types were found and labeled A through J, but some of the major types had several minor modifications. For example, for B there were types B₁, B₂, and B₃, these depending on minor differences in the position of secondary constrictions and relative size of the segment beyond the constriction. Celarier (1959) believed that the conclusions concerning the chromosome associations drawn by Sharma and Bhattacharjee were controversial but at the same time stimulating and challenging. He felt that their differentiation of the sorghum chromosomes as large, medium, and small was not realistic. The chromosomes of the *Parasorghums* are larger than those of the *Sorghums*, but he failed to recognize the distinction of the medium and small categories

within this group. It was Celarier's opinion that such size differences may easily be the result of environmental influences either at the time of collection or during dehydration and imbedding of the material.

More recently, through pachytene studies, Magoon and his co-workers (1961, 1964) have attempted to classify the associations in the meiotic chromosomes of Sorghum. There is evidently no agreement on any pattern of association at this time.

As yet hybrid studies for chromosome number and meiotic behavior have given varied results. Endrizzi (1957), in studying the F₁ hybrids between *Sorghum vulgare* (var. Texas Blackhull Kafir) $2n=20$ and *Sorghum halepense* $2n=40$, found that one hybrid had 30 chromosomes, and ten had 40 chromosomes. The 30 chromosome hybrid had an average of 4.34 I, 4.34 II, and 5.66 III with a maximum of association of nine trivalents. The 40 chromosome hybrids showed an average of 0.97 I, 10.8 II, 0.31 III, and 3.72 IV with a maximum of eight tetravalents. He proposed that these results indicated that at least one genome was common to *S. halepense* and *S. vulgare* and that regular pairing would occur here.

The problem of the relationship of the weedy *Halepensis* to the Arundinacea has not been solved on a cytological basis. Conflicting reports on the number of univalents, bivalents, and tetravalents formed within the species and among the hybrids can be found. Hadley (1953) reported four possibilities in chromosome associations from 30 chromosome de-

rivatives of *S. halepense* -x- *S. vulgare* hybrids.

Assuming that *S. halepense* was of good polyploid origin and the genomes involved between the *Halepensis* and *Arundinacea* were basic sets of 10 chromosomes, Hadley considered these possibilities:

1. *S. halepense* is an autopolyploid AAAA involving the same genome of *S. vulgare* AA. Then the 30 chromosome plant would be AAA with 10 trivalents.
2. *S. halepense* may be AAAA involving a different genome than *S. vulgare* BB. The triploid would be AAB with 10 bivalents and 10 univalents.
3. *S. halepense* may be an allotetraploid AABB involving only one genome equal to *S. vulgare* AA. The triploid would be AAB with 10 bivalents and 10 univalents.
4. *S. halepense* is an allopolyploid AABB with no genome equal to *S. vulgare* CC. The triploid would be ABC with 30 univalents.

He found in the 30 chromosome types 6 III, 4 II, and 4 I which he felt was closer to choice number 1 than any of the others. His suggestion was that *S. halepense* arose as a cross between two 20 chromosome types whose chromosome complements were different.

The study of meiotic behavior in Sorghum can evidently be quite deceiving. What appear to be univalents to one au-

thor may be interpreted as a loosely held bivalent by another (Hadley, 1953). In *S. halepense*, univalents, trivalents, and hexavalents have been reported (Hadley, 1953; Celarier, 1958b). Endrizzi (1957) on the other hand found no chromosome associations higher than tetravalents, and these were limited to one or two with a maximum of six in a single cell.

Factors other than strict chromosome homology and genomic relationships may play a part in meiotic chromosome behavior. The theory of genetic control of chromosome pairing was introduced early by Muller (1922). Differential affinity between chromosomes was discussed by Darlington (1937, 1958) while Stebbins (1950) proposed the concept of preferential pairing.

In the hexaploid wheats, the control of chromosome pairing was demonstrated to be influenced by one chromosome (Riley, Unrau, and Chapman, 1958; Riley, Kimber, and Chapman, 1961). They demonstrated that chromosome five of the B genome carries one or more genes which prevent homoeologous chromosome pairing during meiosis. When chromosome 5-B is absent from the genetic system, pairing between homoeologous chromosomes results in multivalent associations. Chheda and Harlan (1962) have suggested that a genetic control for pairing of homoeologous chromosomes exists in Bothriochloa and that it is transmitted in a Mendelian fashion.

Two systems may be involved in genetic control of pairing since genes for pairing and genetic control of asynapsis

have been proposed by different authors. Doggett (1964) in comparing fertile lines of *S. alnum* to the diploid grain sorghums found that seed set was comparable between the two. He believed that genes for high fertility present in *S. alnum* were at least partially dominant to those for low fertility in crosses with tetraploid grain sorghum. The genetic data of his crosses suggested further that only a few genes were involved in determining high fertility and that they are not tightly linked to undesirable wild characters. He considered the genes were derived from an earlier *S. halpense* parent, and they acted by conditioning regular disjunction.

Pritchard (1965) found that asynapsis was associated with a dwarf character in the progeny between *S. alnum* and perennial sweet Sudan grass. Again working with the same group of plants (Pritchard, 1965), he suggested that preferential chromosome pairing was under genetic control. This, he believed, might be a part of a general diploidization process which has led to a reduction in quadrivalent formation and an increased meiotic stability in tetraploid sorghums.

Stephens and Schertz (1965) have also discovered an asynaptic gene in the cultivated sorghums which resulted in complete male sterility and partial female sterility. Asynapsis in this case was controlled by a single-gene recessive which was not considered to be allelic to the other genes producing male sterility.

The preceding summary gives some indication as to the work that has been done on Sorghum and points out a few of the strong and weak points in describing this heterogenous group. The application of other tools such as the numerical approach to classification will be discussed later.

CHAPTER II

NUMERICAL APPROACH TO AFFINITIES IN
SORGHUM BICOLOR (LINN.) MOENCH

The complex species Sorghum bicolor (Linn.) Moench is recognized to include all cultivated sorghums as well as a group of semiwild plants mostly associated with them as weeds. The extent of morphological variation within S. bicolor is so tremendous that Snowden (1936, 1955) subdivided the complex into 28 cultivated and 24 related wild species. However, lack of genetic barriers between these taxa indicate that they all belong to a single species (de Wet, 1966). For the purpose of this study, techniques of numerical taxonomy were applied to a quantitative analysis of morphological data based on type specimens and herbarium material correlated with type descriptions of the species of Snowden.

Material and Methods

The value of a quantitative study in determining relationships within S. bicolor was demonstrated by Liang and Casady (1966). However, their study was based on plants grown for several generations in various U.S.D.A. nurseries. It has been the experience of investigators at Oklahoma

State University that many lines which have been maintained without special precautions against hybridization have become so altered that they are almost impossible to classify according to Snowden (1936, 1955). For these reasons, only type specimens and original collections that fit the type descriptions in detail were used in this study.

For each of the 52 taxa recognized by Snowden, 38 characters were recorded, as either clearly expressed positive (present or yes) or negative (absent or no). Similarity coefficients were calculated and placed in a matrix table as described by Sokal and Michner (1958), Sokal and Sneath (1963), and Sheals (1965).

The data for the 38 characters of each of the 52 taxa (Table II explains coding of the taxa) were punched on IBM cards, and comparisons were made with the 7040 computer. A total of 1326 correlation coefficients was used to prepare a correlation matrix (Table III) from which further comparisons and computations were made using a Monroe desk calculator.

The clustering of the units from the first matrix followed the procedure outlined by Sokal and Michner (1958). Observation showed that the highest correlation for all pairs was .973 for taxa 5 and 74 which established the first nucleus of the clustering cycle. The taxon which was next considered in this group was number 37 which had the greatest average correlation ($\bar{L}_n = .934$) with 5 and 74. However, after several trials, it was determined that a drop

TABLE II
 CLASSIFICATION OF SORGHUM BICOLOR
 FOLLOWING DE WET (1966)

Number	Taxonomy of Snowden's Taxa	Distribution
	<u>S. bicolor</u> ssp. <u>halepense</u>	
18	S. controversum	Eastern and southern India
31	S. halepense	Mediterranean to northern India
45	S. miliaceum	North West Pakistan to southern India
55	S. propinquum	Southeast Asia
	<u>S. bicolor</u> ssp. <u>bicolor</u>	
	var. <u>aethiopicum</u>	
1	S. aethiopicum	Northern Nigeria to Ethiopia
34	S. lanceolatum	Senegal to Sudan
73	S. virgatum	Egypt and Sudan
	var. <u>arundinaceum</u>	
5	S. arundinaceum	West Africa from Sierra Leone south
74	S. vogelianum	Tropical West Africa
	var. <u>verticilliflorum</u>	
11	S. brevicarinatum	Kenya and Tanzania

TABLE II (Continued)

Number	Taxonomy of Snowden's Taxa	Distribution
14	<i>S. castaneum</i>	Northeastern Congo
37	<i>S. macrochaeta</i>	Congo to Sudan
53	<i>S. panicoides</i>	Ethiopia
56	<i>S. pugionifolium</i>	Punjab of India
63	<i>S. somaliense</i>	Somaliland
70	<i>S. usambarensis</i>	Tanzania
72	<i>S. verticilliflorum</i>	Southern Ethiopia to South Africa
	var. <u>aethiopicum</u>	
	-x- race bicolor	
32	<i>S. hewisonii</i>	Sudan and Ethiopia
68	<i>S. sudanense</i>	Sudan and Egypt
	var. <u>verticilliflorum</u>	
	-x- race guinea	
6	<i>S. aterrimum</i>	West Tropical Africa and upper Nile
23	<i>S. drummondii</i>	West Tropical Africa
50	<i>S. nitens</i>	Tanzania, along river banks
	var. <u>verticilliflorum</u>	
	-x- race bicolor	
49	<i>S. niloticum</i>	Kenya to northeastern Congo and Sudan

TABLE II (Continued)

Number	Taxonomy of Snowden's Taxa	Distribution
	var. <u>verticilliflorum</u>	
	-x- race kafir	
27	S. <i>elliottii</i>	Uganda
	var. <u>bicolor</u>	
	race guinea	
17	S. <i>conspicuum</i>	Tanzania to Mosambique
28	S. <i>exertum</i>	West Tropical Africa
29	S. <i>gambicum</i>	West Tropical Africa
30	S. <i>guineense</i>	West Tropical Africa to Uganda
39	S. <i>margaretiferum</i>	Sierra Leone to north- ern Nigeria
43	S. <i>mellitum</i>	West Tropical Africa to South Africa
60	S. <i>roxburghii</i>	East Tropical Africa and India to Burma
	race kafir	
13	S. <i>caffrorum</i>	Widely distributed in Africa
15	S. <i>caudatum</i>	Widely distributed in Equatorial Africa
19	S. <i>coriaceum</i>	Tanzania to Congo
24	S. <i>dulcicaule</i>	Congo
48	S. <i>nigricans</i>	Widely distributed in Tropical Africa

TABLE II (Continued)

Number	Taxonomy of Snowden's Taxa	Distribution
	race durra	
16	<i>S. cernuum</i>	Asia Minor to India
25	<i>S. durra</i>	Northeast Africa through Arabia to India
59	<i>S. rigidum</i>	Sudan
67	<i>S. subglabrescens</i>	Northeast Africa through Arabia to India
	race bicolor	
4	<i>S. ankolib</i>	Northeast Africa
8	<i>S. basutorum</i>	South Africa
9	<i>S. bicolor</i>	Arabia to Burma
22	<i>S. dochna</i>	India to Burma
26	<i>S. elegans</i>	East Africa to West Africa
42	<i>S. melaleucum</i>	Northeast Africa
44	<i>S. membranaceum</i>	Northeast Africa, India, and China
46	<i>S. miliiforme</i>	East Africa and North- east India
47	<i>S. nervosum</i>	Eastern Asia
52	<i>S. notabile</i>	Northern Nigeria to Sudan
62	<i>S. simulans</i>	Malawii
64	<i>S. splendidum</i>	Southeast Asia

Letter Code for Table IV

Letter Table IV	Taxa Table II
A	5, 74
B	63, 73, 27
C	31, 45
D	19, 48
E	15, 52
F	42, 14
G	46, 60
H	26, 13
I	32, 68
J	47, 16
K	39, 43
L	28, 29, 62
M	8, 44
N	1, 14

TABLE IV
MATRIX 2 OF CORRELATION COEFFICIENTS

CODE	B	C	D	E	F	G	H	I	J	K	L	M	N	4	6	9	11	17	18	22	25	30	34	37	49	53	55	56	59	64	67	70	72	
A	924	765	657	711	765	630	711	926	657	810	723	783	878	754	754	701	860	728	701	701	701	657	860	940	807	807	754	913	754	834	701	887	887	
B		845	647	701	737	620	701	881	647	801	704	765	928	710	852	692	860	656	781	692	692	639	905	878	905	887	781	887	683	790	692	914	932	
C			635	655	581	540	540	729	608	653	540	612	829	533	693	640	720	533	933	667	586	480	746	720	746	746	853	853	506	720	586	526	853	
D				946	891	878	918	729	891	884	916	857	639	826	693	853	586	800	506	853	880	826	613	640	667	667	533	640	800	720	853	640	560	
E					891	864	905	713	837	897	897	816	644	800	720	800	613	800	480	880	853	880	586	667	667	693	586	693	773	720	826	667	613	
F						864	946	810	851	897	900	884	734	906	667	826	426	800	560	853	933	826	640	720	720	720	613	720	826	786	880	693	667	
G							918	657	864	836	906	802	612	826	667	853	560	826	560	853	880	880	586	613	640	667	667	693	720	773	880	613	533	
H								770	891	857	906	884	693	906	693	826	613	800	533	800	933	880	586	667	693	746	613	693	800	773	906	667	613	
I									729	829	742	857	884	826	773	773	746	720	693	773	640	800	880	800	773	720	853	746	880	746	853	853		
J										816	815	884	639	800	640	906	560	800	586	880	906	746	533	613	640	640	586	746	773	826	933	613	560	
K											908	876	739	792	738	845	711	818	604	899	845	818	738	714	765	711	631	792	845	845	765	711		
L												825	687	822	696	840	705	831	569	858	876	894	714	741	768	678	623	696	867	759	858	723	614	
M													744	872	684	845	657	818	757	792	899	738	684	738	738	738	757	738	845	873	872	711	711	
N														711	792	684	818	684	818	630	684	604	845	818	818	818	765	818	651	765	684	899	926	
4															736	842	605	736	526	736	894	789	631	710	684	709	631	684	815	815	789	657	657	
6																736	763	631	631	684	684	684	789	710	789	842	684	736	657	657	631	763	763	
9																	605	789	631	894	894	736	631	657	684	684	631	789	763	868	842	657	605	
11																		657	710	605	605	657	868	894	868	763	763	815	736	684	605	894	789	
17																			526	789	789	710	526	526	684	815	815	842	605	789	684	631	842	
18																				578	578	421	736	710	736	684	842	789	500	710	578	815	815	
22																					842	789	631	657	684	631	631	789	763	815	842	657	605	
25																						789	578	657	684	736	631	736	815	815	894	657	605	
30																							631	657	684	684	578	631	815	657	789	605	552	
34																								921	894	789	736	789	710	710	578	868	868	
37																									868	763	763	868	789	789	657	894	842	
49																										842	736	789	763	710	684	868	815	
53																											789	789	657	657	631	815	815	
55																												842	552	710	578	868	763	
56																													657	868	736	868	815	
59																														736	763	684	631	
64																															815	736	736	
67																																657	605	
70																																		894

Letter Code for Table V

Letter Table V	Taxa Table II
A'	42, 24, 25, 26, 13
B'	19, 48, 15, 52
C'	5, 74, 37
D'	31, 45, 18
E'	17, 16, 67
O'	63, 73, 27, 72, 1, 14, 70

TABLE V
MATRIX 3 OF CORRELATION COEFFICIENTS

CODE	B'	C'	D'	E'	O'	G	I	K	L	M	P	4	6	9	11	17	22	30	34	49	53	55	56	59	64
A'	921	729	585	923	716	907	801	885	913	908	809	922	696	867	560	813	849	849	458	714	750	632	732	831	808
B'		688	586	878	669	883	731	903	919	848	783	824	716	838	608	811	878	865	608	675	689	567	675	797	729
C'			747	679	919	631	916	774	743	772	811	743	743	745	891	730	690	676	904	850	797	770	904	783	824
D'				610	864	559	737	639	655	696	729	538	673	646	727	538	633	458	754	754	727	862	835	511	727
E'					669	887	750	845	851	893	738	808	646	889	592	835	875	781	565	673	646	592	754	781	835
O'						614	896	779	730	757	878	706	818	681	868	706	667	619	900	880	861	820	875	864	782
G							675	836	906	802	758	826	667	853	560	826	853	880	586	640	667	667	693	720	773
I								829	742	857	869	826	773	773	773	746	693	640	800	800	773	720	853	746	880
K									908	876	847	792	845	711	818	818	899	818	738	765	711	631	792	792	845
L										825	837	822	696	840	705	831	858	894	714	768	678	623	696	867	759
M											778	872	684	845	657	818	792	738	684	738	738	757	738	845	873
P												775	857	803	775	721	748	721	830	857	830	721	803	667	775
4													736	842	605	736	736	789	631	684	709	631	684	815	815
6														736	763	631	684	684	789	789	842	684	736	657	657
9															605	789	894	736	631	684	684	631	789	763	868
11																657	605	657	868	868	763	763	815	736	684
17																	789	842	684	631	526	526	684	815	815
22																		789	631	684	631	631	789	763	815
30																			631	684	684	578	631	815	657
34																				894	789	736	789	710	710
49																					842	736	789	763	710
53																						789	789	657	657
55																							842	552	710
56																								657	868
59																									736

in \bar{L}_n of .026 would give a satisfactory limit to the groups. Since the average correlation of number 37 with 5 and 74 was determined to be .934, and this represented a drop of .039 from the original correlation of .973, taxon 37 was not included in the first nucleus. The remainder of the pairs were treated in this same manner so that eventually the original matrix was reduced to 36 items consisting of two groups of 3 taxa each, 13 groups with 2 taxa each, and 20 separate taxa that were not included in the first clustering cycle.

For the second clustering cycle a new matrix was prepared (Table IV), again using the procedure of Sokal and Michner (1958) in which the newly formed groups were considered as single variables. Recomputation was required only for those combinations involving new groups. Correlations involving single taxa were read directly from the first matrix.

The formula for the computation of correlations between new groups was as follows:

$$r_{q.Q} = \frac{\sum qQ}{\sqrt{q + 2\Delta q} \sqrt{Q + 2\Delta Q}}$$

where $\sum qQ$ is the sum of all correlations between members of one group with members of the other group, Δq is the sum of all correlations within the first group, ΔQ is a similar sum within the second group, q is the number of taxa included in the first group and Q is the number of taxa in-

cluded in the second group. When computations for a single taxon (x) and a new group (q) are to be made, the formula was:

$$r_{x.q} = \frac{\sum r_{x.q}}{\sqrt{q + 2\Delta q}}$$

where $x.q$ is simply the sum of all coefficients of \underline{x} paired to all members of \underline{q} . Since $\sqrt{q + 2\Delta q}$ has already been calculated, this computation is quickly done.

The procedure of clustering and calculating new matrices is followed until all combinations come together at one level.

Morphology

The characters employed in this study are those that collectively served to distinguish between every one of the 52 taxa of Snowden (1936, 1955) and not those that he used to recognize the numerous varieties and forms. In addition those characters were used which experience has shown not to vary excessively within a taxon. Those characters which are strongly influenced by environment, such as detailed measurements on leaves, inflorescences, and plant height, were excluded.

Rhizomes. -- Cultivated sorghums and most weedy sorghums are non-rhizomatous and annual or weakly perennial. Well developed rhizomes characterize only *S. controversum*, *S. halepense*, *S. miliaceum*, and *S. propinquum*. Short rhi-

zomatous-like structures are sometimes observed in *S. virgatum* and collections of other weeds which have obviously introgressed with the *S. halepense* group.

Culm-node pubescence. -- Culm-nodes are either glabrous or shortly tomentose in cultivated and weed sorghums. Some truly wild species are characterized by a distinct ring of long hairs at the culm-nodes.

Inflorescence. -- Wild and weed sorghums have rather loose inflorescences, usually with spreading branches. Among the weeds the inflorescences are often large and pyramidal in shape. Most cultivated sorghums have more contracted inflorescences, primarily due to the shortening of the primary axis and branches and sometimes due to an increase in branching. The branches are often whorled in wild species but more or less alternate in the cultivated and weed complex, often with several branches at each node.

Racemes. -- The racemes consist of one or several pairs of spikelets, one of which is sessile and the other is pedicellate. In the weeds and wild species the racemes articulate readily at maturity, while the racemes are persistent in cultivated sorghums.

Spikelets. -- The sessile spikelets are always bisexual while the pedicellate spikelets are reduced to the pedicel or to empty glumes in some wild sorghums. In the weed and cultivated forms, the pedicellate spikelet is either male or neuter and usually well developed. Bisexual pedicellate spikelets are sometimes found and have even been reported to

produce seed (Celarier, 1959). The glumes are glabrous or variously hairy, less than 10-nerved in some wild species and 9 to 22-nerved in weeds and cultivated sorghums. The nerves may be obscured, except near the tip, or prominent throughout. The spikelets vary in shape from lanceolate to almost rotund and ovate, with the lower glume sometimes depressed at the middle. The seed is usually enclosed by the glume except for some cultivars where the grain is exposed by the gaping glumes. The lemmas may be bilobed or entire with a short mucro or a well developed awn.

Distribution. -- Sorghum is widely cultivated in the Old World and was introduced into the New World during historic times (Ball, 1910). Some cultivars are strictly African, and others extend from the Near East to India, while still others are confined to eastern Asia. Except for one collection from the Punjab in India, all non-rhizomatous weed sorghums are strictly African in distribution. The rhizomatous weeds extend from the Mediterranean region to the islands of Southeast Asia.

Taxonomy

The taxa studied and their classification, as suggested by de Wet (1966), are listed in Table II. The similarity coefficients of these 52 taxa (Table III), based on the 38 characters studied for each taxon were used to construct Plate I. Clustering these taxa, as described in the material and methods section, resulted in two groups of

three units each, 13 groups of two units each, and 20 unattached "species." A second matrix, using the new groups, was constructed after the similarity coefficients were calculated (Table IV). The second clustering cycle, using a drop off point of .029, resulted in the formation of six new groups, six unattached groups from the first cycle, and 14 taxa which remained single. Repeating the procedure for a third time (Table V) and using a drop off value of .033, the clustering cycle resulted in the formation of three large complexes. A fourth matrix brought the three large complexes together as illustrated in Plate I.

The three complexes (A, B, and C; Plate I) into which the taxa were arranged through clustering, coincide almost exactly with the subsection *Halepensia* Snowden and the series *Spontanea* Snowden and *Sativa* Snowden of the subsection *Arundinacea* Snowden. The only difference being that subseries *Drummondii* Snowden clustered with series *Spontanea* rather than *Sativa*. This was expected as de Wet (1966) demonstrated that subseries *Drummondii* includes a group of weeds which originated as a result of hybridization between members of the series *Spontanea* and *Sativa*.

In Plate I, complex B, made up of the weed and semiwild varieties, aethiopicum, arundinaceum, and verticilliflorum, are more closely related to complex C (var. bicolor) than to complex A (subspecies halepense). The subspecies halepense (complex A), the perennial weeds, shows about equal affinities to both complexes A and B rather than being

PLATE I

DENODOGRAM SHOWING RELATIONSHIPS
BETWEEN 52 SORGHUM TAXA

- A. Subsp. halepense
- B. Subsp. bicolor
 - var. aethiopicum
 - var. arundinaceum
 - var. verticilliflorum
- C. Subsp. bicolor
 - var. bicolor



more closely associated to one or the other.

Discussion

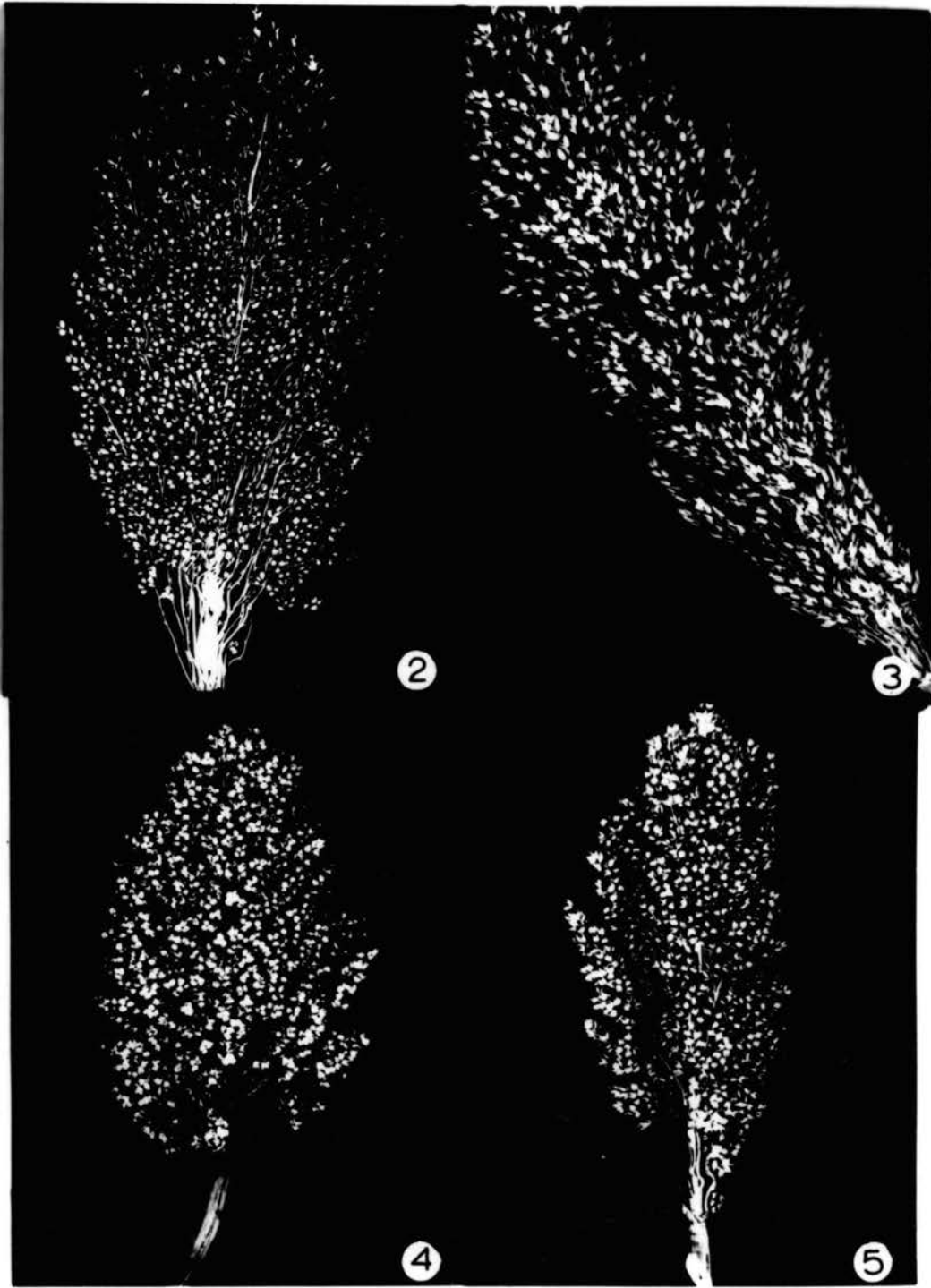
Few if any of the cultivated crops are morphologically more variable than sorghum. Selection by early farmers from among the wide range of climatic adaptation characteristic of S. bicolor made it possible for cultivated sorghum to spread across large areas of the Old World. New hybrid combinations must have been produced almost continuously as geographically isolated cultivars and wild races were brought together as a result of the migrations of man. Such an increase in morphological variation must have been greatly accelerated during the last 500 years. Cultivars and weeds from various geographical regions were introduced into cultivation in newly settled colonies, and extensive hybridization must have taken place. Introduction of sorghum to the New World probably took place during Colonial times (Ball, 1910) and was probably facilitated by the slave trade. Later systematic introduction and breeding during the last 75-80 years have provided a recent center of diversity for cultivated sorghum in the United States.

Cultivated sorghums. -- Snowden (1936) subdivided the cultivated sorghums into six subseries, Drummondii, Guineensis, Nervosa, Bicoloria, Caffra, and Durra (Plate II). In the reorganization of the cultivated and weed sorghums, de Wet (1966) transferred subseries Drummondii to the weed sorghums, combined subseries Nervosa and Bicoloria, and refer-

PLATE II
INFLORESCENCE VARIATION IN CULTIVATED SORGHUMS
(VAR. BICOLOR)

Legend:

- Fig. 2. Race bicolor
- Fig. 3. Race guinea
- Fig. 4. Race durra
- Fig. 5. Race kafir



red to all subseries as cultivated races.

The cultivated sorghums differ from the weed sorghums primarily in having tough racemes that do not articulate at maturity. A number of weeds that have racemes which articulate tardily are assumed to have arisen through hybridization between natural colonizers and cultivars. The cultivated races differ from each other primarily on the following key characters:

1. Grains enclosed by, although usually visible between, the glumes at maturity; glumes at least as long as the grain; inflorescence usually rather loose, more rarely somewhat contracted race bicolor.
1. Grains usually exposed by the gaping glumes, often longer than, and extruded from, the glumes.
 2. Sessile spikelets with the lower glume either transversely wrinkled or depressed at or about the middle, or with a strongly nerved herbaceous tip when in flower; inflorescence usually compact race durra.
 2. Sessile spikelet not as above.
 3. Inflorescence loose, more rarely somewhat compact; sessile spikelets about twice as long as broad when in flower race guinea.
 3. Inflorescence contracted and dense, very rarely somewhat looser; sessile spikelets often almost as broad as long when in flower race kafir.

Kafir corn is widely cultivated in Africa and includes

five taxa of Snowden. These taxa form two distinct groups, the closely allied *S. coriaceum* (19), *S. nigricans* (48), and *S. caudatum* (15), which are connected with the bicolor race through the African *S. notabile* (52), and *S. dulcicaule* (24), and *S. caffrorum* (13) which are allied to three other African members of bicolor, *S. ankolib* (4), *S. melaleucum* (42), and *S. elegans* (26).

Race bicolor is grown primarily in India and eastern Asia, but a few cultivars are also extensively cultivated in Africa. The African representatives are mostly allied to kafir corn. The endemic *S. basutorum* (8) from Basutoland closely resembles African members of *S. membranaceum* (44), and this complex is connected with the kafir race through *S. ankolib* (4). These bicolor sorghums resemble kafir corn in all traits except that the glumes are more distinctly nerved and might better be included in race kafir, as was suggested by de Wet (1966) for *S. basutorum*. The two remaining African representatives of the race bicolor, *S. simulans* (62) and *S. miliiforme* (46), are allied to the guinea race. Indian representatives of bicolor, *S. dochna* (22) and *S. bicolor* (9), are related and quite distinct from African and East Asian members of this race. The widely distributed South East Asian *S. splendidum* (64) is morphologically distinct from all other sorghums and, like the East Asian *S. nervosum* (47), is somewhat related to members of the durra race.

Durra corn is widely cultivated in Arabia, Asia Minor,

northeastern Africa, and northwestern India. The closest allied are *S. cernuum* (16) and *S. subglabrescens* (67), which are somewhat more distantly related to *S. durra* (25). The complex as a whole shows relationships to both race kafir and race bicolor. The endemic cultivar *S. rigidum* (59) from the Blue Nile district of the Sudan is distinctly different from the other durras.

Guinea corn is widely cultivated in Tropical West Africa and is also widespread in East Central Africa, and some members of *S. roxburghii* are grown in India. The taxa of Snowden form four morphological complexes; *S. exertum* (28) and *S. gambicum* (29), which are typically Tropical West African cultivars; *S. margaretiferum* (39) and *S. mellitum* (43), extending into the drier inland regions; *S. conspicuum* (17) and *S. guineense* (30), cultivated across equatorial Africa; and *S. roxburghii* (60), widely cultivated in tropical East Africa and India. The last mentioned group resembles race bicolor more closely than other members of guinea corn. The remaining guinea corns are distinct from all other cultivated sorghums.

Weed sorghums. -- Snowden (1955) divided the weed sorghums between subsections Halepensis (Plate III) and series Spontanea (Plate IV) of the subsection Arundinacea. Subsection Halepensis was recognized as a subspecies of *S. bicolor* by de Wet (1966), and members of Snowden's series Spontanea were reduced in status to three varieties of *S. bicolor* as follows:

PLATE III

INFLORESCENCE VARIATION IN WEED SORGHUMS

(SUBSP. HALEPENSE)

Legend:

Fig. 6. Tropical Ecotype ($2n=40$)

Fig. 7. Mediterranean Ecotype ($2n=40$)

Fig. 8. Tropical Ecotype ($2n=40$)



6



7

8

PLATE IV
INFLORESCENCE VARIATION
IN SEMI-WILD AND WEED
SORGHUMS

Legend:

Fig. 9-10. Var. arundinaceum

Fig. 11. Var. aethiopicum

Fig. 12. Var. verticilliflorum



1. Plants perennial with well developed and extensive rhizomes; racemes fragile; sessile spikelets deciduous at maturity; grains completely enclosed by the longer glumes; inflorescence loose and usually open

subsp. halepense.

1. Plants annual or weakly perennial, without rhizomes or at most with short rhizomatous-like structures; inflorescence variable.

subsp. bicolor.

2. Racemes tough; mature sessile spikelets persistent; grains enclosed by the glumes or exposed and often protruding from the gaping glumes; inflorescence loose to compact

var. bicolor

2. Racemes articulating at maturity; sessile spikelets deciduous; grain completely enclosed by the larger glumes; inflorescence loose and usually open.

3. Leaves 2-7 cm. wide and up to 75 cm. long; inflorescence loose and broad; sessile spikelets usually with a slender 5-10 mm. long awn

var. arundinaceum.

3. Leaves 0.5-3 cm. wide and up to 70 cm. long; inflorescence variable.

4. Leaves mostly about 35 cm. long; inflorescence usually somewhat contracted and narrow; sessile spikelets often with a stout, 10-30 mm. long awn

var. aethiopicum.

4. Leaves often up to 70 cm. long; inflorescence mostly loose and broad; sessile spikelets usually with a slender 10-20 mm. long awn var. verticilliflorum.

Subspecies halepense is characterized by two chromosome races, the tetraploids ($2n=40$), which extend from the Mediterranean region to southern India, and the diploid race, which is widely distributed in South East Asia. The tetraploids form two rather distinct complexes, a small Mediterranean weed with narrow leaves, *S. halepense* (31), which extends to Kashmir, and a more robust tropical weed, *S. miliaceum* (45) and *S. controversum* (18), which extends from West Pakistan to southern India. Morphological characteristics suggest that the tropical complex originated as a result of introgression with cultivated sorghums. The diploid *S. propinquum* (55) differs from the tetraploids primarily in having very small seed and in its distribution. Hackel (1885) and Koernicke (1885) suggested that cultivated sorghums must have originated from this group. However, Piper (1915a, b) correctly pointed out that the prototypes of the cultivated sorghums should be looked for among the non-rhizomatous forms.

The semiwild and weedy members of subspecies bicolor are almost as variable as the related cultivated sorghums. The distribution ranges of the three varieties recognized by de Wet (1966) overlap extensively, and they hybridize freely with each other. Furthermore, they are sympatric with dif-

ferent cultivated races in different regions, and an extensive exchange of genetic material has been going on since the crop was first domesticated. As a matter of fact, some of the taxa recognized by Snowden (1936, 1955) can be reproduced almost exactly by artificial crossings of the assumed parents (Thangam, 1963).

The closely allied *S. hewisonii* (32) and *S. sudanense* (68) exhibit characteristics of var. aethiopicum and of race bicolor. Similarly, *S. aterrimum* (6), *S. drummondii* (23), *S. elliotii* (27), *S. niloticum* (49), and *S. nitens* (50), which Snowden combined into subseries *Drummondii* of series *Sativa* represent hybrids in various combinations between cultivated sorghums and var. verticilliflorum or possibly var. arundinaceum (Table II). Typical representatives of var. arundinaceum are the closely related *S. arundinaceum* (5) and *S. vogelianum* (74), while var. aethiopicum and var. verticilliflorum are best represented only by the taxa *S. aethiopicum* (1) and *S. verticilliflorum* (72) respectively. The remaining taxa of *Spontanea* were divided among these three varieties for convenience, (Table II), but, as was considered by de Wet (1966), they probably represent complex hybrids between varieties.

Prototypes of Cultivated Sorghums

The origins of cultivated sorghums were discussed in detail by Doggett (1965) and de Wet (1966). It seems probable that sorghum domestication started in Africa and that

the races bicolor, kafir, guinea, and durra originated more or less independently in different regions. The predominantly tropical West African guinea corn probably originated from early domestication of var. arundinaceum-like colonizers. Selection from among var. verticilliflorum probably gave rise to kafir corn, and var. aethiopicum-like plants may have been the prototypes of race bicolor. The Near Eastern durra corn, which seems to have developed from local selections out of cultivars belonging to the kafir race, and some members of race bicolor probably reached India before historical times where they developed into a distinct cultivated complex.

Cultivated plants may change rapidly. Strong artificial selection and often unlimited opportunities for hybridization, with otherwise geographically and ecologically isolated forms, make it usually almost impossible to determine exactly what the prototypes of a particular cultivar looked like. In a widely cultivated, extremely variable morphologically wild-weed-cultigen complex such as sorghum, perhaps the best approach is to first look for relics of primitive cultivars. However, it is not easy to decide which morphological traits to associate with such assumed relics.

The wild trait for deciduous sessile spikelets which exist as a simple dominant to persistent spikelets in African materials seems to be just reversed in American collections where rigorous selection has favored the persistent character. This trait must have been introduced through

selection very early in the history of sorghum domestication and now characterizes all cultivars and some of their companion weeds. Transforming a loose and open inflorescence into a compact, highly productive head was a somewhat more complicated process. However, only three major characters contribute to this process: increasing the extent of primary, secondary, and higher order branching; fasciation associated with the breaking up of the node and whorl patterns; and decreasing the length of the internodes on the primary axis and all its branches. Open, rather scantily branched inflorescences may, therefore, suggest primitiveness. Domestication also brought about an increase in seed size to the point where the grains are extruded from the much shorter glumes at maturity. Relatively small seed, more or less enclosed by longer glumes, must also be regarded as primitive characters. However, seeds exposed by gaping glumes are easily accessible to birds, and selection by man against this character probably accompanied selection for yield increase in some cultivars. The ability to survive in disturbed areas without actual cultivation may also suggest primitiveness. However, as was demonstrated in other crops by Heiser (1955), Hinata and Oka (1962), and Harlan and Zohary (1966), weediness is associated with hybridization between the crop and its wild relatives and does not necessarily suggest a prototype of the cultigen.

Kafir corn does not exhibit any of the assumed primitive characteristics. A somewhat open inflorescence and ma-

ture grains which do not exceed the more or less gaping glumes in length (*S. dulcicaule*) seem to be associated with hybridization between race kafir and race bicolor rather than primitiveness. Three closely allied members of race bicolor, *S. splendidum* (64), *S. bicolor* (9), and *S. dochna* (22), are morphologically rather distinct from other members of this complex (Plate I). As a group they are extremely widely distributed, extending from eastern Central Africa through Arabia to East and South East Asia, indicating that these sorghums are probably very old. Like other members of race bicolor, they are characterized by rather open inflorescences and grains that are more or less enclosed by the glumes at maturity. From among these, perhaps, could be selected the primitive relics. However, most of the common cultivars are highly specialized, at least in some characteristics. Most members of *S. dochna* have sweet stems, and the well known broom corn also belongs with this group. As a race, the guinea corns are quite distinct from most cultivated sorghums in having rather loose inflorescences, but their large and exposed grains suggest that they are highly selected for cultivation. Nevertheless, truly primitive relics may also be looked for among this race.

Based on similarity coefficients, var. arundinaceum shows affinities with race guinea and some members of race bicolor. Collectively, var. aethiopicum is allied to both race bicolor and race durra, while the variable var. verticilliflorum shows affinities with all cultivated races.

Additional collecting in remote areas and detailed comparative morphological studies are needed before the problem of prototypes of the different cultivated races can be solved. From a taxonomic point of view the classification of de Wet (1966) still seems acceptable and practical. Morphologically it may perhaps be more correct to combine all the non-rhizomatous weeds into a single variety arundinaceum, and treat the three recognized varieties as races. However, distribution and association with particular cultivated races suggest that, from a phylogenetic point of view, var. arundinaceum, var. aethiopicum, and var. verticilliflorum are distinct taxa.

Conclusions

The application of quantitative techniques to the clarification of the affinities among the members of S. bicolor appears to be a useful tool in the biosystematics of this group. It was demonstrated that the species of Snowden could be grouped into three complexes on the basis of their similarity coefficients.

Two of the complexes which formed the subspecies bicolor of de Wet (1966) included all of Snowden's taxa belonging to his series Spontanea and series Sativa. The affinities between the two complexes were shown to be quite close, and there appears to be no justification to consider them as separate species. The two complexes were subdivided by de Wet into four varieties, var. aethiopicum, var. arundina-

ceum, var. verticilliflorum, and var. bicolor.

The third complex was composed of the four taxa, *S. halepense*, *S. miliaceum*, *S. controversum*, and *S. propinquum*, belonging to Snowden's subsection *Halepensia* which de Wet reduced to the rank of subspecies. This complex was demonstrated to have close affinities to the two complexes which made up subspecies bicolor, but the relationship was not strong enough to warrant including it in that group. However, the similarity coefficients were close enough that the formation of a separate species for this complex would not have been realistic in light of the evidence presented, and it was, therefore, maintained at its subspecific rank.

The overall relationship of all members of the three groups seems to fit quite practically into one large polytypic species, *Sorghum bicolor* (Linn.) Moench, with two subspecies, subsp. *halepense* and subsp. *bicolor*.

CHAPTER III

DISTRIBUTION OF SORGHUM BICOLOR (LINN.) MOENCH

Very little is known about the antiquity of sorghum (Doggett, 1965). This crop is absent from the ancient tombs of Egypt. Hrozny (1913) suggested that the word "dohan" in the Hebrew text of the book of Ezekiel (Chapter IV, Verse 9) may refer to sorghum; however, it is more likely that this millet was Setaria or possibly Panicum. Conclusive archeological evidence of early sorghum cultivation is absent. The often cited carved reliefs of sorghum on a limestone slab which formed part of the palace of Sennacherib at Ninevah (Piedallu, 1923) most likely does not depict sorghum, but the common reed Phragmites communis (Hall, 1928; Plates 30, 33). As archeological data and historical records of early sorghum cultivation are almost completely lacking, conclusions on the origins and domestication of this crop must, for the present, be based on comparative morphological studies correlated with present distribution patterns.

Material and Methods

The sorghums studied were from the collection grown in a uniform grass nursery at the Oklahoma State Agricultural Experiment Station and from herbarium specimens filed with

the Oklahoma State University. The maps are based on field notes of collections made by Dr. J. M. J. de Wet and Dr. Jack R. Harlan, and on material filed at the Royal Botanic Gardens at Kew, England. For the purpose of identification, the monographs of J. D. Snowden (1936, 1955) were followed exclusively.

Distribution of the Weed Sorghums

The weed sorghums were studied morphologically in detail by Snowden (1955). The four rhizomatous taxa, *S. halepense* (Linn.) Pers., *S. miliaceum* (Roxb.) Snowden, *S. controversum* (Steud.) Snowden, and *S. propinquum* (Kunth.) Hitchc., were included in the subsection *Halepensia*, while all the other wild and weedy sorghums of his section *Eusorghum* were included in series *Spontania* of subsection *Arundinacea*. The subsection *Halepensia* was reduced to a subspecies of *S. bicolor* (Linn.) Moench by de Wet (1966), who indicated that it probably did not contribute substantially to the origin of cultivated sorghum. The 17 members of the series *Spontanea* were classified by de Wet as three varieties of *S. bicolor* subsp. *bicolor*. Four of these taxa, *S. elliotii* Stapf, *S. niloticum* (Stapf ex Piper) Snowden, *S. hewisonii* (Piper) Longley, and *S. sudanense* (Piper) Stapf, were considered as hybrids between the weedy and cultivated sorghums. The remaining taxa formed three more or less distinct varieties, with *S. aethiopicum* (Hack.) Rupr. ex Stapf, *S. lanceolatum* Stapf, and *S. virgatum* forming

var. aethiopicum; *S. arundinaceum* (Desv.) Stapf and *S. vogelianum* (Piper) Stapf included in var. arundinaceum; and with the extremely variable var. verticilliflorum made up of *S. brevicarinatum* Snowden, *S. castaneum* C. E. Hubbard et Snowden, *S. macrochaeta* Snowden, *S. panicoides* Stapf, *S. pugionifolium* Snowden, *S. somaliense* Snowden, and *S. verticilliflorum* (Steud.) Stapf.

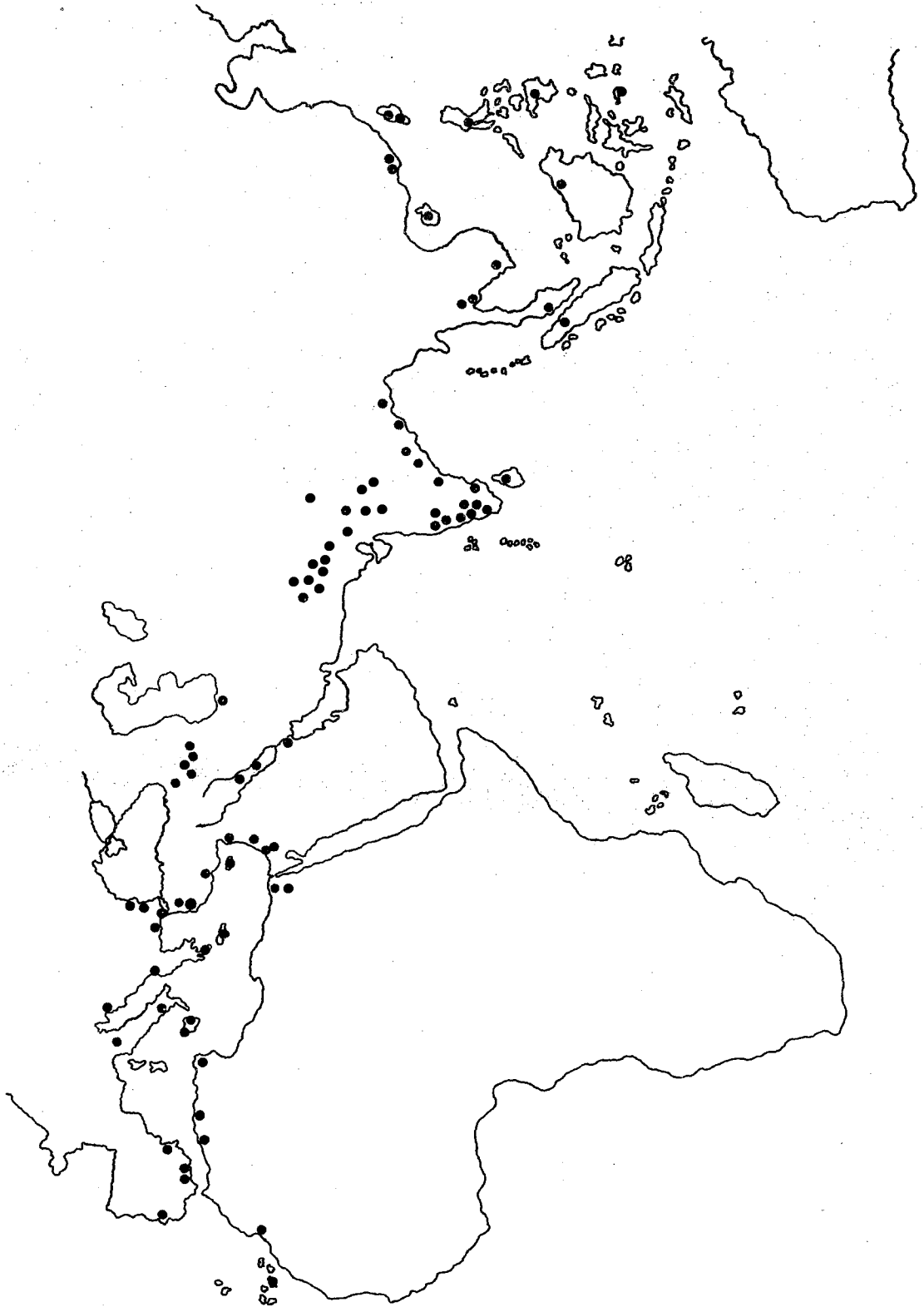
Sorghum bicolor subsp. halepense. -- This subspecies is widely distributed from the Mediterranean region to the islands of South East Asia (Plate V). It is a typical weed, usually encountered in man-made disturbed areas, but it also is adapted to naturally disturbed areas in the tropics. Two rather distinct complexes were described by de Wet (1966), a mediterranean ecotype that extends eastward to Kashmir where it is found in dry rainshadow pockets and a tropical ecotype widely distributed from Kashmir through India. The tropical, South East Asian materials differ from the more western group in having $2n=20$ rather than $2n=40$ chromosomes.

Sorghum bicolor subsp. bicolor. -- This subspecies includes the cultivated sorghums together with their companion weed and semiwild forms. The natural distribution of these semiwild and weedy sorghums is exclusively African. Snowden (1955) recorded an assumed natural collection (*S. pugionifolium*) of var. verticilliflorum from the Punjab, but it probably represents an introduction from Africa during historic times. The weed and semiwild sorghums extend al-

PLATE V

DISTRIBUTION OF SUBSPECIES HALEPENSE

Each Dot Represents a Collection



most continuously from south of the Sahara to the coast of South Africa, avoiding only true desert and dense forest.

The three varieties described by de Wet are each characterized by a more or less well defined distribution range. The common weedy sorghums of tropical and subtropical West Africa belong to var. arundinaceum (Plate VI). This variety extends from Sierra Leone, in the moist belt surrounding the tropical forest along the coast, to about 15° south latitude. It is commonly encountered around waste places, invades cultivated fields, and seems to be naturally adapted to stream banks. In the drier inland regions, extending north of the equator from northern Nigeria eastward to Somaliland and along the Nile Valley to Cairo, var. aethiopicum (Plate VII) is encountered. This variety seems to grow naturally along stream banks but is quite weedy in waste places and often invades cultivated fields. Along the western edge of its distribution, var. aethiopicum overlaps the range of var. arundinaceum, and extensive hybridization between them is obvious in northeastern Nigeria.

The most widely distributed wild-weed complex of Sorghum is that of var. verticilliflorum. Its members have an extremely wide climatic amplitude, extending almost continuously east of 20° east longitude from the South African coast to 10° North latitude (Plate VIII). Along its northern and northwestern ranges of distribution, this variety overlaps the ranges of var. aethiopicum and var. arundinaceum, and extensive hybridization takes place.

PLATE VI
DISTRIBUTION OF SUBSPECIES BICOLOR
VAR. ARUNDINACEUM

Each Dot Represents a Collection



PLATE VII
DISTRIBUTION OF SUBSPECIES BICOLOR
VAR. AETHIOPICUM

Each Dot Represents a Collection

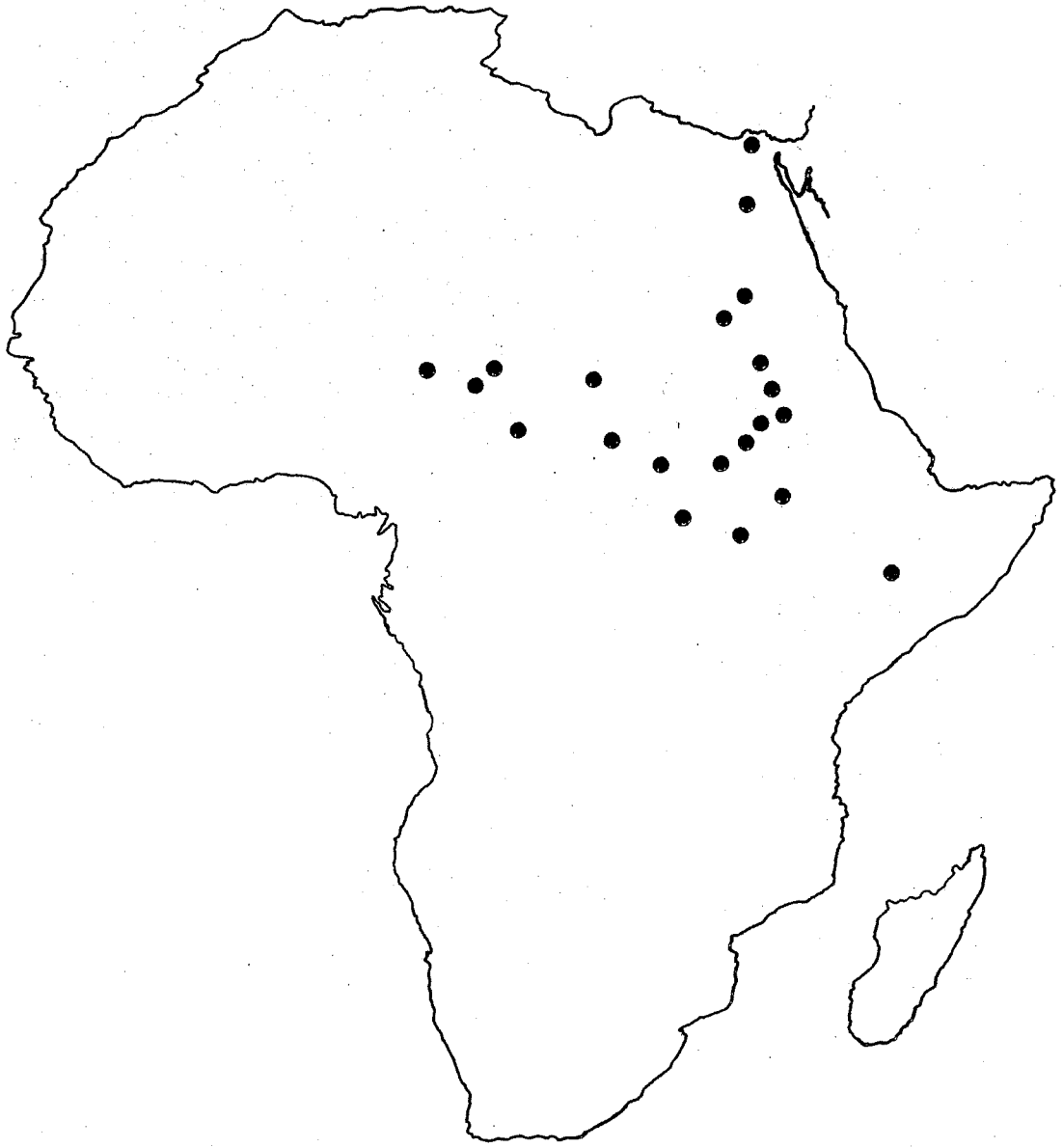


PLATE VIII

DISTRIBUTION OF SUBSPECIES BICOLOR

VAR. VERTICILLIFLORUM

Each Dot Represents a Collection



Distribution of the Cultivated Sorghums

Sorghum is now widely cultivated in the warmer parts of the Old and the New Worlds. The centers of original sorghum cultivation have been obscured by antiquity and the rapid spread of the crop by man. By the first century, it was already widely distributed in the Old World, but it reached the New World only during colonial times. Vavilov (1935) demonstrated centers of sorghum diversity in Ethiopia, India, and China.

Guinea race. -- Guinea corn is the common sorghum of Tropical West Africa (Plate IX). It is widely cultivated in the zone bordering the tropical forest areas with over 1000 mm. of rain per year (Johnson, 1958). This definitely is the center of diversity of the guinea race, with five of Snowden's seven taxa (*S. exertum*, *S. gambicum*, *S. guineense*, *S. margaretiferum*, and *S. mellitum*) confined primarily to West Tropical Africa. Along the eastern edge of the distribution range of guinea corn, hybridization with members of kafir corn gives rise to a complex that extends along eastern Africa south to Zululand (*S. conspicuum*). Selections from this complex are also widely grown in India and Burma (*S. roxburghii*). Distribution and morphological affinities suggest that guinea corn was probably enobled in Tropical West Africa through selection out of var. arundinaceum.

Kafir race. -- This is the dominant sorghum (*S. caffrorum*, *S. caudatum*, *S. coriaceum*, *S. dulcicaule*, and *S. ni-*

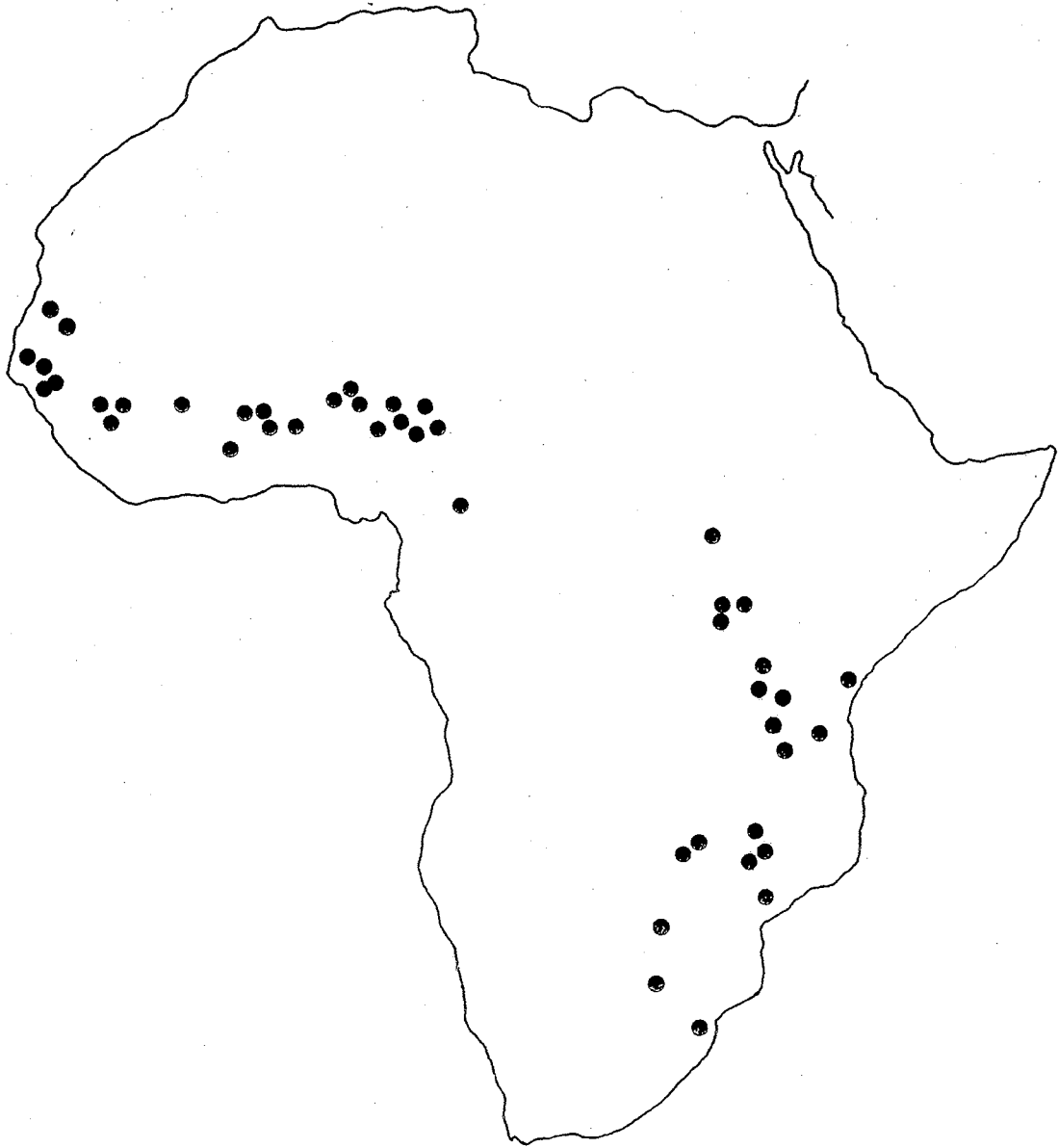
PLATE IX

DISTRIBUTION OF SUBSPECIES BICOLOR

VAR. BICOLOR

RACE GUINEA

Each Dot Represents a Collection



gricans) in Africa south of 5° north latitude and east of 20° east longitude (Plate X). This cultivated complex is sympatric with var. verticilliflorum which it resembles in many morphological characters. It is also widely cultivated in northern Nigeria, and gene flow from race kafir into guinea corn is evident as far east as northern Ghana. There is no apparent center of extreme diversity at this time, as could, perhaps, be expected. Movements of the Bantu people in historic times must have brought almost all major cultivars of kafir corn into contact with each other. Except for relatively recent introductions, it would seem that this race is not cultivated in Asia.

Durra race. -- This is the common sorghum (*S. cernuum*, *S. durra*, *S. rigidum*, and *S. subglabrescens*) of Arabia and Asia Minor (Plate XI). It is also widely cultivated in India and Burma, along the Nile Valley, and in Ethiopia. Two centers of diversity are obvious, one in the Ethiopia-Sudan region and another in India. Comparative morphological studies suggest that durra corns were introduced from East Africa into Arabia and India where selection produced morphologically distinct complexes. Material from Asia Minor combines a gene pool obtained from African, Arabian, and Indian cultivars. Sorghum cultivation was probably introduced into Egypt only after the Arab invasion. Morphologically the durra race is allied to the kafir corns rather than any of the semiwild and weedy varieties. For this reason, de Wet (1966) suggested that the durra race probably originated

PLATE X
DISTRIBUTION OF SUBSPECIES BICOLOR
VAR. BICOLOR
RACE KAFIR

Each Dot Represents a Collection



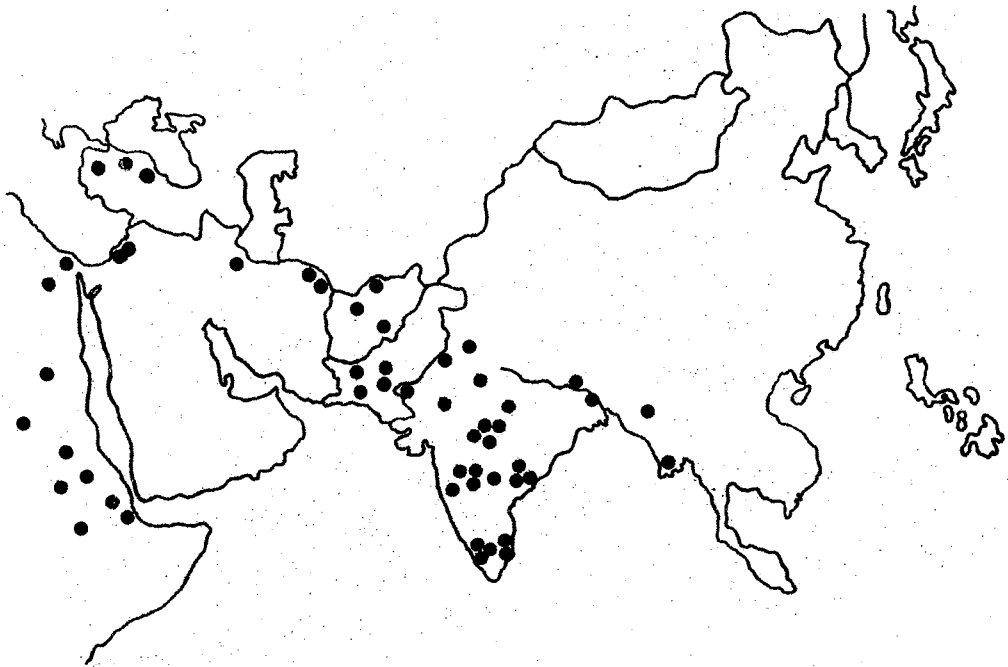
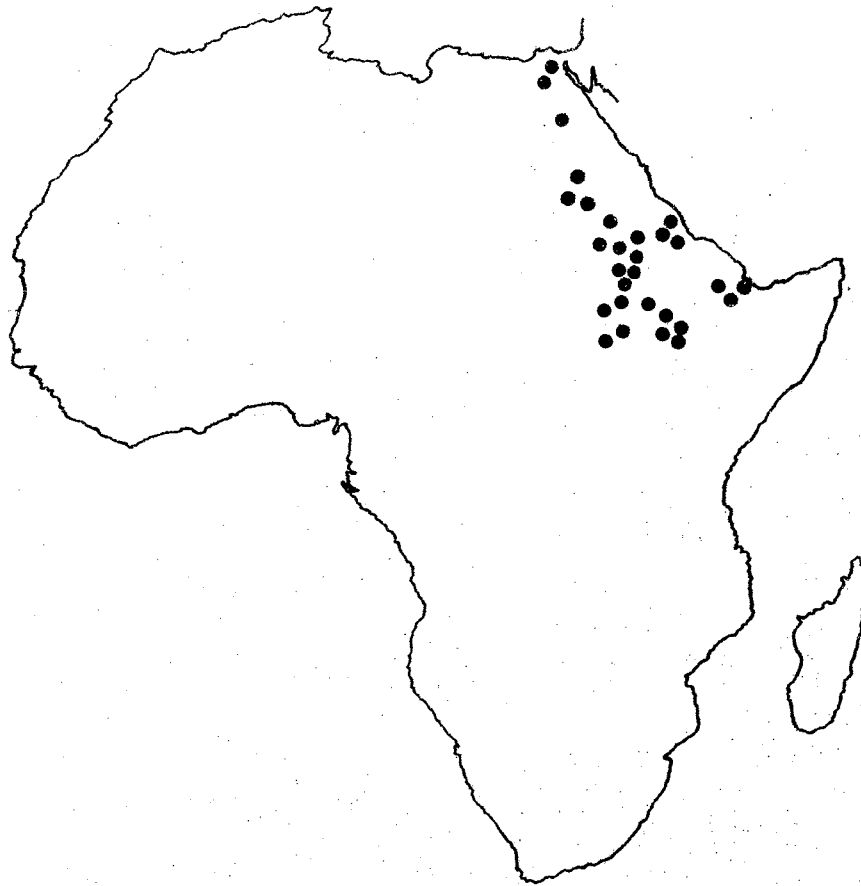
PLATE XI

DISTRIBUTION OF SUBSPECIES BICOLOR

VAR. BICOLOR

RACE DURRA

Each Dot Represents a Collection



from selection from the kafir corns, followed by absorption of some genetic material from race bicolor.

Bicolor race. -- This race has its center of diversity in Asia, but it is also widespread in Africa (Plate XII). Some cultivars are primarily African (*S. ankolib*, *S. elegans*, *S. melaleucum*, *S. notabile*, and *S. simulans*); some are confined to East Asia (*S. nervosum*); a few are grown almost exclusively in India and South East Asia (*S. dochna* and *S. splendidum*), while a number of morphologically very similar cultivars are grown in southern Africa, East Africa, Arabia, India, and China (*S. basutorum*, *S. bicolor*, *S. membranaceum*, and *S. miliiforme*). Snowden (1936) recognized two complexes, the primarily East Asian subseries *Nervosa* and the more widely distributed subseries *Bicoloria*. However, morphological studies suggested that these subseries represent cultivated complexes which probably developed originally from African selections out of a prototype resembling var. aethiopicum.

Discussion

Sorghum was probably first enobled in Africa (Burkill, 1936, 1952). Morphological data correlated with distribution suggest three more or less independent centers of domestication, each with its own distinct prototype. The fact that these centers of domestication are still preserved today is probably due to ecological and ethnic boundaries, as sterility barriers between the different cultivated races do

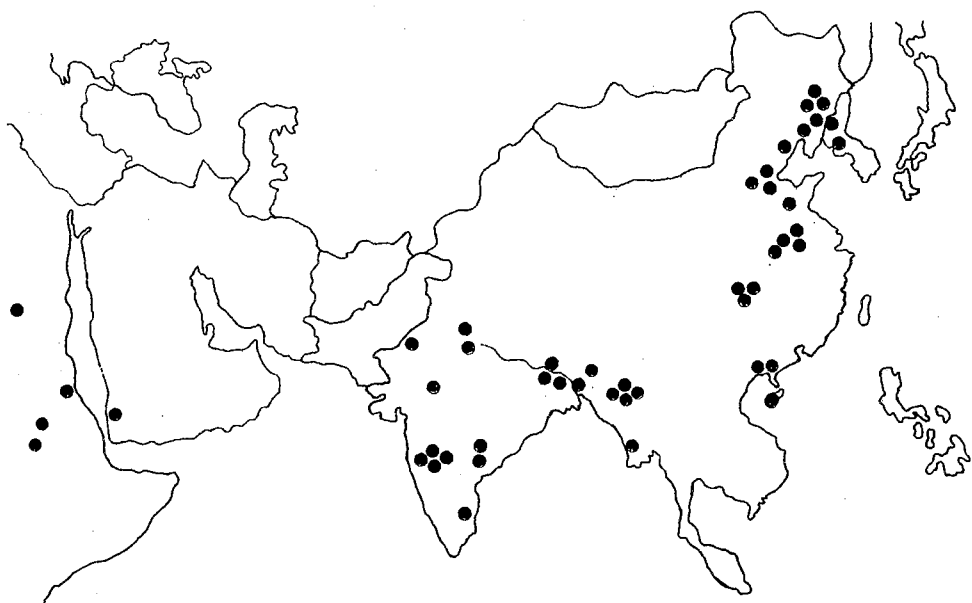
PLATE XII

DISTRIBUTION OF SUBSPECIES BICOLOR

VAR. BICOLOR

RACE BICOLOR


Each Dot Represents a Collection





not exist. The guinea corns are the sorghums of the West African Negroid people. The Bantu grow primarily kafir corn, and the races bicolor and durra are cultivated in Africa primarily by people of Semitic stock. Murdock (1959, 1960) suggested that the Mande people, around the headwaters of the Niger, independently developed agriculture and, among other crops, domesticated sorghum. However, as pointed out by Baker (1962), the practice of plant cultivation was probably introduced to West and South Africa from Ethiopia. Nevertheless, within each of these regions domestication of local native wild varieties must have played a role in the origin of cultivated sorghum. Clark (1962, 1963) and Doggett (1965) indicated that, on the basis of available archeological evidence, the knowledge of cereal cultivation was originally introduced from South West Asia to Egypt about 5000 B.C. From Egypt it spread along the Nile and possibly the Maghrib to the Ethiopian region (about 3000 B.C.) and reached Tropical West Africa sometime later.


The present distribution of native, staple, subsistence crops in Africa has been studied extensively during the last two decades (Shaw, 1947; Church, 1955; Johnson, 1958; Murdock, 1960; Wills, 1962; Portéres, 1962; and Netting, 1965). Two primary factors, rainfall and human food preferences, limit the distribution range of sorghum cultivation. The vegetation map (Plate XIII) is based on the studies of Brown (1965). Comparing vegetation types and rainfall with the distribution of sorghum (Plate XIV), it becomes obvious that


PLATE XIII
VEGETATIONAL TYPES AND ANNUAL RAINFALL
IN AFRICA


 Highveld and Highland Forest:
500-1500 mm. Rainfall

 Semiarid and Bushveld:
100-500 mm. Rainfall

 Savana and Woodland:
500-1500 mm. Rainfall

 Tropical Forest:
1500 mm. Rainfall

 Winter Rainfall

 Desert

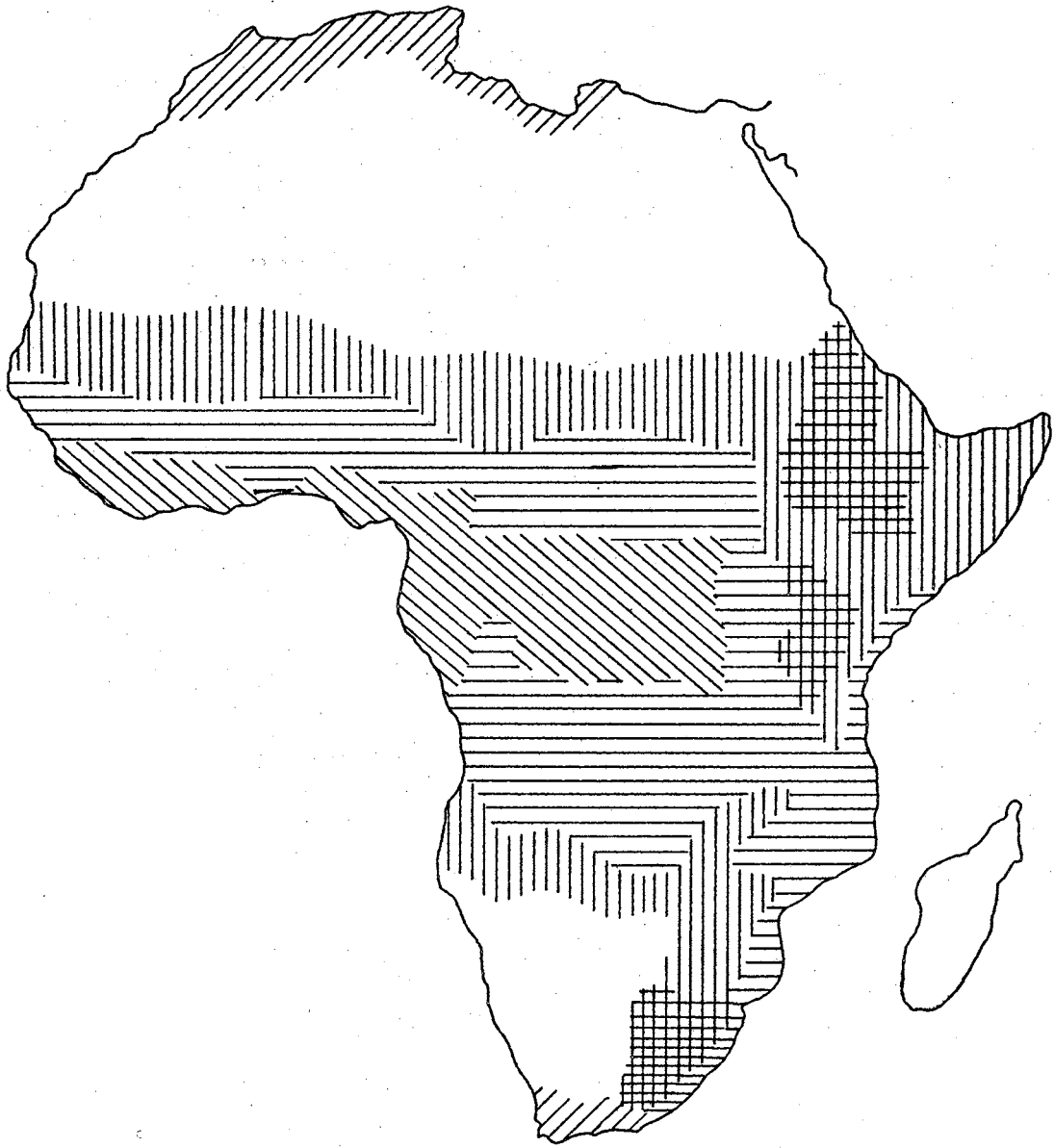


PLATE XIV
DISTRIBUTION OF RICE, ROOT CROPS,
AND SORGHUM



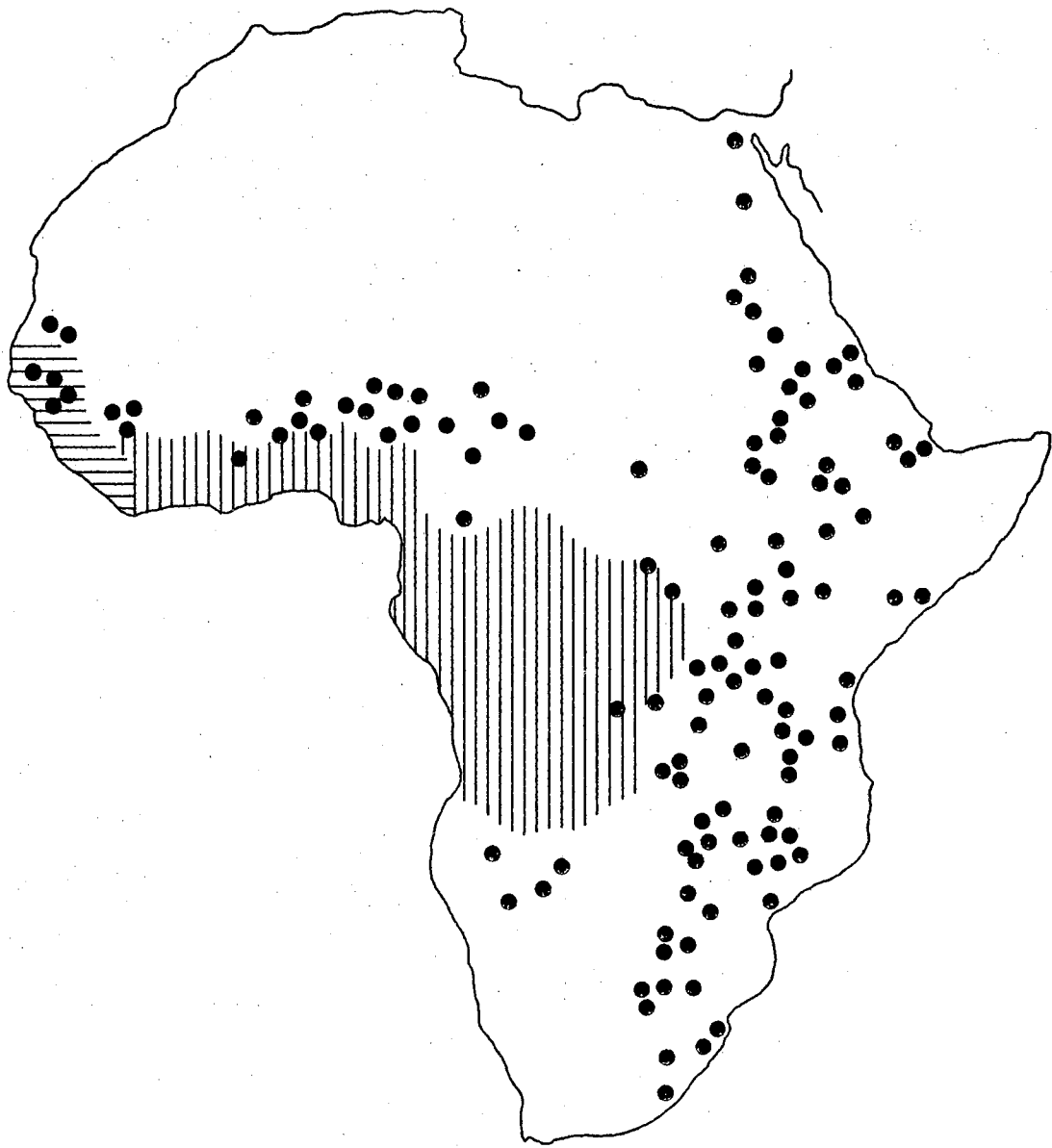
Rice



Root Crops



Sorghum



this cereal is widely cultivated in areas with a rainfall between 500 to 1500 mm. It is only in the tropical forest, the Mediterranean region, and desert areas that sorghum is not cultivated to any great extent. Wheat and barley replace sorghum in the winter rainfall areas and also in desert regions under irrigation. In the wet tropical regions of West Africa, root crops are grown extensively, being replaced at its northern limit by African rice (Oriza glaberrima). Tropical root crops extend far south into the 500 to 1500 mm. rainfall areas of the Congo and Angola (Plate XIV). The crops grown in these tropical and subtropical regions are almost all introduced; as manioc (Manihot esculenta) and sweet potato (Ipomea batatas) from the New World, taro (Colocasia antiquorum) and yam (Dioscorea esculenta) from South East Asia. Two other introduced tropical cultigens, maize (Zea mays) from the New World and banana (Musa sapientum) from South East Asia, are also widely cultivated (Murdock, 1960; Morgan, 1962). Apparently, introduced root crops made survival possible in the tropical forest, and for this reason it seems likely that the people of the drier coastal regions of the Congo and northern Angola did not cultivate the soil until these crops were introduced. For these reasons, sorghum probably never was a staple food crop in these regions.

When and how sorghum cultivation spread from Africa to the East is a matter of conjecture. Durra corn today extends almost continuously from Ethiopia along the Nile to

the Near East across India to Burma and Thailand. However, evidence of sorghum cultivation in ancient Egypt is completely lacking. This is not surprising since the Nile Valley floods during what is the normal growing season for sorghum, and it was farmed in ancient times mainly during the winter when the more preferred cereals, emmer wheat and barley, could be grown. The durra corns probably were introduced into Arabia as early as the Sabian empire and from there spread northward to the Near East along the trade routes (Burkill, 1936). Extensive sea and land trade between Africa, Arabia, India, and even China dates far back into antiquity (Hornell, 1941). It is obvious from the distribution of the bicolor sorghums that this race reached India directly from Africa, whereas durra sorghums probably were introduced into India by the sea route as well as from the Near East. Benson and Rao (1906) suggested that sorghum must have been cultivated in India at least since the first century, as it is mentioned in legends dating at least that far back in history. However, the sanskrit name for sorghum, "Yava-nala," means reed barley or simply reed grain, indicating that sorghum came to India later than barley cultivation.

The apparent absence of sorghum grains from the extensive archeological excavation of early farming sites in the Near East (Braidwood, 1958; Flannery, 1965) suggests that this cereal was introduced into this region in relatively recent times. Sorghum was probably cultivated in the Near

East at least since the first century as Pliny (70) recorded that this cereal reached Rome by the caravans from India. Bretchneider (1893) suggested that sorghum has been cultivated in China since the third century. The Chinese historian Szema Ts'ien (ca. 100 B.C.) did not mention sorghum as one of the staple grains of China (Hrozny, 1913). Distribution of bicolor sorghums suggests that this cereal was introduced into China from India rather than the Near East. However, the presence of durra corns in Korea and adjacent Chinese provinces suggests that sorghum also reached the Far East along the silk route.

Conclusions

The present day distribution of the cultivated sorghums is world wide, and the spread of the weedy sorghums has been closely tied to that of the cultivated crop. The semiwild and weedy relatives of the cultivated forms are restricted to Africa. Almost all the areas of natural distribution of the semiwild forms overlap, and ample opportunity exists for the occurrence of hybridization between them. Selection by man, from early prototypes gave rise to the cultivated forms, and continuous hybridization caused the cultivars and weeds to form a diverse morphological complex.

CHAPTER IV

CYTOLOGY OF SORGHUM BICOLOR

The cytology of the tribe Sorgheae and of the genus Sorghum was discussed in some detail by Celarier (1958a, b; 1959). Cytogenetic studies concerned with plant breeding within S. bicolor are extensive (Laubscher, 1945; Endrizzi, 1957; Kadamov, 1959; Bhatti, Endrizzi and Reeves, 1960; Magoon and Shambulingappa, 1962a, b, c; Doggett, 1964; and Pritchard, 1965). However, very little research on the origin of cultivated and weed sorghum is being done at this time. The present paper summarizes the recent cytogenetic studies on S. bicolor in the biosystematics laboratory at Oklahoma State University.

Material and Methods

The sorghum materials used in this study were from collections grown in a uniform grass nursery, described by Celarier and Harlan (1955), at the Oklahoma Experiment Station, Stillwater. Inflorescences for cytological studies were collected and fixed in Carnoy's fluid, and the developing microsporocytes were stained with aceto-carmin. The chromosome number and degree of cytological abnormalities during meiosis were determined for each accession studied.

Herbarium specimens for all materials are filed with the biosystematics laboratory at Oklahoma State University.

Results

The sorghum collection was classified according to Snowden (1936, 1955), but the data are combined in Table VI following the classification of de Wet (1966).

Sorghum bicolor subspecies halepense. -- The $2n=20$ chromosome race (*S. propinquum*) is characterized strictly by bivalent formation during microsporogenesis. The mediterranean ecotype (*S. halepense*) of the $2n=40$ chromosome race is morphologically and cytologically quite distinct from the tropical ecotype (*S. controversum* and *S. miliaecum*). The chromosomes of the narrow leaved, small mediterranean ecotype are almost strictly associated in bivalents during meiosis, while the more robust tropical ecotype is characterized by 1-5 multivalents in at least some microspore mother cells of each developing anther. However, a 20-20 chromosome distribution was normally found at anaphase (Plate XV). Morphological data indicate that this multivalent formation is the result of introgression with the cultivated sorghums.

Sorghum bicolor subspecies bicolor. -- Cultivated and weed sorghums are characterized by $2n=20$ chromosomes which almost always associated strictly into bivalents during meiosis of the microspore mother cell. Very rarely were collections obtained where one chromosome pair falls apart

TABLE VI
CYTOLOGY OF SORGHUM BICOLOR

Classification	No. Collections Studied	Diploid Chromosome Number	Plate XV Figure	Chromosome Behavior at Meiotic Metaphase
<u>S. bicolor</u>				
subsp. <u>halepense</u>	10	20	1	Regularly 10 II
	142	40	2	Often 20 II, Sometimes up to 5 IV
subsp. <u>bicolor</u>				
var. <u>aethiopicum</u>	12	20	3	Regularly 10 II
var. <u>arundinaceum</u>	35	20	4	Regularly 10 II
var. <u>verticilliflorum</u>	20	20	5	Regularly 10 II
var. <u>bicolor</u>				
race bicolor	57	20	6	Regularly 10 II
race durra	11	20	7	Regularly 10 II
race guinea	12	20	8	Regularly 10 II
race kafir	20	20	9	Regularly 10 II

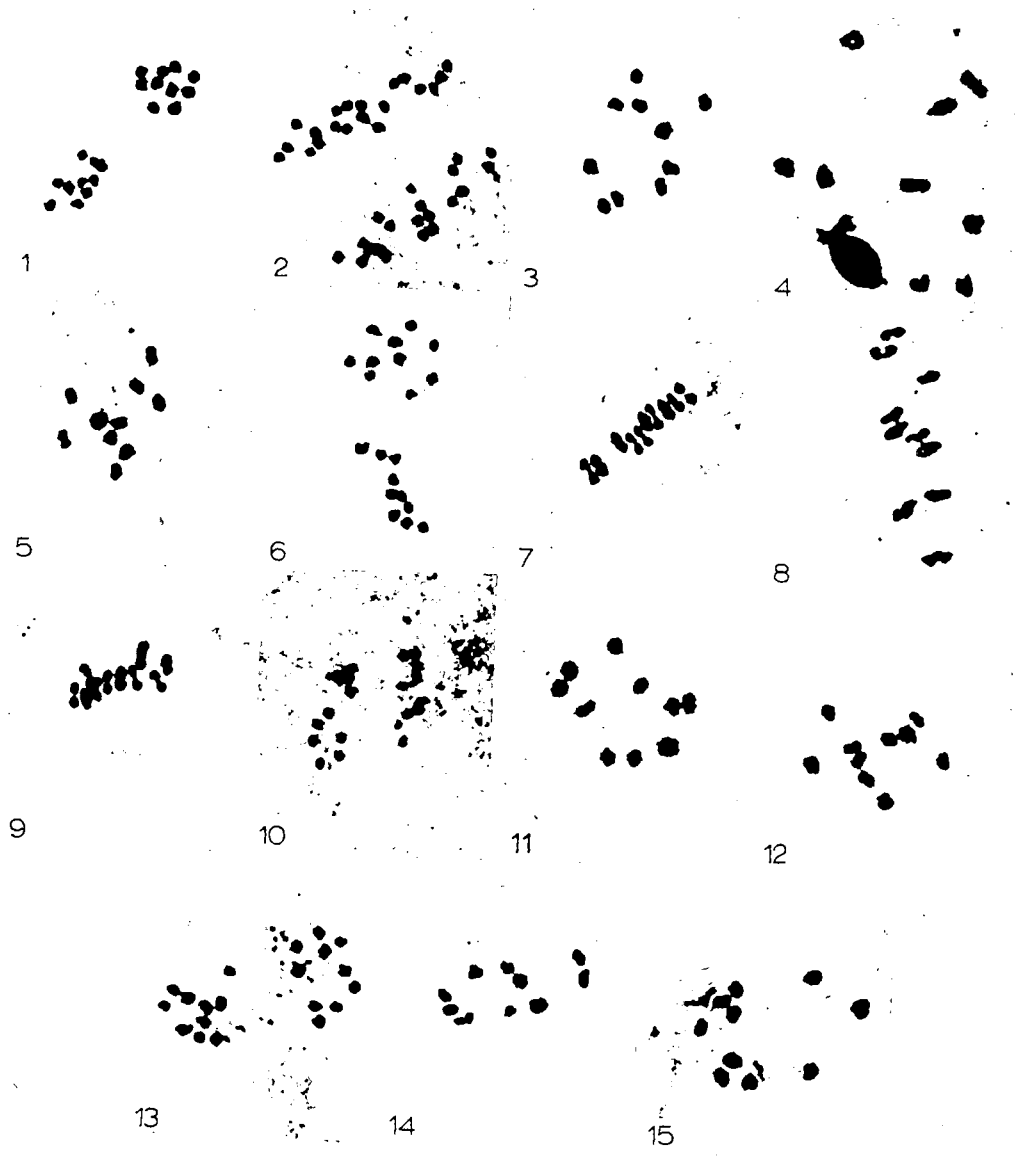
TABLE VI (Continued)

Classification	No. Collections Studied	Diploid Chromosome Number	Plate XV Figure	Chromosome Behavior at Meiotic Metaphase
<u>Hybrids</u>				
var. <u>bicolor</u> -x-				
var. <u>aethiopicum</u>	14	20	10	Regularly 10 II
var. <u>verticilliflorum</u>	30	20	11	Regularly 10 II
var. <u>arundinaceum</u>	2	20	12	Regularly 10 II
var. <u>aethiopicum</u> -x-				
var. <u>verticilliflorum</u>	1	20	13	Regularly 10 II
var. <u>arundinaceum</u> -x-				
var. <u>verticilliflorum</u>	1	20	14	Regularly 10 II
var. <u>verticilliflorum</u> -x-				
subsp. <u>halepense</u>	1	20	15	Mostly 10 II, Sometimes 2 I

PLATE XV

CYTOLOGY IN SORGHUM BICOLOR

See Table VI for Classification of Plate Figure



at late prophase, or where a single tetravalent was observed during early prophase.

Regular chromosome pairing was also observed in hybrids between cultivated sorghums (var. bicolor) and all three varieties of weed sorghums (var. aethiopicum, var. arundinaceum, and var. verticilliflorum). Similarly, hybrids between different varieties of weeds (Table VI) have the chromosomes strictly associating into bivalents. Celarier (1958a) reported complete chromosome homology between *S. propinquum* (*S. bicolor* subsp. halepense) and cultivated sorghum. Essentially strict bivalent formation was also observed in hybrids between this subspecies and *S. bicolor* var. verticilliflorum. In such hybrids one bivalent sometimes falls apart by the beginning of metaphase.

Hybrids between cultivated sorghum and $2n=40$ chromosome members of *S. bicolor* subsp. halepense have either $2n=30$ or $2n=40$ chromosomes. Both the male and female gametes of cultivated sorghum are often cytologically unreduced. The cytology of such hybrids has been discussed at length by Hadley (1953), Endrizzi (1957), Celarier (1958a), and Bennett and Merwine (1966). These studies more or less conclusively demonstrate that the $2n=40$ chromosome mediterranean ecotype of subspecies halepense originated as an autopolyploid, or, at most, as a segmental allopolyploid directly from hybridization among members of *S. bicolor*.

Discussion

Cytological data further emphasize the necessity, demonstrated by comparative morphological studies, to combine the subsections *Halepensia* and *Arundinacea* as recognized by Snowden (1935) into a single species. Essentially complete chromosome homology, or at least normal chromosome pairing without an appreciable loss in fertility, was observed in all hybrid combinations so far studied in cytogenetic detail.

The origin and extent of morphological and cytological variability within subspecies *halepense* are now being studied. Variability within subspecies *bicolor* is very closely associated with man. Natural selection and adaptation to different habitats, together with geographic, ecological, and seasonal isolation, must have played major roles in the evolution of the sorghum prototypes. However, probably for the last 3000 years, artificial selection and isolation or aggregation by man far outweighed the effects of natural evolution in *S. bicolor*.

Truly wild, diploid sorghums are characterized by $2n=10$ chromosomes (Garber, 1950). This would seem to suggest that *S. bicolor* ($2n=20$) is a tetraploid. However, no truly wild diploid or tetraploid species seem to be related to the cultivated-weed complex. Wild species differ from *S. bicolor* not only in gross morphology but also in having distinctly larger chromosomes. Selection by man probably

started from among plants which had already evolved the $2n=20$ chromosome number.

Although geographic isolation played a major role in the origin of the cultivated races of sorghum and their weed companions, obvious cytological differentiation is almost completely absent. This is probably the result of continuous, though limited, gene exchange between races due to natural overlap in distribution as well as transportation by man across geographic barriers. Laubscher (1945) and Bhatti (1963) indicated that in hybrids between various cultivars, genetic segregation is often not as complete as could be expected. This affords some degree of genetic isolation and may be due to partial autosyndetic chromosome association during gametogenesis, suggesting limited genomic differences at least between varieties. However, the extent and degree of genetic isolation within the complex species S. bicolor need to be investigated further.

Conclusion

The cytological studies of S. bicolor showed that chromosome behavior during meiosis of microsporogenesis is essentially regular. The occurrence of univalents and multivalents, in general, was rare with bivalent formation being predominant in most cases. The $2n=40$ chromosome members of subspecies halepense showed the greatest tendency toward multivalent formation with 1-5 tetravalents in some cells of the developing anthers. Celarier (1958a) suggested that the

occurrence of tetravalents and hexavalents in this group was probably the result of secondary association between bivalents. In this report, it is proposed that such chromosome association is the result of introgression between subspecies halepense and subspecies bicolor.

There is no obvious cytological differentiation between var. aethiopicum, var. arundinaceum, var. verticilliflorum, and var. bicolor, but genetic segregation is not as complete as could be expected. From this it is suggested that some degree of genetic isolation exists, but further investigation is needed in order to determine its intensity within this group.

CHAPTER V

SUMMARY

The genus Sorghum is usually subdivided into six sections, Chaetosorghum, Heterosorghum, Parasorghum, Sorghastrum, Stiposorghum, and Sorghum. However, morphological and cytological evidence suggest that only section Sorghum contributed to the origin of the cultivars.

Following the classification of de Wet (1966), the 52 taxa of Snowden (1936, 1955) were shown to be a single biological species, S. bicolor (Linn.) Moench, and that this species could be subdivided into two subspecies, S. bicolor subsp. bicolor and S. bicolor subsp. halepense. The morphologically extremely variable S. bicolor subsp. bicolor is composed of var. bicolor, which includes all of the cultivars, and three weed and semiwild non-rhizomatous varieties, var. aethiopicum, var. arundinaceum, and var. verticilliflorum. Morphological and cytological data suggested that members of subspecies halepense probably originated from hybridization between members of var. aethiopicum and var. arundinaceum, and that subspecies halepense did not contribute toward the origin of cultivated sorghum.

The cultivars of S. bicolor were subdivided into four races: bicolor, kafir, durra, and guinea. Morphological

data and patterns of distribution suggested that the cultivars of race kafir could have originated from var. verticilliflorum-like progenitors, that race guinea could have originated from var. arundinaceum-like ancestors, that race bicolor could have originated from var. aethiopicum-like natural colonizers, and that race durra represents a later selection out of hybrids between race bicolor and race kafir.

Archeological and historical data indicated that sorghum was first cultivated in Africa, probably in present day Ethiopia, some 5000 years ago. The idea of cultivation spread from Ethiopia slowly south and west across Africa, and semi-domesticated races seem to have crossed with the Ethiopian cultivars to form the widely distributed sorghums of West Africa and South Africa. The cultivated race bicolor was transported from the northeast coast of Africa, very likely by boat to Arabia and India. From either or both of these regions, sorghum cultivation soon spread to Assyria and China. At a somewhat later period, cultivars of race durra were introduced to Egypt from the Near East.

LITERATURE CITED

- Ananthasayana, K., P. Chandrasekan, and B. W. X. Ponnaiya. 1964. Studies on some interspecific hybrids in the genus Sorghum. Madras Agri. J. 51: 355.
- Baker, H. G. 1962. Comments on the thesis that there was a major centre of plant domestication near the headwaters of the river Niger. J. Afr. Hist. 3: 229-233.
- Ball, C. R. 1910. The history and distribution of Sorghum. U. S. D. A. Bur. Plant Ind. Bull. 175.
- Bennett, H. W. and N. C. Merwine. 1966. Meiotic behavior of a Hodo Sorgo x Johnsongrass hybrid. Crop. Sci. 6: 127-131.
- Benson, C. and C. K. Subba Rao. 1906. The great millet or Sorghum in Madras. Bull. Dept. Agri. Madras 3(55): 64-91.
- Bhatti, A. G. 1963. Genetic barriers in Sorghum species. W. Pak. J. Agri. Res. 1: 116-139.
- Bhatti, A. G., J. E. Endrizzi, and R. G. Reeves. 1960. Origin of Johnsongrass. Heredity 51: 107-110.
- Braidwood, R. J. 1958. Near Eastern Prehistory. Science 127: 1419-1430.
- Bretchneider, E. 1893. Botanicum Sinicum II. J. Royal Asiatic Soc. China.
- Brown, Leslie. 1965. Africa, a Natural History. Random House, N. Y.
- Burkill, I. H. 1936. The races of Sorghum. Kew Bull. 26: 112-119.
- Burkill, I. H. 1952. Habits of man and origins of the cultivated plants of the old world. Proc. Linn. Soc. Lond. 164: 12-42.
- Celarier, R. P. 1956. Additional evidence for five as the basic chromosome number of the Andropogoneae. Rhodora 58: 135-143.

- Celarier, R. P. 1958a. Cytotaxonomic notes on the subsection Halepense of the genus Sorghum. Bull. Torrey Bot. Club 85: 49-62.
- Celarier, R. P. 1958b. Cytotaxonomy of the Andropogoneae III. Subtribe Sorghae, Genus Sorghum. Cytologia 23(4): 395-418.
- Celarier, R. P. 1959. Cytotaxonomy of the Andropogoneae IV. Subtribe Sorghae. Cytologia 24(3): 285-303.
- Celarier, R. P. and J. R. Harlan. 1955. An Andropogoneae garden in Oklahoma. Taxon 5: 183-186.
- Chheda, H. R. and J. R. Harlan. 1962. Mode of chromosome association in Bothriochloa hybrids. Caryologia 15: 461-476.
- Church, R. J. H. 1955. West Africa. A Study of the Environment and of Man's Use of It. John Wiley and Sons Inc., N. Y.
- Clark, J. D. 1962. The spread of food production in sub-Saharan Africa. J. Afr. Hist. 3: 211-228.
- Clayton, W. D. 1961. Proposal to conserve the generic name Sorghum Moench. (Gramineae) versus Sorghum Adans. (Gramineae). Taxon 10(8): 242-243.
- Darlington, C. D. 1937. Recent Advances in Cytology. 2nd. ed. Blakiston, Phil.
- Darlington, C. D. 1958. The Evolution of Genetic Systems. 2nd. ed. Basic Books, N. Y.
- de Wet, J. M. J. 1966. The origin of Sorghum bicolor. I. Morphological variation. Bot. Gaz. (In Press).
- Doggett, H. 1964. Fertility improvement in autotetraploid Sorghum. 1. Cultivated autotetraploids. Heredity 19: 403-417.
- Doggett, H. 1965. The development of cultivated Sorghums. Crop Plant Evolution. Sir Joseph Hutchinson, Ed. Cambridge Univ. Press, London.
- Durra, B. N. and G. L. Stebbins. 1952. A polyhaploid obtained from a hybrid derivative of S. halepense -x- S. vulgare var. sudanense. Genetics 37: 369-374.
- Endrizzi, J. E. 1957. Cytological studies of some species and hybrids in the Eusorghums. Bot. Gaz. 119: 1-10.

- Endrizzi, J. E. and D. T. Morgan. 1955. Chromosomal interchanges and evidence for duplication in haploid Sorghum vulgare. J. Heredity ⁴⁶66: 201-208.
- Ehrendorfer, F. 1959. Differentiation-hybridization cycles and polyploidy in Achillea. Cold Spring Harbor Symposium 24: 141-152.
- Flannery, K. V. 1965. The ecology of early food production in Mesopotamia. Science 147: 1247-1256.
- Garber, E. D. 1950. Cytotaxonomic studies in the genus Sorghum. Univ. Calif. Publ. Bot. 23: 283-361.
- Hackel, E. 1885. Die kultivirten Sorghum-Formen und ihre Abstammung. Engl. Bot. Jahrb. 7: 115-126.
- Hackel, E. 1889. Andropogoneae. In De Candolle; Monographiae phanerogamarum. 6: 499-520.
- Hadley, H. H. 1953. Cytological relationships between Sorghum vulgare and Sorghum halepense. Agron. J. 45: 139-143.
- Hall, H. R. 1928. Babylonian and Assyrian Sculpture in the British Museum. Les Editions G. van Oest, Paris and Brussels.
- Harlan, J. R. 1965. The possible role of weed races in the evolution of cultivated plants. Euphytica 14: 173-176.
- Harlan, J. R. and D. Zohary. 1966. Distribution of the wild wheats and barley. Science (In Press).
- Heiser, C. B. 1955. The origin and development of the cultivated sunflower. Amer. Bio. Teacher 17: 162-167.
- Hinata, K. and H. I. Oka. 1962. A survey of Oryza perennis and O. sativa. Jap. J. Gen. 37: 314-328.
- Hornell, J. 1941. Sea trade in early times. Antiquity 15: 233-256.
- Hrozny, B. 1913. Ancient history of Western Asia, India, and Crete. Philosophical Library, N. Y.
- Johnson, B. F. 1958. The Staple Food Economics of Western Tropical Africa. Stanford Univ. Press.
- Kadamov, S. K. 1959. Hybridization of Sorghum species. Bull. Sci. Tech. Inf. Uzbek. Sci. Ser. 4: 3-10 (Abst.)

- Kidd, H. J. 1956. The morphology of the panicle in cultivated Sorghums. Ph.D. Thesis (Unpublished) Washington Univ., St. Louis.
- Koernicke, F. 1885. Andropogon Sorghum Brot. Die mohrhirse. In Koernicke, F. and H. Werner; Handbuch des Getreidebaues 1: 294-315.
- Krishnaswamy, N., V. S. Raman, and P. Chandrasekhran. 1956. An interspecific hybrid of grain sorghum and Johnson-grass. *Curr. Sci.* 25: 195-197.
- Laubscher, F. X. 1945. A genetic study of Sorghum relationships. *So. Afr. Dept. Agri. Sci.* 6: 76-79.
- Liang, G. H. L. and A. J. Casady. 1966. Quantitative presentation of the systematic relationships among twenty-one Sorghum species. *Crop Sci.* 6: 76-79.
- Magoon, M. L., P. L. Mancham, and M. S. Ramana. 1964. Cytological and morphological studies in the genus Sorghum. *Cytologia* 29: 42-60.
- Magoon, M. L. and M. S. Ramana. 1961. Cytology of some Eusorghums. *Genet. Iber.* 13: 129-148.
- Magoon, M. L. and K. G. Shambulingappa. 1962a. Studies on polyploids in the genus Sorghum. *Genet. Iber.* 14: 105-124.
- Magoon, M. L. and K. G. Shambulingappa. 1962b. Cytomorphological studies on some species and species hybrids in the genus Sorghum. *Züchter* 32: 317-324.
- Magoon, M. L. and K. G. Shambulingappa. 1962c. Cytological and morphological studies on some interspecific hybrids in Eusorghums. *Zeitschr. Vererbungslehre* 93: 14-24.
- Magoon, M. L., K. G. Shambulingappa, and M. S. Ramana. 1961. Chromosome morphology in meiosis in some Eusorghums. *Cytologia* 26: 236-252.
- Morgan, W. B. 1962. The forest and agriculture in West Africa. *J. Afr. Hist.* 3: 235-239.
- Muller, H. J. 1922. Variation due to change in individual gene. *Amer. Nat.* 56: 32-50.
- Murdock, G. P. 1954. Africa - Its People and Their Culture History. McGraw-Hill, N. Y.

- Murdock, G. P. 1960. Staple subsistence crops of Africa. *Geogr. Rev.* 50: 521-540.
- Netting, R. M. 1965. Heritage of survival. *Nat. Hist.* 74: 14-21.
- Piedallu, A. 1923. *Le Sorgo, son Historie, ses applications.* Challamel, Paris.
- Piper, L. V. 1915a. Andropogon halepense and Andropogon sorghum. *Proc. Biol. Soc. Wash.* 28: 25-44.
- Piper, L. V. 1915b. The prototype of cultivated sorghums. *J. Amer. Soc. Agron.* 7: 109-117.
- Plinius, Caius Secundus. 60-70 (approx.) *Historiae naturalis.* ed. Harduinus, libre XXXVII, 2, 105.
- Portéres, R. 1962. Berceaux agricoles primaires sur le continent africain. *J. Afr. Hist.* 3: 195-210.
- Pritchard, A. J. 1965. Cytological and genetical studies on hybrids between Sorghum alnum Parodi ($2n=40$) and some diploid ($2n=20$) species of Sorghum. *Euphytica* 14: 307-314.
- Riley, R., J. Unrau, and V. Chapman. 1958. Evidence on the origin of the B genome in wheat. *J. Hered.* 49: 91-98.
- Riley, R., G. Kimber, and V. Chapman. 1961. Origin of genetic control of diploid-like behavior of polyploid wheat. *J. Heredity* 52: 22-25.
- Satish Rao, C., B. W. X. Ponnaiya, and V. S. Raman. 1964. Studies on the morphology and fertility of male-sterile kafir-grain Sorghum hybrids and their progeny. *Madras Agri. J.* 51: 355.
- Sethupathy, R., P. Chandrasekaran, and B. W. X. Ponnaiya. 1964. Studies on some interspecific hybrids in Eusorghum. *Madras Agri. J.* 51: 356.
- Shambulingappa, K. G. and M. L. Magoon. 1953. Cytomorphological studies in the genus Sorghum. *Indian J. Genet.* 23: 275-289.
- Sharma, A. K. and D. Bhattacharjee. 1957. Chromosome studies in Sorghum 1. *Cytologia* 22: 287-311.
- Shaw, H. K. 1947. The vegetation of Angola. *J. Ecol.* 35: 23-48.

- Sheals, J. G. 1965. The application of computer techniques to Acarine taxonomy: a preliminary examination with species of the Hypoaspis - Androlaelaps complex (Acarina). Proc. Linn. Soc. Lond. 176: 11-21.
- Snowden, J. D. 1935. A classification of the cultivated Sorghums. Kew Bull. No. 1935: 221-254.
- Snowden, J. D. 1936. The Cultivated Races of Sorghum. Adlard and Son, London.
- Snowden, J. D. 1955. The wild fodder Sorghums of the section Eusorghum. J. Linn. Soc. Lond. 55: 191-260.
- Sokal, R. R. and C. D. Michner. 1958. A statistical method for evaluating systematic relationships. Univ. of Kansas Sci. Bull. 38: 1409-1438.
- Sokal, R. R. and P. H. A. Sneath. 1963. Principles of Numerical Taxonomy. W. H. Freeman, San Francisco.
- Stapf, O. 1917. Sorghum. In Prain; Fl. Trop. Afr. 9: 104-154.
- Stebbins, G. L. 1950. Variation and Evolution in Plants. Columbia Univ. Press, N. Y.
- Stephens, J. C. and K. F. Schertz. 1965. Asynapsis and its inheritance in Sorghum vulgare Pers. Crop. Sci. 5: 337-339.
- Thangam, M. S. 1963. Studies on the progenies of Sorghum aethiopicum crossed with cultivated Sorghum. Madras Agri. J. 50: 332-333.
- Thangam, M. S., B. W. X. Ponnaiya, and V. S. Raman. 1964. Interspecific hybridization in Eusorghum with special reference to the cross S. halepense (2n=40) -x- S. durra (2n=20). Madras Agri. J. 51: 353-354.
- Vavilov, N. I. 1935. The origin, variation, immunity, and breeding of cultivated plants. (Translated by K. S. Chester. 1950) Chron. Bot. 13: 1-364.
- Vinall, H. N., J. C. Stephens, and J. H. Martin. 1936. Identification, history, and distribution of common Sorghum varieties. U. S. D. A. Tech. Bull. 506.
- Wills, J. B. (Ed.) 1962. Agriculture and Land Use in Ghana. Oxford Univ. Press, London.
- Zohary, D. 1960. Studies on the origin of cultivated barley. Bull. Res. Council Israel 9d: 21-42.

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