

THE INHERITANCE OF STAMINATE PEDICELLED SPIKELETS
OF SORGHUM, Sorghum bicolor (L.) Moench,
AND ITS INFLUENCE ON HYBRID SORGHUM SEED PRODUCTION

by

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INTRODUCTION

Since the beginning of hybrid sorghum [Sorghum bicolor (L.) Moench] production, synchronization of anthesis of the male and female parents has been a problem in hybrid seed production. Anthesis synchronization of hybrid sorghum parents has been attempted by differential planting dates, fertilization, irrigation, clipping, and flaming of the parents. Lengthening the duration of anthesis of either parent should facilitate anthesis synchronization of the parents. This paper reports an investigation of staminate pedicelled spikelets of sorghum, reported by several researchers (4, 8, 10, 14, 16), as a means to lengthen the anthesis period of male parents. The results of an inheritance study of staminate pedicelled spikelets are also reported.

REVIEW OF LITERATURE

As described by authorities (5, 9, 14), the inflorescence of sorghum is a panicle with several orders of branching. The spikelets are borne in groups to form a raceme. The racemes are 2-4 noded, and each node bears one sessile and one pedicelled spikelet, except that the terminal node bears one sessile and two pedicelled spikelets. The sessile spikelets are ordinarily hermaphroditic, and the pedicelled spikelets are usually staminate or neuter.

Long (11) compared the pedicelled and sessile spikelets of sudangrass, Sorghum bicolor var. sudanense (Hitchc.), with those of johnsongrass, Sorghum halepense (L.) Pers. He found aborted pistils in the pedicelled spikelets of johnsongrass which indicated the now staminate spikelets were

once perfect. Further study of the meristematic tissue positions indicated that both the sessile and pedicelled spikelets of johnsongrass at one time had two perfect flowers. Cross sections of sudangrass spikelets showed all the rudimentary parts corresponding to those of johnsongrass, indicating an original two flowered condition in both spikelets of both grasses. Karper and Stephens (9) found the sessile spikelet of sorghum to contain two flowers, the lower abortive and the upper perfect. The staminate pedicelled spikelet contained an aborted lower flower, and stamens of a staminate upper flower. In discussing sorghum and related genera, Garber (6) noted the gradual reduction of the pedicelled spikelet from a staminate to neuter condition in Eu-Sorghum, Para-Sorghum, and Stiposorghum to a neuter only condition in Chaetosorghum and Heterosorghum. The pedicelled spikelet was completely suppressed in Sorghastrum, and finally the pedicel was suppressed in Cleistachne.

The anthesis habits of staminate pedicelled spikelets have been studied by a number of investigators (1, 9, 12, 15). However, Schertz and Stephens (13), reporting on inherited characters of sorghum, did not mention the inheritance of staminate pedicelled spikelets.

From a study of seven Indian sorghum cultivars, Patel and Patel (12) reported the percentage of pedicelled spikelets that were staminate ranged from 0 in Sholapuri 1 to 40 in Althan Deshi 6. In the cultivars with staminate pedicelled spikelets, the upper portion of the panicle and the tips of each branchlet contained a larger proportion of staminate pedicelled spikelets. They found staminate pedicelled spikelets to account for up to 35% of the total anther bearing spikelets (sessile and pedicelled) of a panicle. Staminate pedicelled spikelet pollen grains germinated better

and faster than those of sessile spikelets in 5% glucose, whereas, sessile spikelet pollen germinated better in 10% glucose solutions. Successful crosses were made with pollen from staminate pedicelled spikelets placed on the stigmas of emasculated sessile spikelets. They stated that staminate pedicelled spikelets started and finished blooming 3 to 4 days later than the sessile spikelets. The duration of anthesis in cultivars with staminate pedicelled spikelets ranged from 12 to 16 days, whereas, the duration in cultivars with neuter pedicelled spikelets ranged from 9 to 11 days. Graham (7) pointed out that the duration of anthesis in individual sorghum panicles varied with the size of the inflorescence and the number of flowers, with the average time for sessile spikelets being about 7 days.

Ayyangar and Rao (1) and Karper and Stephens (9) reported the later period of anthesis by staminate pedicelled spikelets. In the case of hermaphroditic pedicelled spikelets reported by Ayyangar and Rao (2), the sessile and pedicelled spikelets bloomed at the same time.

Stephens and Quinby (15) made a detailed study of anthesis, pollination, and fertilization in sorghum at Chillicothe, Texas. They found that sorghum cultivars completed sessile spikelet anthesis in 6 to 9 days under August temperatures and with sufficient soil moisture. Staminate pedicelled spikelets started and finished blooming 2 to 4 days later than sessile spikelets. Seed set was obtained in emasculated sessile spikelets pollinated with staminate pedicelled spikelet pollen.

Ayyangar and Rao (3) found no differences in anther size of the pedicelled versus sessile spikelets, thus showing no difference in sexual atrophy. Both types of anthers were found to have an average length of 3.25 mm and an average width of 998 microns. Microscopic examination of the pollen

from pedicelled and sessile spikelet anthers showed no difference in percentages of abortive pollen, those pollen grains devoid of solid contents. Those workers, therefore, concluded that neither the size nor the nature of the pollen population was affected by the pedicelled condition. However, a decided difference was found in the effectiveness of the pollen. Forty-eight percent seed set was obtained in emasculated sessile spikelets pollinated with sessile spikelet pollen, and only 17.7% seed set was obtained when pollinated with staminate pedicelled spikelet pollen. On a culture medium of 41% sucrose and 0.75% shredded agar, sessile spikelet pollen germinated 60.4% with an average pollen tube length of 260 microns, whereas, staminate pedicelled spikelet pollen germinated 37.7% with a pollen tube length of only 92 microns.

MATERIALS AND METHODS

The pure line sorghum cultivars Combine 7078, Japanese Dwarf broom-corn, and KS 6; the sorghum plant introductions P.I. 88022, P. I. 181074, and P.I. 217831; and the unreleased sorghum pure line 67R1115 were observed to exhibit staminate pedicelled spikelets. The pure line sorghum cultivars Redlan and Combine Kafir-60, were observed to exhibit neuter pedicelled spikelets. For simplicity, the term lines will be used in the remainder of this paper to designate all sorghum materials.

Crosses for the staminate pedicelled spikelet inheritance study included Combine Kafir-60 X Combine 7078, Combine Kafir-60 X 67R1115, Combine Kafir-60 X Japanese Dwarf broomcorn, and Combine Kafir-60 X P.I. 88022. The reciprocal cross Combine 7078 X Combine Kafir-60 was made to study the effect of cytoplasm on staminate pedicelled spikelet inheritance.

To prevent outcrossing, panicles of the F_1 progenies were covered with kraft paper bags before anthesis. The F_2 progenies were grown in the field in 1969. Individual pedicelled spikelets containing anthers were classed as staminate. If no anthers were found in the individual pedicelled spikelets by the completion of sessile spikelet anthesis, the pedicelled spikelets were classed as neuter. Not knowing how many genes were involved, I made four classifications (staminate, staminate minus, neuter plus, and neuter) of the pedicelled spikelet condition in the F_2 progenies. The F_2 plants were classed staminate if the percentage of pedicelled spikelets that were staminate appeared to be the same as in the staminate pedicelled spikelet parent. They were classed staminate minus if the percentage of staminate pedicelled spikelets was slightly less than in the staminate pedicelled spikelet parent. The F_2 progenies were classed neuter if the percentage of staminate pedicelled spikelets was no more than in the neuter pedicelled spikelet parent. They were classed neuter plus if the percentage of staminate pedicelled spikelets was slightly more than in the neuter pedicelled spikelet parent and less than those of the staminate minus classification. There was no attempt to classify the pedicelled spikelets staminate or neuter on the basis of viable pollen.

A dual purpose study was conducted on Redlan, Combine Kafir-60, Combine 7078, Japanese Dwarf broomcorn, KS 6, and 67R1115. The duration of pollination (cross-pollination) part of this study involved the number of days a panicle shed viable pollen. The other part of the study was a visual comparison of anthesis characteristics and duration of the sessile and pedicelled spikelets in an individual panicle. Twelve panicles of each line were used for the duration of pollination (cross-pollination) study,

which was the number of days one panicle would continue to pollinate a cytoplasmic male sterile panicle, as expressed by seed set. The first day anthesis was noticed, pollen was collected in a kraft paper bag and transferred to a cytoplasmic male sterile panicle. This was repeated every day on a different cytoplasmic male sterile panicle until two or three days after completion of all visible anthesis of the pollinator line. Two dates of planting, ten days apart, of cytoplasmic male sterile lines of Combine Kafir-60, Martin, KS 24, KS 9, Wheatland, Westland, 60MHL362, and Redlan gave an extended period of receptive cytoplasmic male sterile panicles. A number of cytoplasmic male sterile panicles were covered with kraft paper bags before anthesis. A portion of those panicles were used in the cross-pollination study, and the remainder were left bagged until the end of season to determine the degree of seed set from selfing. Because of essentially 0% seed set in bagged panicles not pollinated, over five seeds set per panicle were figured as resulting from cross pollination by the fertile panicle rather than selfing. Pollinations were made on the cytoplasmic male sterile panicles as available, regardless of cytoplasmic male sterile lines. Twelve panicles were used for the other part of the study involving visual comparison of the anthesis in sessile and pedicelled spikelets. This was done by recording the first and last dates of sessile spikelet anthesis and the first and last dates of pedicelled spikelet anthesis.

A few of the remaining panicles of plants in the duration of pollination plot were selected at random and sampled by removing an representative number of branchlets from each whorl in the panicle. A count was made of the staminate and neuter pedicelled spikelets, and their associations

with terminal or non-terminal sessile spikelets of racemes were recorded.

RESULTS

Inheritance Study

In a comparison of the F_1 progenies with their parents in the 1968 field nursery, the staminate pedicelled spikelet character appeared to be partially dominate, as it was not expressed to quite the extent in the F_1 's as it was in parents with staminate pedicelled spikelets. The parents that expressed the staminate pedicelled spikelet character in the field did not in all cases express the character under greenhouse conditions.

The segregations of the F_2 progenies for neuter and staminate pedicelled spikelets are shown in Table 1 and 2. Table 1 records the data as the plants were initially classified in the field. Assuming independent inheritance (no linkage) chi-square values gave no indication that any of the F_2 progenies acceptably fit any typical dihybrid ratio. However, the ratios indicated a coupling phase of two linked genes having similar effects. The F_2 progenies 1, 2, and 3 acceptably fit a 3 staminate: 1 neuter ratio ($P= 0.50-0.25$) by combining staminate minus with staminate and neuter plus with neuter. Progeny 4 acceptably fit a 3:1 ratio ($P= 0.10-0.05$) when the staminate minus and neuter plus were combined with the staminate class. Progeny 5 did not acceptably fit a monohybrid ratio with any combination of classes. However, when the staminate minus and neuter plus were combined with the staminate class, it more nearly fit a 3:1 ratio ($P= 0.05-0.025$). Progenies 1 and 2 which were reciprocal crosses showed no difference in inheritance, indicating no cytoplasmic effect.

Table 1. Initial classification of the segregating F_2 progenies and their parents for the pedicelled spikelet condition. Manhattan, Kansas, 1969.

Cross or Parent	Number of Plants				Total
	Staminate	Staminate Minus	Neuter Plus	Neuter	
Combine Kafir-60 X Combine 7078, F_2	239	44	32	51	366
Combine 7078 X Combine Kafir-60, F_2	238	25	30	50	343
Combine Kafir-60 X 67R1115, F_2	513	98	97	121	829
Combine Kafir-60 X Japanese Dwarf broomcorn, F_2	890	71	65	381	1407
P.I. 88022 X Combine Kafir-60, F_2	271	96	47	168	582
Combine 7078	65				
67R1115	31	1	1		
Japanese Dwarf broomcorn	65	2			
P.I. 88022	40				
Combine Kafir-60			19	194	

Table 2. Combined classification of the F_2 progeny classes listed in Table 1. Manhattan, Kansas, 1969.

Cross	F_2 progeny number	Number of plants			Chi-Square	P-Value
		Total	Staminate	Neuter		
Combine Kafir-60 X Combine 7078, F_2	1	366	283	83	1.053	0.50-0.25
Combine 7078 X Combine Kafir-60, F_2	2	343	263	80	0.559	0.50-0.25
Combine Kafir-60 X 67R1115, F_2	3	829	611	218	0.778	0.50-0.25
Combine Kafir-60 X Japanese Dwarf broomcorn, F_2	4	1407	1026	381	3.186	0.10-0.05
P.I. 88022 X Combine Kafir-60, F_2	5	582	414	168	4.425	0.05-0.025

1/ Chi-square calculated on basis of 3:1 segregation.

Duration of Pollination

Table 3 gives the average pollination period of lines with staminate and neuter pedicelled spikelets. Combine Kafir-60 gave 8.2 days of pollination, which was significantly (0.01 level of probability) less than any of the lines with staminate pedicelled spikelets. KS 6 gave 9.1 days of pollination, 0.1 days less than Redlan. The pollination period of Redlan was significantly less (0.05 level of probability) than 67R1115 and also significantly less (0.01 level of probability) than Japanese Dwarf broom-corn and Combine 7078. Japanese Dwarf broomcorn increased the pollination period by 2.0 days over Redlan and 3.0 days over Combine Kafir-60. Combine 7078 increased the days of pollination by 1.2 days over Redlan and 2.2 days over Combine Kafir-60. Orthogonal comparisons were made of the group of lines with neuter pedicelled spikelets with the group of lines with staminate pedicelled spikelets. The group with staminate pedicelled spikelets gave significantly more (0.01 level of probability) days of pollination than the group with neuter pedicelled spikelets.

Visual comparisons of anthesis durations of six sorghum lines are recorded in Table 4. Sessile spikelet anthesis varied from 6.6 days in KS 6 to 8.0 days in Redlan. Pedicelled spikelet anthesis ranged from 5.9 days in Japanese Dwarf broomcorn to 7.5 days in Combine 7078. The duration of pedicelled and sessile spikelet anthesis for individual lines was very close in all but Japanese Dwarf broomcorn. Anthesis lag in pedicelled versus sessile spikelets ranged from 2.1 days in Japanese Dwarf broomcorn to 3.2 days in Combine 7078. Total anthesis periods of Combine Kafir-60 and Redlan were significantly less, (0.01 level of probability) than any of the

Table 3. Pollination period of sorghum lines with staminate or neuter pedicelled spikelets. Manhattan, Kansas. 1969.

Line designation	No. of plants crossed	Pedicelled spikelet condition	Average ^{1/} pollination periods (days)
Combine Kafir-60	12	Neuter	8.2
Redlan	12	Neuter	9.2
67R11115	12	Staminate	9.9
KS 6	12	Staminate	9.1
Japanese Dwarf broom-corn	12	Staminate	11.2
Combine 7078	12	Staminate	10.4
		LSD 5%	.7
		LSD 1%	1.0
		C.V. 9.3%	

^{1/} The pollination period was the number of days one panicle would pollinate cytoplasmic male sterile panicles as expressed by seed set.

Table 4. Visual comparisons of anthesis duration of sorghum lines with neuter or staminate pedicelled spikelets. Manhattan, Kansas. 1969.

Line designation	Pedicelled spikelet condition	Duration of anthesis (days)		Anthesis lag of pedicelled spikelets (days)	1/ Total anthesis period (days)	2/ Percent staminate pedicelled spikelets increased total anthesis period
		Sessile spikelets	Pedicelled spikelets			
Combine Kafir-60	Neuter	7.5			7.5	
Redlan	Neuter	8.0			8.0	
67R1115	Staminate	7.5	7.4	2.5	10.0	25
KS 6	Staminate	6.6	6.8	2.8	9.4	30
Japanese Dwarf broomcorn	Staminate	7.9	5.9	2.1	10.0	21
Combine 7078	Staminate	7.5	7.5	3.2	10.7	30
					LSD 5%	1.0
					LSD 1%	1.3
					C.V.	43.8%
						12.9%

1/ Lag was the number of days of staminate pedicelled spikelet anthesis beyond sessile spikelet anthesis. Lag was non-significant at .05 level of probability.

2/ Period from first day of sessile spikelet anthesis to last date of pedicelled spikelet anthesis.

Table 5. Distribution and percentages of staminate versus neuter pedicelled spikelets observed in six lines with staminate pedicelled spikelets. Manhattan, Kansas. 1969.

	Lines					
	Dwarf Japanese broomcorn	Combine 7078	P.I. 217831	KS 6	67R1115	P.I. 181074 Average
No. of heads studied	3	3	3	2	4	4
Percent of pedicelled spikelets which were staminate	35.3	72.4	83.2	86.7	47.6	69.5 65.8
Percent of total flowers with anthers that were staminate pedicelled spikelets	33.3	46.6	55.1	51.9	37.8	46.3 45.2
Percentage of non-terminal pedicelled spikelets that were staminate	30.6	68.3	83.9	89.4	39.2	66.9 63.0
Percentage of terminal pedicelled spikelets that were staminate	38.8	76.5	82.8	84.5	55.2	71.8 68.3
Percentage of total staminate pedicelled spikelets that were terminal	63.9	52.8	64.0	53.2	61.1	54.4 58.2

1/ Terminal and non-terminal refers to position on racemes.

four lines with staminate pedicelled spikelets. An increase in anthesis duration of 3.2 days was observed between Combine 7078 and Combine Kafir-60. The lowest increase of staminate over neuter pedicelled spikeleted lines was 1.4 days anthesis duration between KS 6 and Redlan. Orthogonal comparisons were made between the group of lines with staminate pedicelled spikelets and the group of lines with neuter pedicelled spikelets. The group with staminate pedicelled spikelet gave significantly more (0.01 level of probability) days of pollination than the group with neuter pedicelled spikelets. Percent increase in total pollination period due to pedicelled spikelet anthesis ranged from 21% in Japanese Dwarf broomcorn, to 30% in KS 6 and Combine 7078.

Distribution of Staminate Pedicelled Spikelets

Distribution of staminate pedicelled spikelets within the panicles of six lines with staminate pedicelled spikelets are recorded in Table 5. Over 50% of the total pedicelled spikelets were staminate in most cases, the average being 65.8%. Pedicelled spikelets accounted for an average of about one-half, 45.2%, of the total spikelets with anthers (sessile and pedicelled). An average of 63.0% of the non-terminal pedicelled spikelets of racemes were staminate. An average of 68.3% of the terminal pedicelled spikelets of racemes were staminate, accounting for an average of 58.2% of the total staminate pedicelled spikelets of a panicle.

DISCUSSION AND CONCLUSIONS

While the segregation of the F_2 progenies cannot be completely explained, it suggested a fairly simple staminate pedicelled spikelet inheritance,

involving probably one major partially dominate allele with modifiers or two linked genes having similar effects. Definite conclusions should not be made without an F_3 generation study. Differences in the combining of classes in progenies 1, 2, and 3 and progenies 4 and 5 cannot be completely justified. Many segregates in progeny 4 were dwarf plants, the panicle of which remained partly in the boot, possibly causing neuter pedicelled spikelets. Japanese Dwarf broomcorn, one of the parents of progeny 4, exhibited staminate pedicelled spikelets; however, in some cases classifications were based on the tiller panicles rather than primary culm panicles. Only primary culm panicles were used to class the F_2 progenies, as tiller panicles were not present in all cases. Japanese Dwarf broomcorn may not be as good a staminate pedicelled spikelet parent as previously thought. The segregation of progeny 5 cannot be explained, however, it came nearer to fitting a 3:1 ratio than any other typical genetic ratio. The deviation from an expected 3:1 ratio may have represented a chance event that could be expected in drawing innumerable 582-plant samples from an infinite number of F_2 plants. The partial dominance of staminate pedicelled spikelets, as indicated by the F_1 progenies, may have caused misclassification in all F_2 progenies. As indicated by non-expression in the greenhouse in some cases, the staminate pedicelled spikelet character is definitely influenced by environmental factors. Therefore, environmental influence may have also caused misclassification.

The data indicated that staminate pedicelled spikelets accounted for an average of 45.2% of the total spikelets with anthers (sessile and pedicelled) in the lines with staminate pedicelled spikelets. According to Ayyangar and Rao (3), the pollen population, not being affected by the

pedicelled condition, would be increased by 45.2% also. This would give a much better pollen supply for seed production purposes.

KS 6, a short panicle line with staminate pedicelled spikelet, gave less days of pollination than Redlan, a long panicle line with neuter pedicelled spikelet. As suggested by Graham (7), the reason may have been that the size of the inflorescence and the number of flowers influenced the duration of anthesis.

In the lines with staminate pedicelled spikelet, the duration of anthesis in the pedicelled spikelets and sessile spikelets of individual lines were almost the same. The pedicelled spikelet lag, duration of staminate pedicelled spikelet anthesis beyond sessile spikelet anthesis, was the most important factor causing an increase in total pollination period. There were significant variations between staminate pedicelled spikelet lines in total duration of anthesis. There were non-significant variations between staminate pedicelled spikelet lines in the lag of staminate pedicelled spikelet anthesis beyond sessile spikelet anthesis. Although the pedicelled spikelet anthesis lag was non-significant these variations in the limited number of lines studied suggested that it may be possible to select, by careful observations and screening, even better material, exhibiting greater duration of pollination.

In conclusion, the staminate pedicelled spikelet character, being fairly simply inherited, could be incorporated into parents of hybrid sorghum relatively easy. Materials containing a higher percentage of staminate pedicelled spikelets with an anthesis lag as large as possible should be selected. Extension of the pollination period and an increase in the amount of pollen of hybrid sorghum male parents could be the deter-

mining factors in a hybrid sorghum seed crop. It is not known to what extent the results reported in this research problem would be applicable under other environments or with other sorghum lines.

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ABSTRACT

Five sorghum, Sorghum bicolor (L.) Moench, crosses were made to study the inheritance of staminate pedicelled spikelets. The inheritance study was made on the F_2 generation at Kansas State University, 1969, Manhattan, Kansas. The segregation of the F_2 progenies suggested a fairly simple staminate pedicelled spikelet inheritance, involving probably one major dominate allele with modifiers or two linked genes having similar effects. Definite conclusions should not be made without an F_3 generation study.

A dual purpose study was conducted on four sorghum lines with staminate pedicelled spikelets and two lines with neuter pedicelled spikelets. The duration of pollination (crossing pollination) part of the study was the number of days one panicle would continue to pollinate a cytoplasmic male sterile panicle, as expressed by seed set. Increases in the pollination period by the lines with staminate pedicelled spikelet were highly significant over the lines with neuter pedicelled spikelets. The other part of the study involved visual comparisons of anthesis duration of sorghum lines with neuter or staminate pedicelled spikelets. These comparisons also showed a highly significant increase in the anthesis period by the lines with staminate pedicelled spikelets, due to duration of the staminate pedicelled spikelet anthesis beyond sessile spikelet anthesis.

The distribution of staminate pedicelled spikelets within the panicle was studied on six sorghum lines with staminate pedicelled spikelets. An average of 65.8% of the pedicelled spikelets were found to be staminate. Staminate pedicelled spikelets accounted for 45.2% of the total spikelets with anthers.