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THE EFFECT OF SORGHUM KERNEL SMUTS ON THE DEVELOPMENT OF THE HOST[1]

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INTRODUCTION

Covered kernel smut, caused by *Sphacelotheca sorghi* (Lk.) Clint., is the most common and destructive disease of the sorghum crop in the United States. Although the loose kernel smut, caused by *Sphacelotheca cruenta* (Kühn) Potter, occurs occasionally in the United States, it is of less economic importance. Preventive measures for these smuts are well known, and no other cereal smuts may be more easily and economically controlled by means of specifics than these two. It is common knowledge that cereal plants affected with systemic smuts do not develop normally, but little is known of the cause of the abnormalities.

The purpose of the present study was to learn what morphologic changes occur in the organs of sorghum plants when attacked by these kernel smuts. The investigations at Manhattan, Kans., begun in 1929, were continued over a period of 7 crop years, during which great variations of temperature and precipitation occurred. Not all phases of the work, however, were carried on during the entire period. The present report covers the following phases of the work: (1) A study to determine the effect of *Sphacelotheca sorghi* and *S. cruenta* on the height of plant, diameter of stalk, and width of leaf of sorghum varieties; (2) a study of several varieties of sorghum infected with the two species of kernel smut to determine the parts of the host that are morphologically changed and to locate the regions responsible for a reduction in height; (3) a study of the number of nodes and tillers which occur in smutted and unsmutted plants of White Durra C. I. 81, Manchu Brown kaoliang C. I. 171, Evergeen Dwarf broomcorn C. I. 822, and Acme broomcorn C. I. 243; (4) a study of node differentiation in smut-infected plants; (5) observations on the vegetative proliferation of sorghum panicles following infection by *S. cruenta;* and (6) a study to obtain further information on the relation between size and shape of smut sori produced by the different physiologic races of *S. cruenta* on different varieties of sorghum.

REVIEW OF LITERATURE

In wheat affected with bunt, slight differences in height between diseased and normal plants, as well as other abnormalities, have been observed by various investigators (*1, 5, 8, 9, 16, 20, 23*),[2] but the cause of the difference in height between smutted and unsmutted plants has not been definitely determined. In recent years a physiologic race of *Tilletia tritici* has been described which produces a marked dwarfing

[1] Received for publication March 16, 1942. Contribution No. 406, Department of Botany, Kansas Agricultural Experiment Station.

[2] Italic numbers in parentheses refer to Literature Cited, p. 164.

of the wheat plant, but here again no report has been made on the cause of the reduction in height (*10, 24*). Viennot-Bourgin (*22*) found that in wheat bunt, a reduction in height of culms was due not so much to a shortening of the internodes as to a decrease in their number. Barrus (*2*) observed that wheat plants affected with bunt were shorter than healthy plants because of the general decrease in the length of the internodes, all internodes sharing equally in the decrease. He further observed that—

> In the case of wheat plants affected by loose smut where mature culms are shorter than healthy ones, the difference is due to the failure of the upper internode of affected plants to develop as much as healthy ones do.

It is known that the culms of smutted oat plants are frequently shorter than those of unsmutted plants of the same variety.

The literature bearing on the morphologic changes in the host that cause the reduction in height of smutted plants is not extensive, and the reports presented to date have been based upon observations rather than upon detailed studies. This is especially true of the kernel smuts of sorghum, *Sphacelotheca sorghi* and *S. cruenta* (*3, 4*).

Reed and Melchers (*19*) found that plants infected with *Sphacelotheca sorghi* headed as soon as normal plants and were essentially as tall as normal plants. On the other hand, plants attacked by *S. cruenta* were shorter than normal ones, headed earlier, and frequently produced more tillers. Infected plants also showed an enlargement of glumes and developed slenderer heads.

No detailed review of literature on the taxonomy or life histories of the two sorghum kernel smuts seems necessary; they are very similar (*19*). Primary infection occurs during the early growth of the sorghum seedlings, generally from germinating chlamydospores which adhere to the seed. After infection the mycelium invades the meristematic tissue of the seedling, keeping pace with the growing point. At flowering time and as soon as the sorghum heads emerge from the sheath, affected ovaries in the florets are easily recognized by the white smut galls (sori) and the absence of normal stamens.

METHODS AND MATERIALS

The seed of the sorghum varieties was obtained from self-pollinated heads and was considered pure for the variety. The smut was prepared and applied to the seed which was then planted and cultural crop practices were followed as described by Melchers (*12, 13*). Smutted and unsmutted plants grew from seed of the several varieties used in these investigations, and notes and measurements were taken when the plants had made their maximum growth. Fifteen smutted plants of each variety, or as many more as were available, were measured each year. No difficulty was encountered in measuring 15 or more unsmutted plants in the same row in which the smutted individuals grew. These served as check or control plants.

The height measurement was taken from the tip of the panicle to the base of the plant at the soil line. The diameter of the stalk was obtained just below the second leaf from the top of the plant by means of calipers. The diameter of the stalk in these studies includes the thickness of the stalk and leaf sheath. Leaf width was measured at its widest point and the second leaf from the top was always chosen for the measurement.

The varieties used belong to the main groups of sorghum; that is, forage, grain sorghums, and broomcorn. The experimental material consisted of such varieties and hybrids as Red Amber, Red Amber hybrids, and Kansas Orange among the sorgos; feterita, feterita hybrids, White Yolo, milos, Blackhull kafir, White Durra, and kafir × milo hybrid K. B. 2561 among the grain sorghums; Darso, Weskan, Schrock, Manchu Brown kaoliang, and Grohoma among the miscellaneous sorghums; and Acme and Evergreen Dwarf broomcorn.

The inoculum of *S. sorghi* consisted of a composite, in equal amounts, of three physiologic races (p. r. [3] 1, 2, and 3) of the organism known to attack the kafir, milo, and feterita groups, while the *S. cruenta* inoculum consisted of p. r. 1 and 2 used separately. These physiologic races have already been described (*12*, *15*).

EXPERIMENTAL RESULTS

EFFECT OF SMUT INFECTION ON HEIGHT OF PLANT, DIAMETER OF STALK, AND WIDTH OF LEAF

Although *Sphacelotheca sorghi* and *S. cruenta* are closely related, they react differently on the same variety of sorghum and vary in general appearance (*14*, *19*). Preliminary studies to determine the morphologic changes that occur in sorghum plants attacked by *S. cruenta* were begun in 1929. Two varieties of sorghum were of special interest that year because smutted plants were decidedly shorter than unsmutted plants. Measurements showed that the smutted plants of Manchu Brown kaoliang C. I. 171 had a mean decrease in plant height, stalk diameter, and leaf width of 54.2, 42.9, and 65.9 percent, respectively. Smutted plants of Acme broomcorn C. I. 243 had a mean decrease in plant height, stalk diameter, and leaf width of 45.0, 42.9, and 47.4 percent, respectively. These studies were then enlarged to include a representative group of 25 varieties of sorghum and both *S. cruenta* and *S. sorghi* were used. Four years' data obtained in 1931, 1932, 1935, and 1936 were averaged for each variety as shown in table 1.

There was some variability in height reduction among varieties of plants infected with *S. sorghi*, although the average reduction for the varieties taken as a group was only 1.9 percent. That *S. sorghi* does not greatly reduce the height of sorghum plants confirms the results obtained in other studies (*17*, *19*). In this connection Tyler (*21*) has shown that F_1 chlamydospore lines of *S. sorghi* may vary in respect to their ability to stunt sorghum during the parasitic phase. Acme broomcorn, kafir×feterita, Kansas Orange, Manchu Brown kaoliang, and Red Leaf feterita each showed a reduction in height of more than 10 percent, while the smutted plants of Weskan, Premo, Early White milo, kafir × milo 26–3–1–1, and Blackhull were taller than the unsmutted plants (table 1).

Both physiologic races of *S. cruenta* materially and consistently reduced the height of infected plants (table 1). Among the varieties tested this reduction ranged from a few to 38 percent for *S. cruenta* p. r. 1 and to 55 percent for *S. cruenta* p. r. 2, with the average for all the varieties for both physiologic races close to 18 percent (table 1).

[3] Physiologic race hereafter will be designated by the abbreviation p. r.

TABLE 1.—*The effect of sorghum kernel smut infection on the height, diameter of stalk, and width of leaf of sorghum plants, Manhattan, Kans., 1931, 1932, 1935, and 1936* [1]

Variety	Accession No.[2]	Average deviation from normal plant of plants attacked by—								
		Sphacelotheca sorghi p. r.[3] 1–3			*Sphacelotheca cruenta* p. r. 1			*Sphacelotheca cruenta* p. r. 2		
		Height of plant	Diameter of stalk	Width of leaf	Height of plant	Diameter of stalk	Width of leaf	Height of plant	Diameter of stalk	Width of leaf
		Pct.	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
Acme broomcorn	C. I. 243	−14.7	−21.6	−12.5	−38.3	−58.5	−64.4	−37.3	−33.8	−33.9
Blackhull	K. B. 3047	+5.4	−17.5	−15.3	−8.6	−36.6	−17.6	−9.9	−27.3	−15.6
Darso	C. I. 615	−7.7	−21.9	−14.6	−8.2	−25.2	−15.9	−13.9	−19.7	−12.3
Dwarf Shantung kaoliang	C. I. 293				−23.8	−25.0	−36.2	−18.7	−17.6	−21.0
Early White milo	C. I. 480	+7.2	−10.0	−13.3	−18.2	−43.0	−34.6	(4)	(4)	(4)
Feterita	S. P. I. 51989	+1.8	−20.4	−20.9	−13.0	−41.8	−38.9	−15.4	−28.5	−12.5
Feterita hybrid (feterita × kafir)	F. C. 8917	−5.3	−16.3	−21.1	−17.8	−36.7	−34.9	−27.1	−38.5	−33.3
Grohoma	C. I. 920	+2.4	−22.8	−12.2	−13.9	−30.2	−25.0	−2.2	−28.5	−25.8
Kafir × feterita	K. B. 2686	−13.9	−15.5	−14.8	−14.0	−38.3	−30.2	−11.9	−29.0	−30.0
Kafir × milo 26-3-1-1	K. B. 2561	+8.6	−22.8	−22.6	+.3	−18.5	−15.1	(4)	(4)	(4)
Kansas Orange	F. C. 9108	−12.4	−32.3	−16.6	−33.7	−45.7	−42.5	−24.2	−34.7	−32.4
Manchu Brown kaoliang	C. I. 171	−10.5	−22.8	−20.4	−28.0	−46.1	−42.2	−28.4	−34.9	−45.7
Pierce kaferita	K. B. 2547	−7.9	−18.6	−11.4	−13.3	−31.0	−31.7	−55.3	−28.6	−39.1
Premo	F. C. 8929	+12.6	−19.9	−16.5	−13.3	−35.9	−26.5	−15.6	−17.3	−20.4
Red Amber	F. C. 1534	+.5	−15.4	−8.4	−26.8	−30.3	−40.8	−19.6	−20.6	−14.1
Red Amber × feterita	K. B. 2570	+.9	−19.7	−24.9	(4)	(4)	(4)	−6.7	−19.5	−21.3
Do	K. B. 2562	−4.0	−21.4	−19.7	(4)	(4)	(4)	−14.2	−22.6	−14.8
Do	K. B. 2501	+.6	−20.2	−17.0	(4)	(4)	(4)	−16.4	−24.9	−22.4
Red Leaf feterita	K. B. 2543	−12.2	−11.8	−12.5	−18.9	−41.2	−36.8	−6.7	−25.2	−15.8
Schrock selection	C. I. 616	+3.2	−14.3	−9.9	−24.3	−38.8	−32.8	−15.2	−33.3	−13.5
Shallu	C. I. 85	−5.6	−20.0	−23.1	−25.8	−42.4	−30.2	−20.0	−26.8	−20.2
Weskan	K. B. 2522	+8.8	+2.3	−12.8	−8.3	−27.3	−33.1	−1.8	−26.8	−24.3
White Durra	C. I. 81	+1.4	−17.1	−12.4	−23.0	−51.4	−47.6	−22.8	−26.7	−25.0
White-seeded darso (selection).	K. B. 3002	−7.3	−18.5	−16.9	−10.2	−49.4	−22.8	−17.4	−24.4	−22.1
White Yolo	C. I. 699	+2.7	−14.8	−20.8	(4)	(4)	(4)	−18.2	−21.0	−23.8
Average of all varieties measured.		−1.9	−18.1	−16.3	−18.6	−37.8	−33.3	−18.2	−27.0	−23.4

[1] The figures given represent the averages of varieties grown 4 years (1931, 1932, 1935, and 1936), except Premo, which was grown 3 years.

[2] C. I. refers to accession number of the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.
K. B. refers to Kansas Botany, Kansas State College, Manhattan.
S. P. I. refers to accession number of the Division of Plant Exploration and Introduction, Bureau of Plant Industry, U. S. Department of Agriculture.
F. C. refers to accession number of the Division of Forage Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.
H. C. refers to cereal number of Fort Hays, Kans., Branch Experiment Station.

[3] p. r=Physiologic race.

[4] This sorghum seems to be immune, since no smut appeared in it for the years and the physiologic race of smut concerned.

Sphacelotheca sorghi brought about an average reduction in stalk diameter of 18 percent, while *S. cruenta* p. r. 1 and 2 caused reductions of 38 and 27 percent, respectively. Certain varieties showed an appreciable reduction in the diameter of stalk, while others were affected much less.

Sphacelotheca sorghi and *S. cruenta* exhibited a similar tendency with respect to reduction of leaf width, the former reducing it on an average 16 percent and *S. cruenta* p. r. 1 and 2 approximately 33 and 23 percent, respectively. In some instances the reduction exceeded the average leaf width of all the varieties.

From the data in table 1, one must conclude that the height of sorghums was not appreciably changed by *S. sorghi* infection. but that infection by *S. cruenta* did reduce it markedly (fig. 1, *A*). There was no great difference between the average percentage reduction in height of sorghum plants affected with *S. cruenta* p. r. 1 and 2; how-

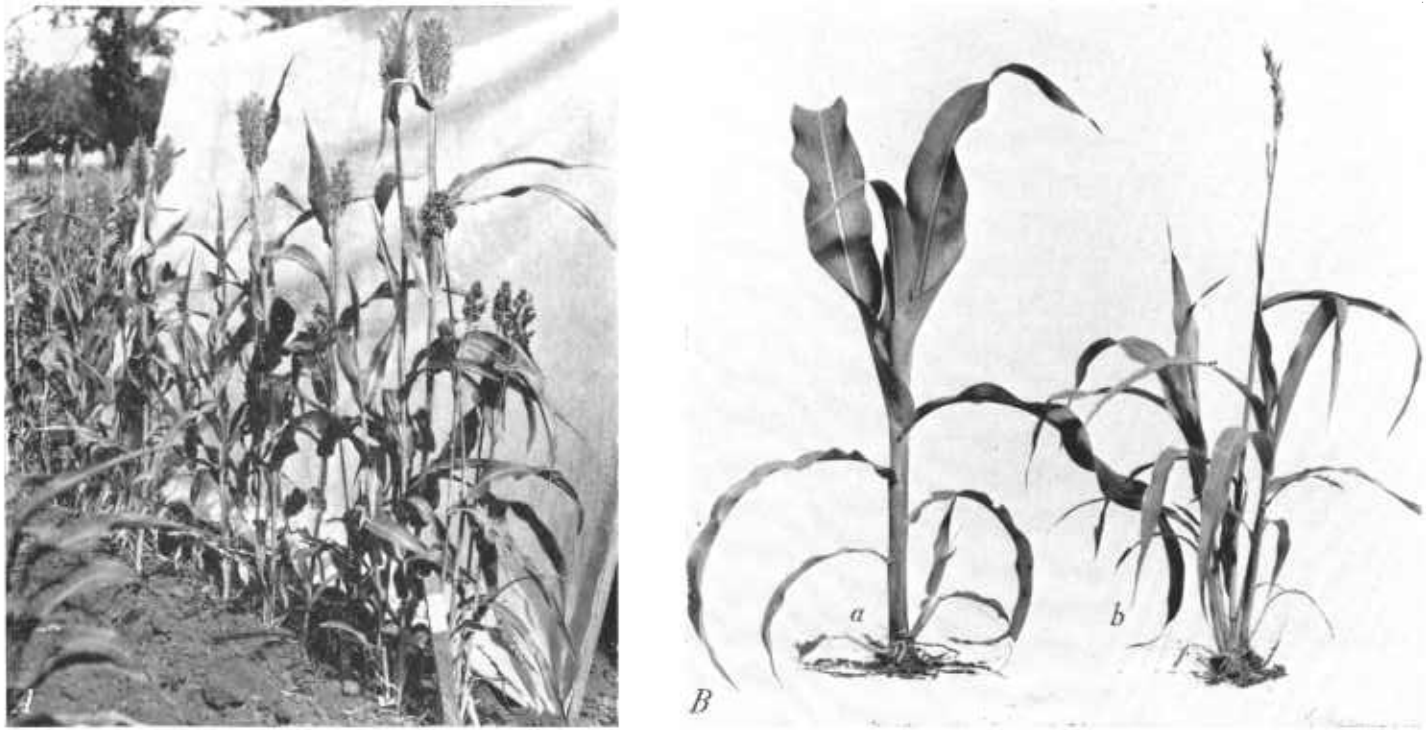


FIGURE 1.—*A*, Manchu Brown kaoliang, showing the effect of loose kernel smut of sorghum (*Sphacelotheca cruenta* p. r. 1) on the height of infected plants. The unsmutted plants had not made their complete growth when the photograph was taken; at a later date the contrast would have been greater. *B*, White Durra sorghum, showing the effect of smut infection on the growth of the host: *a*, Unsmutted plant; *b*, plant infected with *S. cruenta* p. r. 1. The plants were 1½ months old when the photograph was made.

ever, the average percentage reduction in diameter of stalk and width of leaves of plants affected with *S. cruenta* p. r. 1 was significantly greater than that for *S. cruenta* p. r. 2.

Reductions in height of plant, diameter of stalk, and width of leaf bring about a loss in total weight of plant, particularly in the case of attack by *S. cruenta*. It has been known for some time that the nutritive value of smutted sorghum plants is greatly reduced through the destruction of the grain but that the presence of sorghum smut itself is neither poisonous nor otherwise harmful to livestock when fed (*7*). The present studies show that considerably less tonnage of fodder is to be expected from plants attacked by *S. cruenta* and *S. sorghi*, particularly the former.

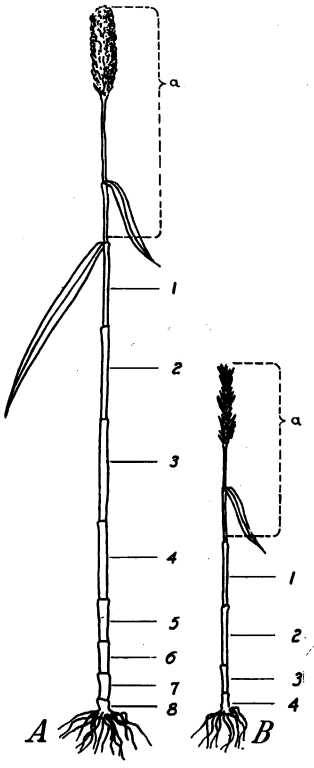


FIGURE 2.—Schematic sketch of a normal sorghum plant and of one infected with the loose kernel smut, *Sphacelotheca cruenta*. All but the topmost leaves have been removed, exposing the nodes. *A*, Normal plant with internodes numbered; *B*, plant attacked by *S. cruenta* showing reduced number of internodes; *a*, panicle and peduncle.

After these more general studies were completed, it seemed desirable to study in detail two varieties of sorghum to determine whether the difference in height between smutted and unsmutted plants was due to a reduction in the number of nodes per plant, to a difference in the length of the internodes, or to a combination of these factors. White Durra C. I. 81 and Manchu Brown kaoliang C. I. 171 were selected for this study.

Reed and Faris (*18*) observed that Valley kaoliang affected with *S. cruenta* had shorter stems with fewer nodes than normal plants or than those infected by *S. sorghi*. Measurements of internode lengths and counts on the number of nodes of smutted and unsmutted plants were made in 1936 at Manhattan, Kans., on White Durra C. I. 81 and Manchu Brown kaoliang C. I. 171. A study was also made of the effect of the two species of smut on the length of the peduncle [4] and panicle of the sorghum plant and on the length of the four internodes below the peduncle in order to locate specifically the regions responsible for difference in height. Since most of the plants attacked by *S. cruenta* did not produce over four or five nodes above the soil line, it was thought best not to consider comparative measurements below the fourth node.

Figure 2 is a schematic sketch of a normal sorghum plant and of one attacked by the loose kernel smut. The various parts of the plant used in the measurement studies are illustrated. The comparative average lengths of the panicle and peduncle combined (fig. 2, *A and B*, *a*), as well as the length of the first to fourth internodes inclusive, of normal and smutted plants are presented in table 2.

[4] The peduncle is the part of the stem joining the panicle with the first node below the panicle.

TABLE 2.—*Results showing effect of sorghum kernel smut infection on length of peduncle and panicle combined, and on each of the 4 internodes below the peduncle of the sorghum plant, Manhattan, Kans., 1936*

WHITE DURRA C. I. 81

Sorghum kernel smut	Length of peduncle and panicle		Length of internode below peduncle								Combined length [1]	
			First		Second		Third		Fourth			
	Normal	Smutted	Normal	Smutted	Normal	Smutted	Normal	Smutted	Normal	Smutted	Normal	Smutted
	Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
S. sorghi p. r. 1–3	50.8	48.4	13.1	12.3	12.2	10.7	11.5	10.8	12.2	11.6	99.8	93.8
S. cruenta p. r. 1	56.7	59.3	15.5	21.8	12.1	11.1	11.4	7.8	12.7	5.4	108.4	105.4
S. cruenta p. r. 2	54.5	53.4	14.2	15.2	12.8	12.1	12.8	10.4	11:0	9.9	105.3	101.0

MANCHU BROWN KAOLIANG C. I. 171

S. sorghi p. r. 1–3	53.0	55.1	13.7	17.2	15.9	15.5	16.7	15.7	15.9	14.0	115.2	117.5
S. cruenta p. r. 1	48.5	47.8	12.1	15.8	13.3	11.7	13.8	8.7	15.9	6.9	103.6	90.9
S. cruenta p. r. 2	52.9	43.8	15.9	13.6	16.0	11.9	15.8	9.7	14.6	7.8	115.2	86.8

[1] Panicle, peduncle, and first 4 internodes below.

There was no marked difference in the combined length of peduncle and panicle of the normal and smutted plants in the two varieties White Durra and Manchu Brown kaoliang for either species of smut, with perhaps the exception of *S. cruenta* p. r. 2 on Manchu Brown kaoliang. The greatest difference occurred in internode length of plants attacked by *S. cruenta* p. r. 2, although those infected with p. r. 1 showed the same trend (table 2). If only *S. cruenta* is considered, there is an appreciable difference between smutted and normal plants in internode length below the peduncle, but the variation in length in comparable internodes is not always consistent. It is, however, consistent for the third and fourth internodes of both varieties, and a marked reduction in the length of these internodes in the smutted plants is noted (table 2). Other varieties of sorghum, such as Acme broomcorn, were just as severely stunted by *S. cruenta* as the two varieties considered here.

As stated previously, smutted plants developed fewer nodes. In a comparison of infected and normal plants, corresponding internodes were not comparable as to position. For example, internode 4 of a plant smutted with *S. cruenta* was essentially at the ground line while internode 4 was about the middle of a normal plant (fig. 2).

Significant differences may be noted for *S. cruenta* p. r. 1 and 2 if the combined lengths from the tip of the panicle, to and including the fourth internode, of smutted and normal plants of Manchu Brown kaoliang are considered (table 2). Some differences are also noted in White Durra but these are less striking. These figures do not represent the total height of plants but rather that part from the tip of the panicle down to and including the fourth internode. The reduced height in plants infected with *S. cruenta* apparently was due in part to the shorter internodes, but the entire reduction in height cannot thus be explained. Smutted plants in the field were frequently about one-half the height of normal plants of the same variety (fig. 1, *A*).

The effect of smut on the total number of nodes visible above the ground was analyzed and the results are given in table 3. The data are expressed in terms of the smutfree [5] plants. Plants of the same varieties attacked by *S. sorghi* had approximately the same number of nodes as unsmutted plants. The same varieties, however, when infected with the two physiologic races of *S. cruenta* had fewer nodes (table 3). The average decrease was 3.5 and 1.5 nodes in plants attacked by *S. cruenta* p. r. 1 and 2, respectively. The reduced height of smutted plants apparently was due more to the reduced number of nodes than to the length of the internodes, according to the 1936 data (table 3).

TABLE 3.—*Results showing effect of sorghum kernel smut infection on the number of nodes in the sorghum plant, Manhattan, Kans., 1936*

Treatment	Average number of nodes per plant [1]		Average decrease in number of nodes
	White Durra C. I. 81	Manchu Brown kaoliang C. I. 171	
S. sorghi p. r. 1-3:			
Smutfree	7.5	8.6	
Smutted	8.5	7.7	0
S. cruenta p. r. 1:			
Smutfree	7.7	7.5	
Smutted	3.7	4.5	3.5
S. cruenta p. r. 2:			
Smutfree	6.9	8.0	
Smutted	6.2	5.8	1.4

[1] Visible nodes above ground.

In 1937 the studies were enlarged to include four varieties of sorghum. Data on the height of plant, diameter of stem, leaf width, and the number of nodes in smutted, smutfree, and check [6] plants of the varieties Evergreen Dwarf broomcorn C. I. 822, Acme broomcorn C. I. 243, White Durra C. I. 81, and Manchu Brown kaoliang C. I. 171 are given in table 4. The comparisons were based on smutfree plants, although either smutfree or check plants could have been used with no appreciable difference in the final results.

An analysis of the data in table 4 shows that in smutted plants the total length of panicle and peduncle and the four internodes below was generally less than that of the smutfree plants. The difference usually was less in plants attacked by *S. sorghi* than in those attacked by *S. cruenta*. The reductions in length of internode could not in themselves, however, be responsible for the great reduction in total height of smutted plants. Similar conclusions were reached from the studies in 1931, 1932, 1935, and 1936. The measurements included only the length of the plants from the tips of the panicles down through the fourth internodes.

[5] "Smutfree" means that plants grew from treated seed and were free from internal smut infection.

[6] Check plants grew from untreated seed and produced normal panicles. Since some of them may have carried infection in the stalk even though the heads were not smutted, a smutfree control was used in 1937 as a safeguard in making comparative measurements.

TABLE 4.—*Results showing effect of sorghum kernel smut infection on length of panicle and peduncle combined, length of 4 internodes below the peduncle, total height of plant, diameter of stem, width of leaf, and number of nodes per plant, Manhattan, Kans., 1937*

Variety	Treatment	Length of panicle and peduncle	Length of internode below peduncle				Combined length of panicle, peduncle, and internodes 1 to 4	Height of entire plant	Reduction in height of smutted plant	Diameter of stem	Width of leaf	Average nodes per plant [1]	Average decrease in nodes per plant [2]
			First	Second	Third	Fourth							
		Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Pct.*	*Cm.*	*Cm.*	*No.*	*No.*
Evergreen Dwarf broomcorn C. I. 822.	*S. sorghi* p. r. 1–3:												
	Smutted	62.3	7.6	6.6	8.0	9.1	93.6	139.4	4.5	1.1	6.4	8.6	0.8
	Smutfree	69.8	7.3	6.8	7.6	8.8	100.3	145.9	-----	1.4	7.8	9.4	-----
	Check	66.6	6.0	6.7	7.7	8.3	95.3	143.8	-----	1.4	7.5	9.4	-----
	S. cruenta p. r. 1:												
	Smutted	47.3	8.0	10.0	9.8	9.5	84.6	84.2	44.0	.6	3.5	4.7	4.9
	Smutfree	69.5	8.0	6.3	7.7	8.3	99.8	150.3	-----	1.5	7.4	9.6	-----
	Check	73.8	7.0	8.3	8.9	9.8	107.8	153.0	-----	1.6	7.9	9.2	-----
	S. cruenta p. r. 2:												
	Smutted	57.2	9.5	9.0	9.0	9.2	93.9	104.1	32.7	1.0	3.8	5.8	3.7
	Smutfree	73.8	7.0	7.2	8.4	8.9	105.3	154.6	-----	1.6	7.8	9.5	-----
	Check	70.9	8.0	8.6	9.5	9.2	106.2	149.8	-----	1.6	7.8	10.2	-----
Acme broomcorn C. I. 243.	*S. sorghi* p. r. 1–3:												
	Smutted	71.4	9.0	10.1	9.5	9.4	109.4	151.9	6.6	1.2	6.1	9.1	.9
	Smutfree	82.6	9.0	9.6	9.2	9.2	119.6	162.7	-----	1.8	7.4	10.0	-----
	S. cruenta p. r. 1:												
	Smutted	70.0	11.0	8.0	8.0	9.0	106.0	136.0	14.7	1.3	5.5	8.0	1.7
	Smutfree	77.5	7.0	9.2	9.1	9.1	111.9	159.4	-----	1.7	7.3	9.7	-----
	S. cruenta p. r. 2:												
	Smutted	58.5	10.0	7.0	7.0	9.5	92.0	106.5	30.6	1.1	4.7	6.2	3.5
	Smutfree	73.3	9.0	8.6	9.6	9.4	109.9	153.4	-----	1.7	7.3	9.7	-----
	Check	72.0	8.0	7.9	8.8	8.9	105.6	155.0	-----	1.6	7.6	10.0	-----
White Durra C. I. 81.	*S. sorghi* p. r. 1–3:												
	Smutted	60.4	15.2	16.1	16.2	14.8	122.7	141.1	11.5	1.1	6.8	6.2	.1
	Smutfree	66.2	21.2	16.9	17.1	16.1	137.5	159.4	-----	1.3	7.8	6.3	-----
	Check	68.4	22.0	19.3	16.7	16.0	142.4	167.2	-----	1.3	8.2	6.7	-----
	S. cruenta p. r. 1:												
	Smutted	63.6	22.0	21.5	14.5	12.0	133.6	115.4	26.1	.9	5.5	3.8	3.0
	Smutfree	65.2	20.0	17.3	18.0	17.0	137.5	156.2	-----	1.4	8.1	6.8	-----
	Check	67.5	19.8	19.4	17.6	16.2	140.5	162.0	-----	1.5	8.4	6.6	-----
	S. cruenta p. r. 2:												
	Smutted	57.1	18.5	17.4	15.5	12.9	121.4	115.8	24.5	1.0	5.6	5.2	1.9
	Smutfree	67.3	21.4	18.8	15.9	15.4	138.8	153.3	-----	1.5	8.5	7.1	-----
	Check	66.8	35.0	10.0	19.4	18.0	149.2	141.6	-----	1.3	12.8	6.8	-----
Manchu Brown kaoliang C. I. 171.	*S. sorghi* p. r. 1–3:												
	Smutted	62.4	22.0	17.6	17.8	16.8	136.6	150.3	8.9	1.2	6.6	6.5	.3
	Smutfree	59.8	18.2	19.9	18.8	19.3	136.0	165.0	-----	1.3	7.6	6.8	-----
	Check	58.8	19.0	19.3	19.2	17.4	133.7	164.9	-----	1.2	7.6	6.6	-----
	S. cruenta p. r. 1:												
	Smutted	47.8	10.8	9.9	12.2	11.6	91.4	93.0	35.3	.7	4.5	4.8	1.3
	Smutfree	55.8	17.5	17.2	16.6	18.6	125.7	143.8	-----	1.1	7.2	6.1	-----
	Check	54.5	13.5	13.5	14.4	14.2	110.1	142.6	-----	1.2	7.5	6.5	-----
	S. cruenta p. r. 2:												
	Smutted	64.0	19.0	15.5	16.0	14.5	129.0	147.0	17.4	1.1	6.9	6.0	1.0
	Smutfree	63.8	17.6	19.8	19.0	18.9	139.1	177.9	-----	1.3	8.5	7.0	-----
	Check	60.8	16.5	16.8	16.6	17.5	128.2	172.0	-----	1.4	8.2	6.8	-----

[1] Above ground or visible nodes.
[2] The difference in number of nodes is based on "smutfree" and smutted plants.

Sphacelotheca sorghi reduced the height of the plant slightly, while *S. cruenta* p. r. 1 and 2 reduced it materially, as already shown in these studies. The percentage reduction for smutted plants of the four varieties infected by the two species of smut showed a range for

S. sorghi of 4.5 to 11.5 percent; for *S. cruenta* p. r. 1, 14.7 to 44 percent; and for p. r. 2, 17.4 to 32.7 percent. These reductions in height are illustrated by figure 1, *A*, showing plants of Manchu Brown kaoliang infected by *S. cruenta* p. r. 1.

The average number of nodes per plant for each variety and the average decrease in the number of nodes in smutted plants as compared with smutfree plants are given in the last two columns of table 4. The average decrease in number of nodes for the four varieties was 0.5, 2.7, and 2.5 in plants affected with *S. sorghi*, *S. cruenta* p. r. 1, and *S. cruenta* p. r. 2, respectively (table 4). Plants affected with *S. sorghi* had essentially the same number of nodes above ground as the smutfree plants. This explains why they were approximately the same height. Plants infected with *S. cruenta* always had fewer nodes, and in many instances only half as many nodes, as smutfree plants.

While the reduced height of smutted plants may be brought about by a combination of shortened internodes and fewer nodes, the latter factor is the more important. The two species of smut differ markedly in the extent to which they effect reductions in different varieties, but the general tendency is for *S. cruenta* definitely to dwarf the host.

The reduction in the stalk diameter of smutted plants of the four varieties was significant in most cases and in accord with previous results.

The effect on leaf width was most pronounced in the case of *S. cruenta* infection, although it was also noticeable in the case of *S. sorghi*.

EFFECT OF SMUT INFECTION ON GROWTH CYCLE

A striking characteristic of sorghum infected with *S. cruenta* is the tendency for smutted plants to head several days to 2 weeks earlier than unsmutted plants (*3*, *19*). One of the field characteristics of the development of the loose kernel smut of sorghum is for the host to speed up its growth cycle. In figure 1, *B*, which shows plants of White Durra at 1.5 months of age, the smutted plant (*b*) has headed, while the noninfected plant (*a*) is still about 2 weeks from heading. This difference in time of heading between smutted and normal plants was very much less noticeable in plants attacked by *S. sorghi;* generally such plants do not head more than a day or two before the normal plants.

EFFECT OF SMUT INFECTION ON NODE DIFFERENTIATION

A possible explanation for the differences observed in node development in smut-infected and normal plants may be derived from histologic studies. In the present investigations the embryos of Western Blackhull kafir, Darso, Scarborough broomcorn, Pygmy milo, and feterita were removed from dormant seed and from seed which had germinated for 24 hours. It was found that about five nodes besides the coleoptilar and scutellar nodes had differentiated in the embryo of the normal sorghum seed, a condition similar to that occurring in the embryo of corn and other grasses. Supporting evidence by Evans and Grover (*6*) is found in their morphologic studies of eight species of grasses other than sorghum.

As the seed germinates and grows, additional nodes are successively differentiated at regular intervals in the apical meristem of the plant.

After the rudiments of the panicle are differentiated, no additional nodes are formed. This differentiation occurs early in the ontogeny of the plant. The number of nodes in the embryo of inoculated or uninoculated sorghum seed of the same variety or strain would naturally be the same. Some of the young plants are infected with the smut as the inoculated seed germinates. The smut invades and follows the meristematic tissues of the plant as the latter grows to maturity, affecting its metabolism in such a way that fewer nodes are formed prior to the differentiation of the panicle. The plant heads earlier than the unsmutted plant and is dwarfed, a condition which is due primarily to the reduction in the number of internodes.

In this connection a supplementary experiment was conducted in the field and in the greenhouse in 1941 with 10 varieties of sorghum. The seed was not smutted, since the authors wished to study the normal growth of the plant. By varying the environmental conditions an average increase of 50 percent was obtained in the number of nodes in the greenhouse plants as compared with the same varieties in the field. It is believed, therefore, that the number of nodes which a sorghum plant eventually develops depends partly on the inherent nature of the variety or strain and partly on environmental factors which affect the general metabolism of the plant.

Since plants affected with *S. cruenta* are much more dwarfed than those affected with *S. sorghi*, the invasion of the meristematic tissues of the seedling by *S. cruenta* probably had a greater effect on the metabolism of the varieties and strains tested than did *S. sorghi*, and consequently a greater influence on node development.

It is not known whether a chemical depressant is given off by the specific smut fungus that causes the host to respond in this manner, or whether the mere association of the mycelium of the smut fungus in the meristematic tissues of the plant is partly responsible for the differentiation of fewer nodes. The former explanation seems the more plausible. Different varieties and strains of sorghum respond differently to the same smut. The same variety or strain may respond differently to the two races of *S. cruenta* and *S. sorghi* (table 4).

EXCESSIVE TILLERING

A difference in tillering, very pronounced in a few varieties, was observed between smutted and unsmutted plants. All stalks or culms are considered as tillers in this discussion. A summary of the data on 25 varieties of sorghum shows that plants attacked by *S. cruenta* p. r. 1 had an average of 1.4 more tillers per plant than normal plants; those attacked by *S. cruenta* p. r. 2 had 0.6 more tillers, and those attacked by *S. sorghi* had 0.5 more tillers, than normal plants. Tillers produced by plants attacked by *S. cruenta* were short, slender, and sometimes decidedly "Sudan grasslike." A striking example of this is shown in figure 3, *A, b*, typical for Shallu C. I. 85. A representative picture of what occurs in many varieties, in this instance Acme broomcorn, is shown in figure 3, *B, a*.

If the varieties White Durra, Manchu Brown kaoliang, Shallu, and Acme broomcorn are considered from the point of view of tillers produced, it will be found that those attacked by *S. cruenta* p. r. 1 produced excessive tillering, while those attacked by *S. cruenta* p. r. 2 and *S. sorghi* showed only a moderate increase in tillering. Two

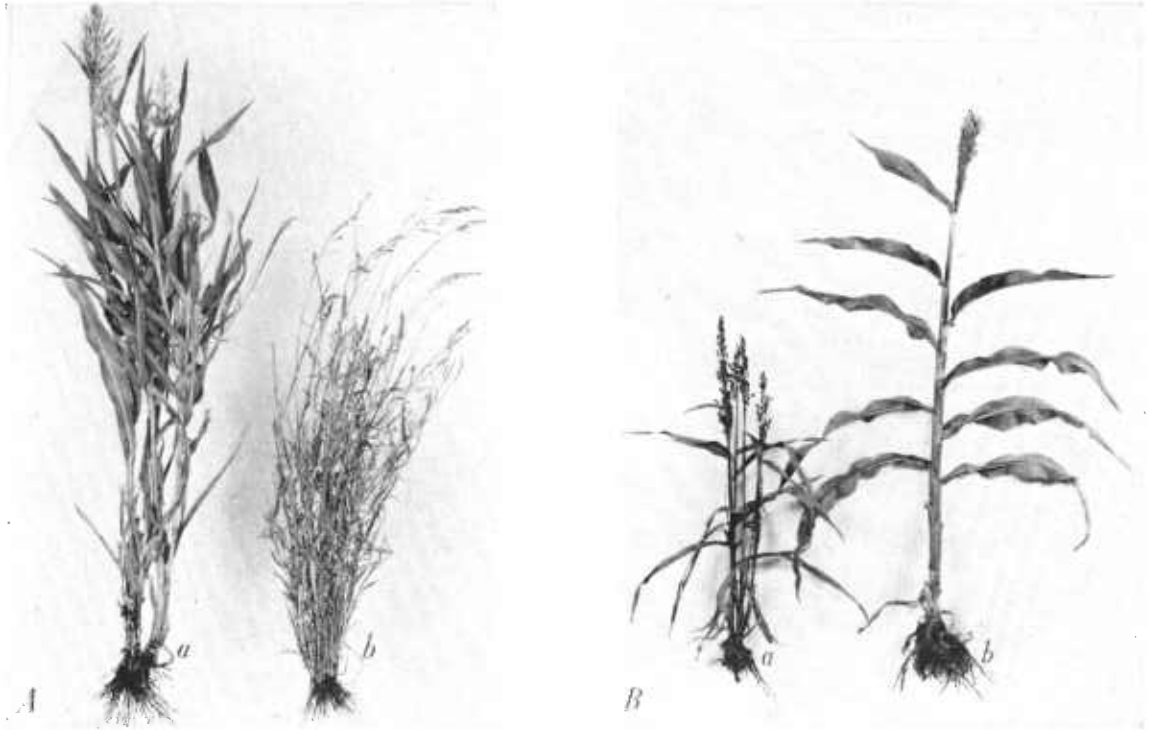


FIGURE 3.—On some varieties of sorghum the effect of loose kernel smut (*Sphacelotheca cruenta* p. r. 1) is to produce excessive tillering. *A*, *a*, A normal plant of Shallu; *b*, a smut-infected plant of Shallu. The "Sudan grasslike" but more prostrate growth is a striking feature of this variety (photographed Oct. 20, 1936). Such prolific tillering is not typical of all varieties.
B, *a*, Acme broomcorn, showing the increased tillering characteristic of many sorghum varieties attacked by *S. cruenta;* *b*, normal plant of Acme variety (photographed Aug. 8, 1930).

years' data were obtained, but since the general tendency was the same for each year, the results for 1936 only are given. The data in table 5 show the comparative differences in amount of tillering for these varieties on August 18. Had the number of tillers been counted in October when the photograph (fig. 3, *A*) was taken, the number in both normal and smutted plants would have been greater than those given in table 5. It is apparent that a smutted plant has a tendency to produce more as well as shorter shoots. This tendency varies in varieties and may be influenced both by seasonal conditions and the age of the plant.

TABLE 5.—*Results showing the effect of smut infection in sorghums on tiller production, Manhattan, Kans., 1936* [1]

Smut species and sorghum variety	Number of tillers per plant		Increase in number of tillers
	Normal	Smutted	
S. sorghi p. r. 1–3:			
White Durra	2.1	1.9	−0.2
Manchu Brown kaoliang	2.0	2.6	.6
Shallu	2.3	3.8	1.5
Acme broomcorn	1.7	3.1	1.4
S. cruenta p. r. 1:			
White Durra	1.6	3.9	2.3
Manchu Brown kaoliang	1.4	3.3	1.9
Shallu	2.6	4.9	2.3
Acme broomcorn	1.3	6.1	4.8
S. cruenta p. r. 2:			
White Durra	1.5	3.0	1.5
Manchu Brown kaoliang	1.5	1.9	.4
Shallu	2.3	3.5	1.2
Acme broomcorn	1.8	3.7	1.9

[1] Data taken August 18.

VEGETATIVE PROLIFERATION OF SMUTTED PANICLES

During the course of these investigations, it was observed that pronounced proliferation of smutted panicles occurred in certain varieties of sorghum attacked by *Sphacelotheca cruenta* (fig. 4, *A, b*). Reed (*17*) and Reed and Melchers (*19*) mentioned this as a characteristic of this species of smut. In the experimental plots in Kansas increased proliferation has not been observed in unsmutted panicles of the same varieties growing in the same row, nor has it been noted in plants attacked by *S. sorghi*. A similar, but usually more intensified proliferation has been observed in Kansas and elsewhere on sorghum plants attacked by *S. reilianum* (Kühn) McAlp., which causes head smut (fig. 4, *A, a*). Apparently this abnormal condition is the expression of a stimulus brought about by conditions other than smut infection, since Karper and Stephens (*11*) describe a similar, heritable abnormality on unsmutted Blackhull kafir panicles in Texas. In 1940 several plants of Wheatland sorghum collected in Stevens County, Kans., had a type of proliferation not due to smut infection. The writers believe this may be similar to the one described by Karper and Stephens (*11*). A normal panicle of Wheatland, a greatly proliferated panicle, and a deformed spikelet are illustrated in figure 4, *B*.

The proliferation caused by the loose kernel smut infection is more pronounced in some varieties than others. In the group of 25 varieties examined over a period of several years, those in which proliferation

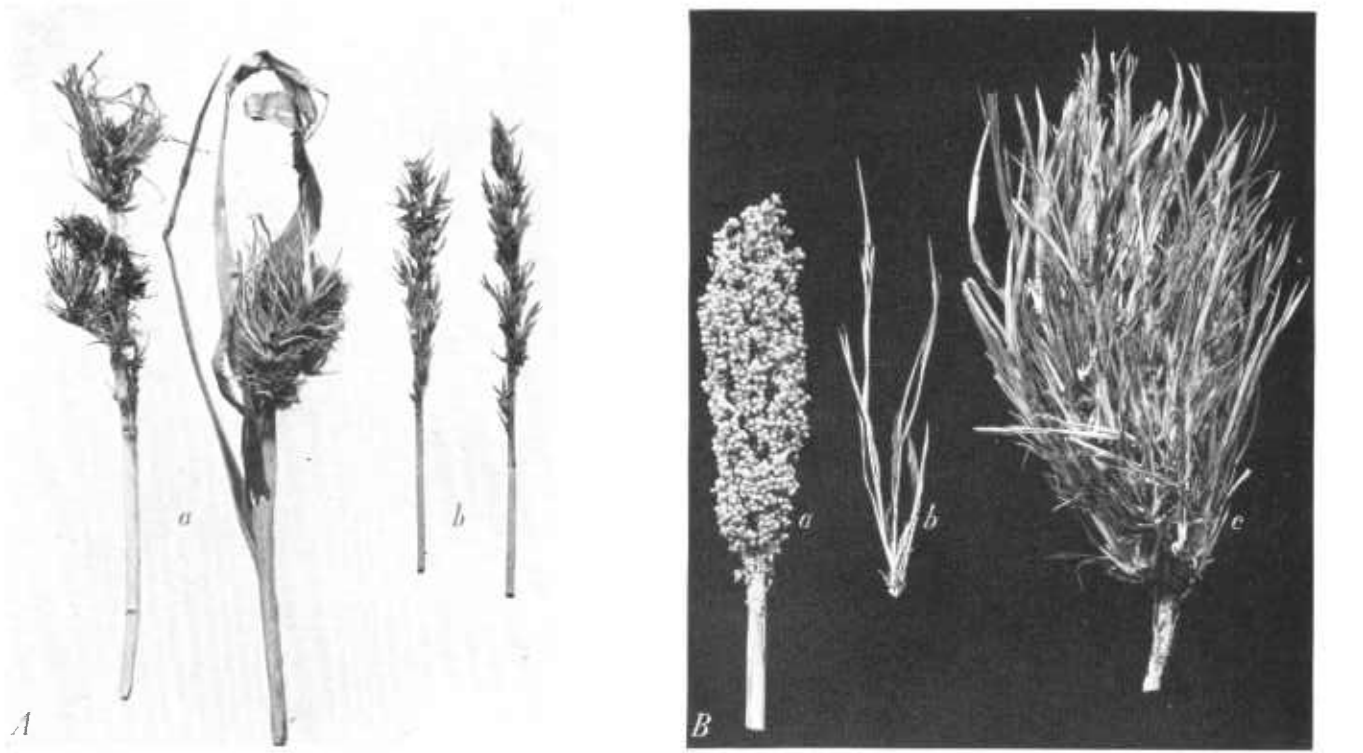


FIGURE 4.—*A*, Two types of proliferation brought about by smut infection in sorghum: *a*, Head smut (*Sphacelotheca reiliannum*); *b*, loose kernel smut (*S. cruenta*). *B*, *a*, Normal head of Wheatland sorghum; *b*, deformed spikelet; *c*, greatly proliferated paniele. This proliferation was not due to smut infection; possibly it has a genetic explanation.

was observed to be very marked were Shallu, Acme broomcorn, Kansas Orange sorgo, and Coon darso. Essentially, the abnormality is a type of fasciation with small shoots developing from tissue which generally gives rise to the floral organs of the spikelet. A smutted panicle with numerous abnormal spikelets becomes very noticeable because of the "brushy" appearance of the panicle (fig. 4, *A*, *b*). The pronounced dark-green color of the proliferated part contrasts vividly with the normal green of the remainder of the plant. It is similar to the dark-green color that develops in heads of wheat plants attacked by *Tilletia levis*.

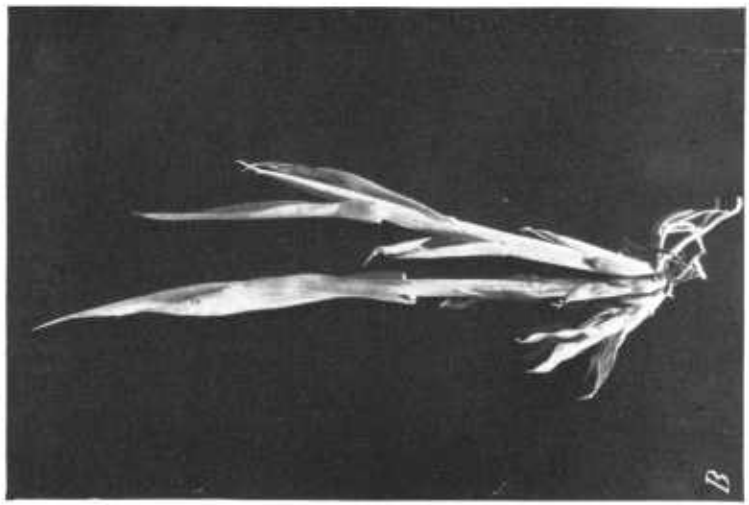
The extreme case of panicle proliferation shown in figure 5, *A*, is a plant of kafir×feterita infected with *S. cruenta* p. r. 2, which was selected by C. O. Johnston, who made a further study of its development. Some of the smutted spikelets vegetated rapidly after rains in late August. No seed developed in the head. A few spikelets produced anthers, as shown in figure 5, *A*, *a*. The spikelet shown in figure 5, *A*, *b* was removed, placed in water, and allowed to stand in the laboratory where it produced roots, as shown in figure 5, *B*. Later it was placed in soil in the greenhouse, but it lived only a few weeks. On dissection, it was found to contain two or three aborted spikelets, which seemed to indicate that the structure was proliferated flowering parts.

SIZE OF SMUT SORI

Considerable variation has been observed in the size of the smut sori on different varieties of sorghum. This feature was not studied in detail, but it is apparent that the sori on certain varieties are particularly long and curved. The differences in size and color of the smut sori and peridia of different physiologic races of *S. sorghi* have already been described (*15*). Recently observations on the size of sori and color of peridia have been made by Tyler (*21*) in connection with genetic studies in *S. sorghi*.

When kafir × feterita K. B. 2686 was infected with *S. cruenta* p. r. 1 and 2, there was a marked difference in the appearance of the sori of the two races. Several years' data showed that the average length of the sori of p. r. 1 was about 1 cm., while that of p. r. 2 was about 1.5 cm. (fig. 6, *A*). The differences were not seasonal. The variation in length of the sori on other varieties of sorghum inoculated with the two physiologic races of *S. cruenta* was less noticeable, although there was a tendency for those produced by p. r. 1 to be slightly longer. Only 2 years' study has been made on this phase of the work, and further observations with other varieties would be desirable.

Figure 6, *B*, shows certain differences between physiologic races 1 and 2 of *S. cruenta* on White Durra. These differences were observed for several seasons on this variety. Figure 6, *B*, *e*, is a normal head of White Durra and *f* is smutted, showing glume proliferation and the absence of awns. Smutted panicles of White Durra in which the sori involve the rachilla (fig. 6, *B*, *a* to *d*, and *g* to *j*) have been observed during certain seasons on a few varieties affected with *S. cruenta* physiologic race 2, but not on the same varieties affected with *S. cruenta* physiologic race 1 under the same environmental conditions.



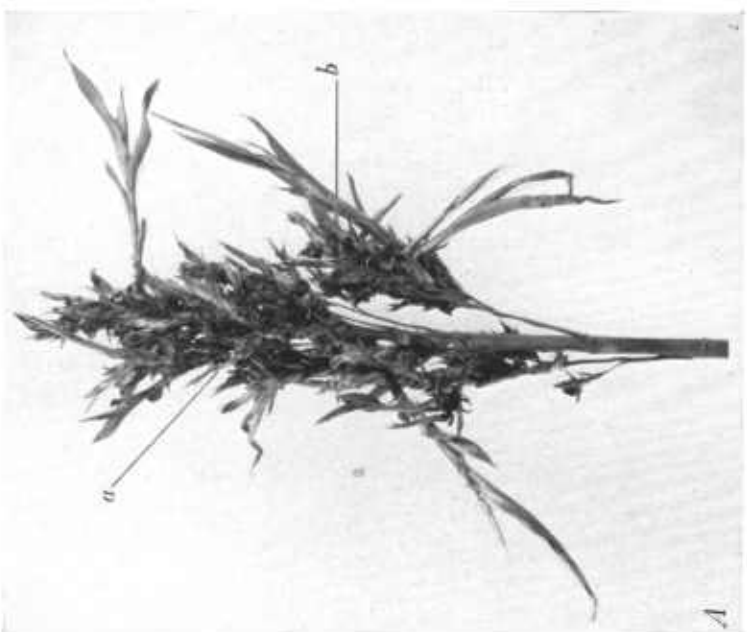


FIGURE 5.—Loose kernel smut of sorghum causes pronounced proliferation of sorghum panicles in some instances. *A*, *a*, A normal spikelet showing anthers; *b*, a proliferated spikelet (plant) which was removed and placed in water. *B*, The same spikelet as that shown at *A*, *b*; it developed roots when placed in water but did not survive when planted in soil. (Photograph by C. O. Johnston.)

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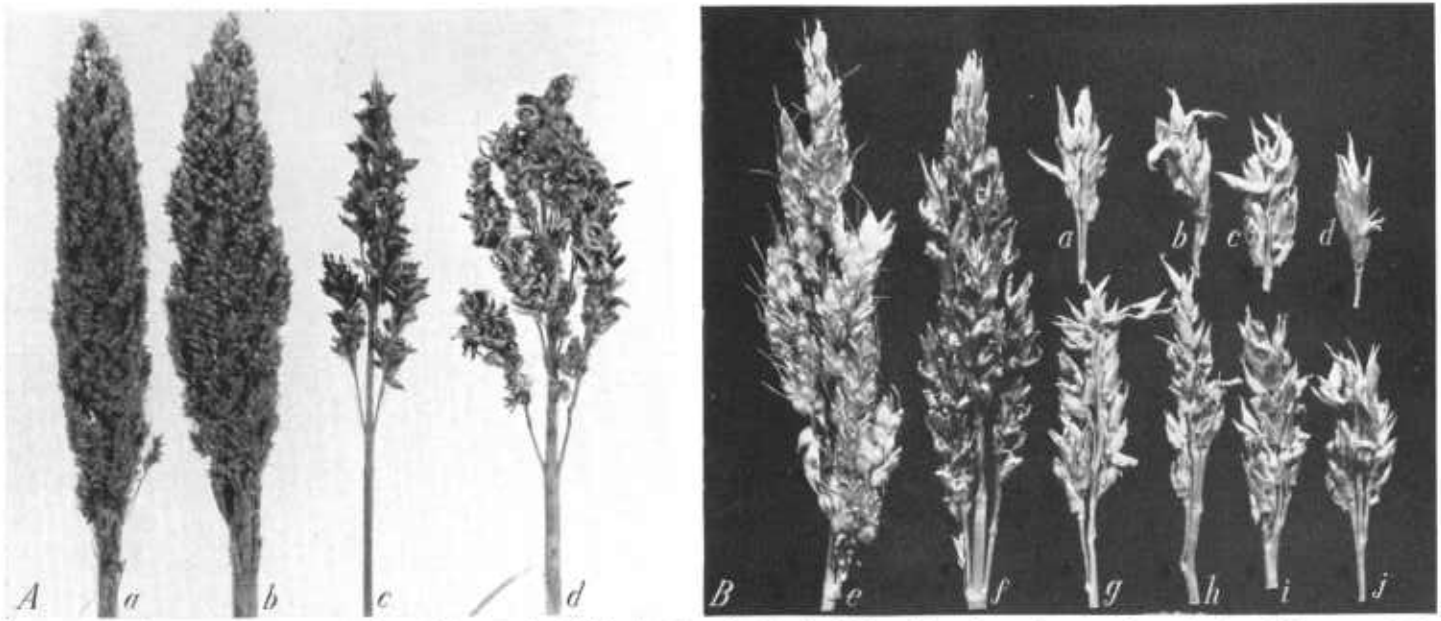

FIGURE 6. *A*. Normal and smutted panicles of a hybrid, kafir×feterita K. B. 2686, collected on the same day, showing differences in the size and appearance of the smut sori of two physiologic races of *Sphacelotheca cruenta*. *a*. Unsmutted panicle. Note stamens, proof that smut is not present. *c*. Panicle taken from the same row as *a*, attacked by *S. cruenta* p. r. 1. b. Unsmutted panicle for comparison with smutted panicle *d*, both selected from the same row. The smut in *d* is *S. cruenta* p. r. 2. Compare the large, curved, or horn-shaped sori with the fragile, moderate-sized, straight sori of p. r. 1 shown in *c*.

B. Morphologic differences between the sori of *S. cruenta* p. r. 1 and 2 on White Durra (X 2); *a*, *b*, *c*, and *d*, and *g*, *h*, *i*, and *j*, Branches of panicles affected with *S. cruenta* p. r. 2, showing the tendency of the sori to involve the rachilla. This condition was common in 1937 with this race of smut on White Durra. *e*, A normal panicle of White Durra. *f*, A panicle of White Durra affected with *S. cruenta* p. r. 1 in which the sori are confined to the ovaries; note the proliferation of the glumes.

In some varieties infected with physiologic race 1, the fungus limits its sporulating area to the ovaries of the flower, as shown in figure 6, *B*, *f*.

LACK OF AWN DEVELOPMENT

The group of sorghums known as milos have short awns or barbs on the glumes, a characteristic which distinguishes them from other

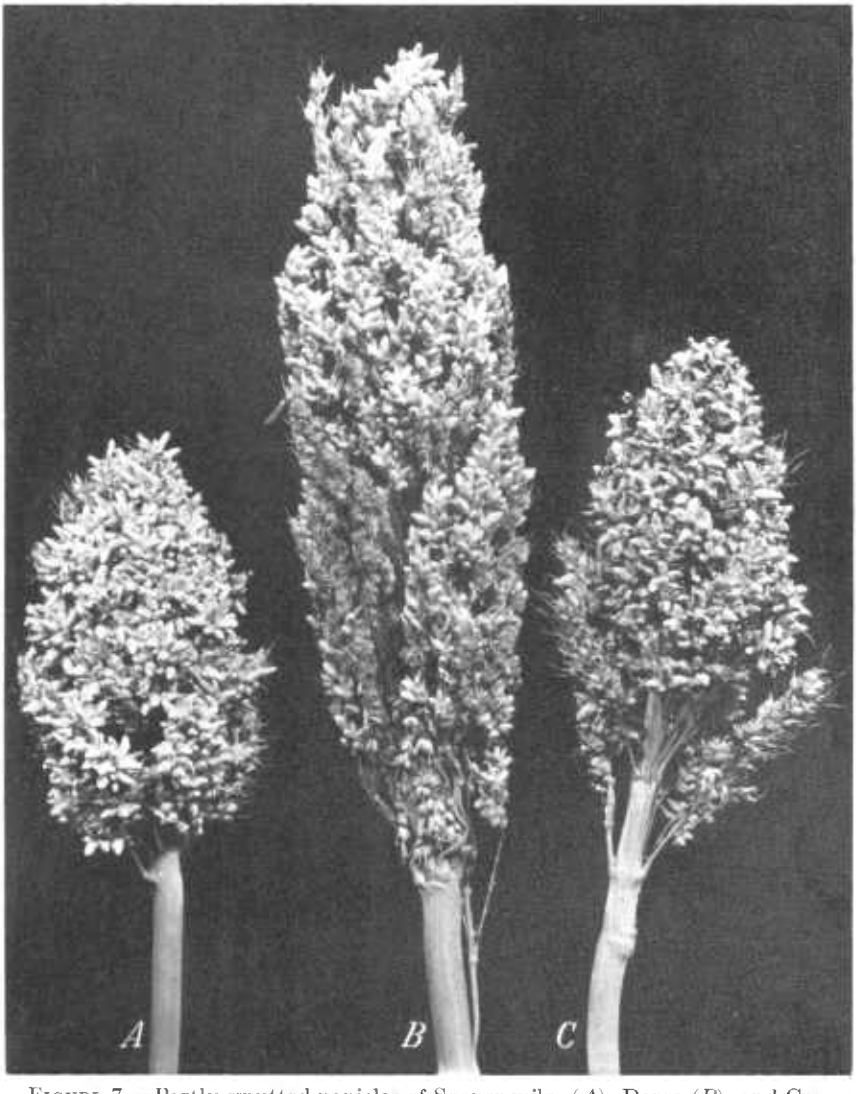

FIGURE 7.—Partly smutted panicles of Sooner milo, (*A*), Darso (*B*), and Cream milo (*C*). The smut is *Sphacelotheca sorghi* physiologic races 2. Note the lack of development of the awns on the glumes of the smutted spikelets. This is characteristic of the milo group.

sorghums. The milos are generally considered resistant to *S. sorghi* and *S. cruenta*, although recent studies have proved that certain physiologic races attack them (*14*, *15*). When a milo head or part of

a panicle is infected with the kernel smut organism, there is a partial or entire lack of awn development on the spikelets attacked, as is shown in figure 7. The fungus in this instance was *S. sorghi* physiologic race 2; the effect of *S. cruenta* physiologic race 1 on White Durra is shown in figure 6, *B, f*. In the latter case there was a complete suppression of awn development since all the spikelets were affected by the smut.

SUMMARY AND CONCLUSIONS

A study was made of 25 varieties, selections, and hybrids of sorghum to determine the effect of the kernel smuts *Sphacelotheca sorghi* and *S. cruenta* on the normal development of the host. Data on the reduction in height of plant, diameter of stalk, and width of leaf showed that sorghum varieties react differently to these two smuts. The average reduction in height from the normal of the varieties tested with *S. sorghi* was 2 percent; with *S. cruenta* physiologic races 1 and 2, 19 and 18 percent, respectively. The average reduction in diameter of stalks infected with *S. sorghi* was 18 percent, whereas in stalks infected with *S. cruenta* physiologic races 1 and 2 the average was 38 and 27 percent, respectively. The average reduction in leaf width of smutted plants as compared with the normal for all the varieties infected with *S. sorghi* was 16 percent; while with *S. cruenta* physiologic races 1 and 2, it was 33 and 23 percent, respectively. In general, therefore, the reductions in height, diameter of stalk, and width of leaf were greater in plants infected with *S. cruenta* than in those infected with *S. sorghi*. Furthermore, *S. sorghi* infection did not consistently reduce the height of the plant, although it materially reduced the diameter of the stalk and the width of the leaves.

These reductions in plant parts by both of the kernel smuts are of economic importance since they result in a reduction in the tonnage of grain and forage that may be expected from badly smutted crops.

A study was made to find what causes the reduction in height of smutted plants. The reduced height of plants infected by *S. cruenta* was found to be due partly to shortened internodes, but primarily to a reduced number of internodes. Plants attacked by *S. cruenta* had fewer nodes than those attacked by *S. sorghi*. In several instances the varieties attacked by the former had only half as many nodes as smut-free plants.

A histologic explanation of the causal factors concerned in node reduction of smut-infected sorghum plants is believed by the writers to be as follows. The smut fungus invades and follows the apical meristematic tissue of the sorghum plant. This invasion affects the metabolism of the growing plant in such a way that it forms fewer nodes prior to the differentiation of the panicle than does a normal plant. Consequently the infected plant heads earlier than the non-infected plant and is dwarfed primarily because of the reduction in the number of internodes. Whether it is chiefly a chemical stimulus initiated by the specific smut fungus that causes the host to respond in this manner, or whether some additional action of the mycelium in the meristematic tissue is partly responsible is not known. The authors believe the first explanation to be the more plausible. In respect to the extent of node reduction, varieties and strains of sorghum

differ. Also, the same variety or strain may differ in its response to attack by the different races of *S. cruenta* and *S. sorghi*.

The growth cycle of plants attacked by *S. cruenta* is speeded up; the plants head from a few days to about 2 weeks earlier than unsmutted plants. In general, plants attacked by *S. sorghi* head at approximately the same time as smut-free plants.

In 25 varieties of sorghum plants attacked by *S. cruenta* physiologic race 1 had an average of 1.4 more tillers than normal plants; the plants attacked by *S. cruenta* physiologic race 2 had 0.6 more tillers; and those attacked by *S. sorghi* had 0.5 more tillers. The results indicate a tendency for smutted plants to tiller more abundantly than smut-free plants, and in certain varieties this characteristic is very pronounced.

The proliferation of glumes of some varieties of sorghum infected with *S. cruenta* was very striking in the field because of the brushlike appearance and abnormally dark-green color of the glumes. Plants attacked by *S. sorghi* showed neither of these characteristics.

In the experiments conducted, the size and shape of sori were found to vary according to the species and race of smut and the variety of sorghum attacked. However, too few varieties were studied for definite conclusions to be formed and additional data would be desirable. It is apparent that kafir × feterita K. B. 2686 when infected with *S. cruenta* physiologic race 2 has longer and more curved sori than when affected with *S. cruenta* physiologic race 1 or *S. sorghi*.

A singular effect of sorghum kernel smut on the florets of milo and milo hybrids is the lack of development of awns which is a characteristic of normal florets in this group of sorghums.

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