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Reproduction and morphology of two annual taxa of Sporobolus (Poaceae).

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REPRODUCTION AND MORPHOLOGY OF TWO ANNUAL TAXA OF SPOROBOLUS (POACEAE)

A Thesis

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THESIS ACCEPTANCE

Accepted for the faculty of the Graduate College, University of Nebraska, in partial fulfillment of the requirements for the degree Master of Arts, University of Nebraska at Omaha.

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E. W. S.

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ABSTRACT

Morphology and reproduction were studied in two annual taxa of *Sporobolus* (Poaceae) at eight locations in eastern Nebraska. Estimated percent cleistogamy was 93.2% in *S. neglectus* and 83.8% in *S. vaginiflorus* in specimens collected throughout the 1982 growing season. Anthers of cleistogamous florets were smaller in size and lower in number than anthers of chasmogamous florets. Pollen-ovule ratios were significantly lower in cleistogamous than in chasmogamous florets and cleistogamous florets showed precocious development. Agamospermous reproduction may also be present in the taxa. The lack of intermediate forms between the two taxa in the locations studied may be attributable to the high incidence of cleistogamous reproduction.

INTRODUCTION

Two annual taxa of the genus *Sporobolus* R. Br. (Poaceae) occur in eastern Nebraska (Great Plains Flora Assoc., 1977). *Sporobolus neglectus* Nash and *Sporobolus vaginiflorus* (Torr.) Wood are weedy annuals of disturbed areas. They are apparently indistinguishable vegetatively (Sutherland, 1975), thus, identification is based on differences in spikelet morphology (Pohl, 1966; Reeder, 1975). Shinners (1954) united the taxa under *S. vaginiflorus* based on specimens from Texas with intermediate spikelet morphology.

Cleistogamous reproduction in the taxa was reported by Hackel (1906) and Ritzerow (1908). The taxa follow a general tendency of cleistogamous grasses to have confined florets and reduced floral structures. Panicles are commonly sheath-enclosed (Fernald, 1950) and the florets borne on such panicles are unable to open at anthesis. In addition, anthers are frequently reduced in size and anthers and lodicules are sometimes reduced in number (Fernald, 1950; Hackel, 1906; Ritzerow, 1908).

Agamospermy is not known to occur in any annual grass and was not found in *S. vaginiflorus* by Brown and Emery (1958). However, extremely reduced and apparently non-functional anthers (Fernald, 1950) in both *S. neglectus* and *S. vaginiflorus* suggest its presence.

The primary objectives of this study were: (1) to determine if *S. neglectus* and *S. vaginiflorus* occur sympatrically in eastern Nebraska, and if their flowering phenologies overlap; (2) to determine if the taxa remain distinct in sympatric populations or whether intermediates, as described by Shinners (1954), are found; (3) to quantify chasmogamous and cleistogamous reproduction in the taxa; (4) to correlate spikelet morphology with the types of reproduction present; and (5) to determine if there is a relationship between the frequency of chasmogamous reproduction present and the occurrence of intermediate forms. Secondary objectives were to describe the life histories of the taxa and to differentiate them vegetatively.

METHODS AND MATERIALS

The life histories of the taxa were studied in natural populations in eastern Nebraska from May 1982 through July 1983. Observations were made at eight sites (see Appendix). All of the study sites were along roadways which had been subject to frequent mowing during previous growing seasons. Sporobolus neglectus and S. vaginiflorus occurred sympatrically at seven of the eight study sites. Specimens were collected at all eight sites during the 1982 growing season. More extensive collections, however, were made from sites #1 and #2 from the time of first flowering until the completion of fruit dispersal. Specimens were preserved by pressing.

Field identification of the species was difficult. Populations of seedlings were tentatively located in the spring of 1982 based on habitat and such non-quantified characters as color, fine texture and wiry, geniculate culms. The occurrence of the two species sympatrically and their lack of distinctive vegetative characters made them indistinguishable during most of the growing season. Even following the onset of flowering, field identification was difficult due to the small spikelet size.

Morphological and reproductive characters were examined on 95 randomly selected specimens collected between August 15, 1982 and October 15, 1982. Characters of spikelet morphology were recorded for two spikelets per specimen, the terminal spikelet of the terminal panicle and the terminal spikelet of a mid-culm panicle. Fruit length, anther length and number, and the presence or absence of cleistogamy were recorded when possible for six florets per specimen, three florets from the terminal panicle and three florets from a mid-culm panicle. In each panicle the terminal floret, a mid-panicle floret, and the lowest floret were used. The frequency of cleistogamy of these six florets in 65 specimens was used as an estimate of percent cleistogamy. The occurrence of developing fruits with persistent anthers in post-flowering florets is an indication of the failure of the florets to open at anthesis and was used as a measure of cleistogamous reproduction.

Measurement of vegetative characters, spikelet characters, anther length and fruit length were made with an ocular micrometer on a dissecting microscope. Anther number was determined by counting the number of anthers in unopened florets. Mean pollen diameter was determined by measuring the maximum diameter of 15 pollen grains per anther using an ocular micrometer on a compound microscope. The pollen was mounted in lactophenol cotton blue (0.02% cotton blue in 1:10 acetic acid:lactophenol) before measuring and pollen stainability, as an indicator of viability, was noted simultaneously. Pollen-ovule ratios were determined by counting the number of pollen grains removed from unopened anthers.

Germination studies were done on a random sample of fruits collected in October, 1982 from mature plants. Seedlings were grown to maturity in the greenhouse and were used for observation of early vegetative growth.

Statistical analyses were performed using Minitab Release 81.1

programs (Ryan, Joiner and Ryan, 1981) on a VAX 11/780 computer.

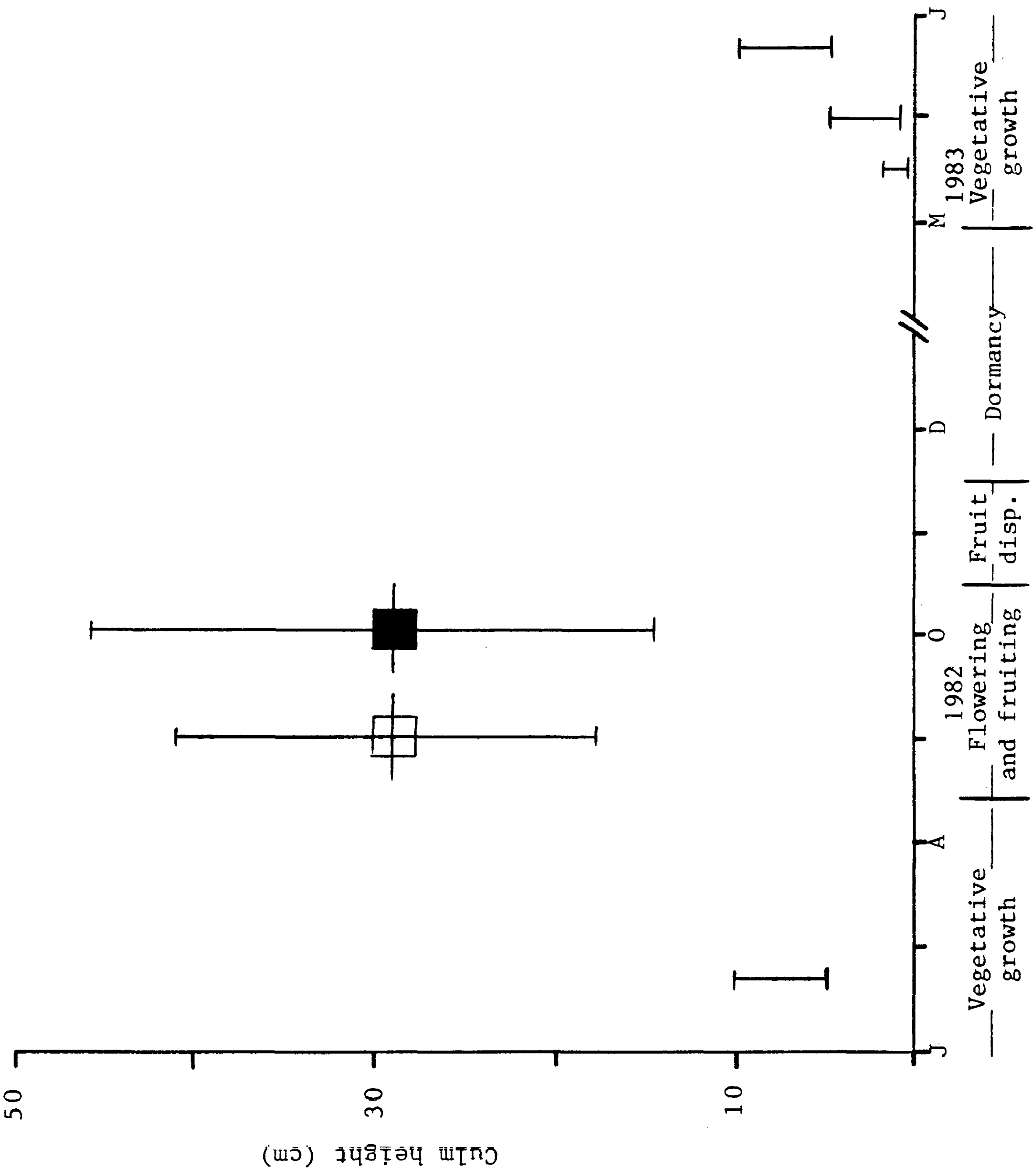
RESULTS

Life History

Sporobolus neglectus and *S. vaginiflorus* were found to be locally abundant in eastern Nebraska, but somewhat restricted in their range of habitats. They were always found along roadways or other open areas which were subject to periodic drying and frequent disturbance such as mowing. Although they were not found in areas where other weedy species were abundant, they were sometimes associated with limited stands of weedy grasses such as *Digitaria spp.* (crabgrasses) and *Setaria spp.* (foxtails), and other weedy annuals.

The major life history events of the species are shown in Fig. 1. In 1982, I was unable to recognize seedlings in the field until late June. In 1983, germination occurred in late April in the 1982 study areas, with seedlings in both years attaining a height of 5-10 cm by late June. I was unable to distinguish the two taxa vegetatively, therefore the range of heights shown from May to August includes both taxa. The first plant in flower was observed on August 20, 1982 at site #8 and was identified as *S. vaginiflorus*. Plants at all other study sites began flowering within the following 12 days. The two species flowered synchronously at all of the study sites. The mean height of each taxon is shown for collections made between August 15, 1982 and October 15, 1982 when plants were essentially mature and could be separated by spikelet characteristics. A one-way analysis of variance of collection data showed no significant change in height during this time period for either taxon. Although *S. vaginiflorus*

Figure 1. Phenology and culm height of *S. neglectus* and *S. vaginiflorus* in natural populations, June 1982 - July 1983. Vertical bars represent range of culm heights (May - August). Mean, one standard error and range shown during flowering and fruiting period for both species (closed square is *S. vaginiflorus*, open square is *S. neglectus*).



Culm height (cm)
50
30
10
J
A
O
D
M
J
Vegetative growth
1982
Flowering and fruiting
Fruit disp.
Dormancy
1983
Vegetative growth

had a wider range of heights, there was no significant difference in mean height of the two taxa during the same time period.

In these taxa the spikelets, each consisting of one floret, are borne on one or more panicles per culm. Single culms produce as many as six panicles, often with a panicle at each node. All panicles, except in many cases the terminal one, were sheath-enclosed until after fruit set. Fruits matured on or about October 15 in 1982 and dispersal followed. In many plants fruit dispersal and exposure of the sheath-enclosed panicle by spreading back of the sheath occurred simultaneously. In 1982, plant death and fruit dispersal coincided with the time of killing frost (early November), but the freezing temperatures may not have been the primary cause of these events. Fruit dispersal was complete by November 15, 1982.

Germination

Sporobolus vaginiflorus had significantly higher germination rates in the light than in the dark ($\chi^2 = 56.17$, $p < 0.01$) and fruits stored at room temperature germinated significantly better than those stored in the cold ($\chi^2 = 4.24$, $p < 0.05$). There was no significant change in germination rates following cold storage (0-4° C) for 13, 24, and 90 days for S. vaginiflorus. All treatments, except darkness, showed significantly higher germination rates for S. vaginiflorus, which had an overall germination rate of 73.3% (S.E. = 3.36). This was significantly higher ($\chi^2 = 5.64$, $p < 0.05$) than the 65.4% (S.E. = 2.58) overall rate for S. neglectus. Sporobolus neglectus showed no significant differences in germination rates for germination in the light or the dark, nor following cold storage of fruits for periods of 13, 24 and 90 days.

Morphology

Measurement and observation of glume length, lemma length and lemma pubescence on the terminal spikelet of the terminal panicle resulted in two distinct groups (Fig. 2); (1) specimens with pubescent lemmas greater than 3.0 mm in length and glumes more than 3.0 mm long which corresponded to descriptions of *S. vaginiflorus*, and (2) specimens with glabrous lemmas less than 3.0 mm long and glumes less than 3.0 mm long which corresponded to *S. neglectus*. Specimens were assigned tentative species designations based on these differences. (The spikelet with a glume 2.5 mm long and a pubescent lemma shown in Fig. 2, was atypical of the specimen since all other glumes on the specimen's terminal panicle were greater than 3.5 mm in length, and this specimen was designated as *S. vaginiflorus*.) Other characters, both vegetative and reproductive, were analyzed based on species designations using the above criteria.

There were highly significant differences between the species in mean values for all terminal and mid-culm spikelet characters measured (Table I). The combined data from terminal and mid-culm spikelets also showed highly significant differences between the species. However, its usefulness for recognition was limited because of differences within species due to location of spikelets on the culm (Table II). Spikelet measurements for both species were

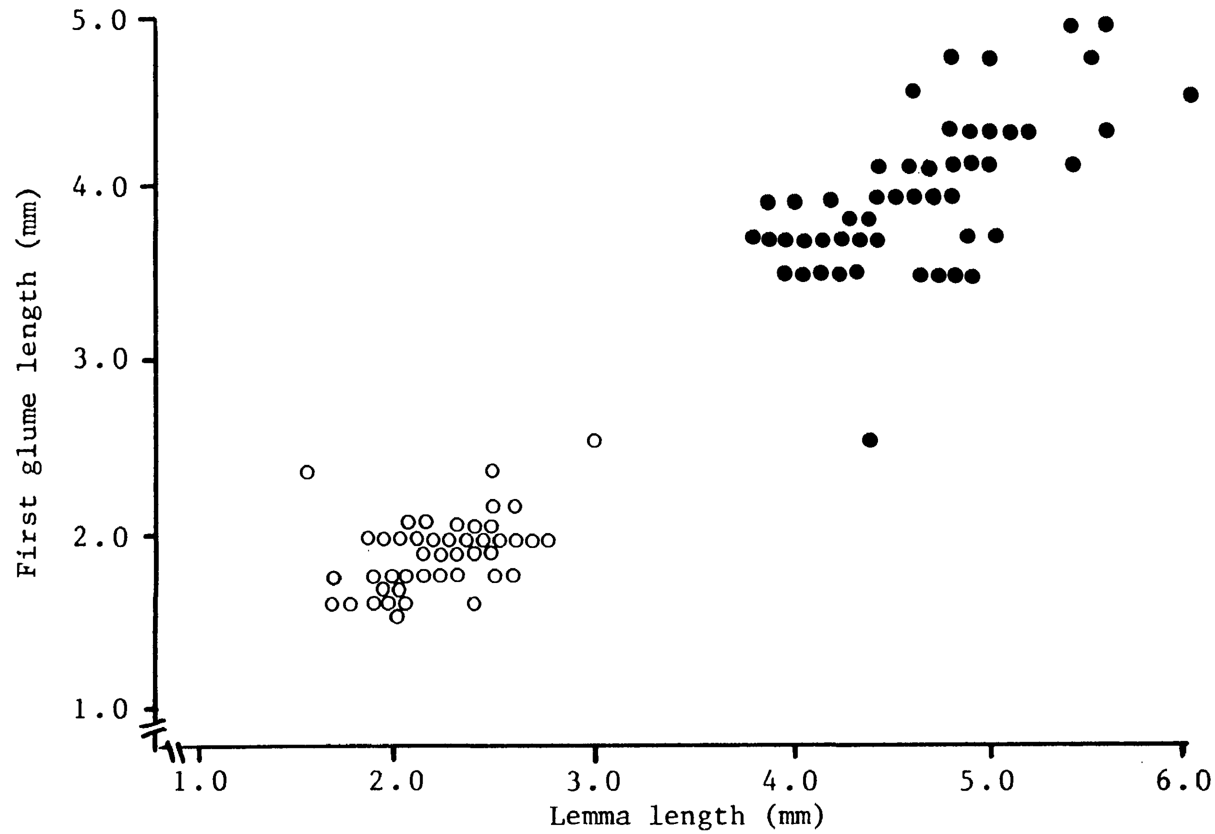


Figure 2. Scatter diagram of first glume length and lemma length, terminal spikelet of terminal panicle. Closed circles are pubescent lemmas, open circles are glabrous lemmas. (n = 95)

Table I. Differences in terminal and mid-culm spikelet characters by species [a]

	n	Glume 1 length (mm)	Glume 2 length (mm)	Lemma length (mm)	Lemma width (mm)
Terminal spikelet characters					
Sporobolus neglectus	45	1.91 ± 0.03	2.08 ± 0.04	2.29 ± 0.05	0.49 ± 0.010
Sporobolus vaginiflorus	50	3.99 ± 0.06	4.50 ± 0.06	4.64 ± 0.07	0.67 ± 0.015
t-value [b]		29.15**	33.60**	27.87**	9.84**
Mid-culm spikelet characters					
Sporobolus neglectus	45	1.78 ± 0.06	1.88 ± 0.07	1.96 ± 0.04	0.44 ± 0.014
Sporobolus vaginiflorus	50	3.53 ± 0.10	3.76 ± 0.10	3.96 ± 0.10	0.57 ± 0.017
t-value		15.23**	15.84**	17.96**	6.25**
Combined data of terminal and mid-culm spikelet characters					
Sporobolus neglectus	90	1.82 ± 0.03	1.96 ± 0.03	2.12 ± 0.04	0.46 ± 0.008
Sporobolus vaginiflorus	100	3.76 ± 0.06	4.13 ± 0.07	4.30 ± 0.07	0.62 ± 0.012
t-value		28.82**	28.67**	27.39**	10.32**

[a] Values represent mean ± one S.E.

[b] The significance of the t-tests is as follows: $p < 0.01$, **.

Table II. Differences in terminal and mid-culm spikelet characters by location [a]

	n	Glume 1 length (mm)	Glume 2 length (mm)	Lemma length (mm)	Lemma width (mm)
Sporobolus neglectus					
Terminal	45	1.91 ± 0.03	2.08 ± 0.04	2.29 ± 0.05	0.49 ± 0.010
Mid-culm	45	1.78 ± 0.06	1.88 ± 0.07	1.96 ± 0.04	0.44 ± 0.014
t-value [b]		1.85	2.56*	5.58**	3.31**
Sporobolus vaginiflorus					
Terminal	50	3.99 ± 0.06	4.50 ± 0.06	4.64 ± 0.07	0.67 ± 0.015
Mid-culm	50	3.52 ± 0.10	3.76 ± 0.10	3.96 ± 0.10	0.57 ± 0.017
t-value		4.07**	6.44**	5.36**	4.37**

[a] Values represent mean ± one S.E.

[b] The significance of the t-tests is as follows: $p < 0.01$, **; $p < 0.05$, *.

lower and generally showed greater variability (larger standard error) in the mid-culm panicle. For all except one, mid-culm characters for both species showed highly significant reductions in size. The exception was first glume length in S. neglectus which only approached significance (p = 0.07). The lower mid-culm values were not attributable to immaturity since even the smallest spikelets in both species contained maturing ovaries. Spikelet characters of the mid-culm panicle showed some overlap (Fig. 3), and therefore, were less useful for distinguishing species than spikelet characters of the terminal panicle (Fig. 2).

Analysis of vegetative characters (Table III) was based on separation of the species using criteria shown in Fig. 2. There was a significant difference in mean mid-culm blade width, but even this character shows a great deal of overlap between the species (Fig. 4).

Reproduction

Cleistogamous florets were present in all individuals of both species, with some specimens being entirely cleistogamous. Chasmogamous florets, when present, were always located in the upper portion of the terminal panicle. Frequently, cleistogamous florets matured earlier than chasmogamous florets of the same specimen, as evidenced by the presence of maturing ovaries with persistent anthers at the time of anthesis in chasmogamous florets. Only rarely was there chasmogamous fruit production (developing fruits without persistent anthers).

Percent cleistogamy was significantly higher in S. neglectus (93.2%) than in S. vaginiflorus (82.8%) as estimated from data from

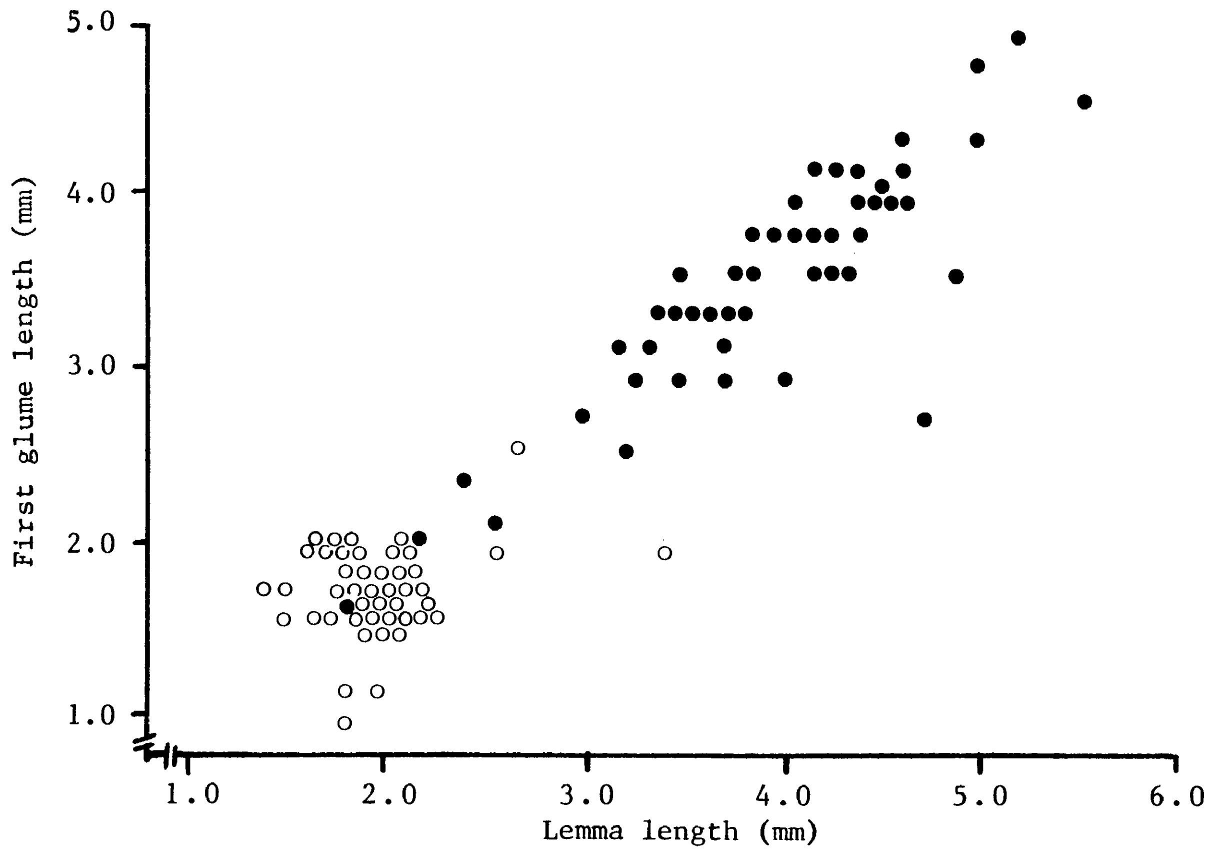


Figure 2. Scatter diagram of first glume length and lemma length, terminal spikelet of mid-culm panicle. Closed circles are pubescent lemmas (S. vaginiflorus), open circles are glabrous lemmas (S. neglectus). Species designation based on morphology of terminal spikelet of terminal panicle shown in Fig. 2. (n = 95)

Table III. Differences in vegetative characters [a]

Character	*Sporobolus neglectus* (n = 45)	*Sporobolus vaginiflorus* (n = 50)	t-value [b]
Culm height (cm)	29.16 ± 0.98	28.92 ± 0.95	- 0.18
Mid-culm width (mm)	0.57 ± 0.01	0.56 ± 0.01	- 0.80
Mid-culm internode length (mm)	44.51 ± 1.24	48.36 ± 1.65	1.86
Mid-culm blade length (mm)	35.84 ± 1.73	32.28 ± 1.74	- 1.45
Mid-culm blade width (mm)	1.41 ± 0.02	1.27 ± 0.03	- 4.17**

[a] Values represent mean ± one S.E.

[b] The significance of the t-tests is as follows: $p < 0.01$, **.

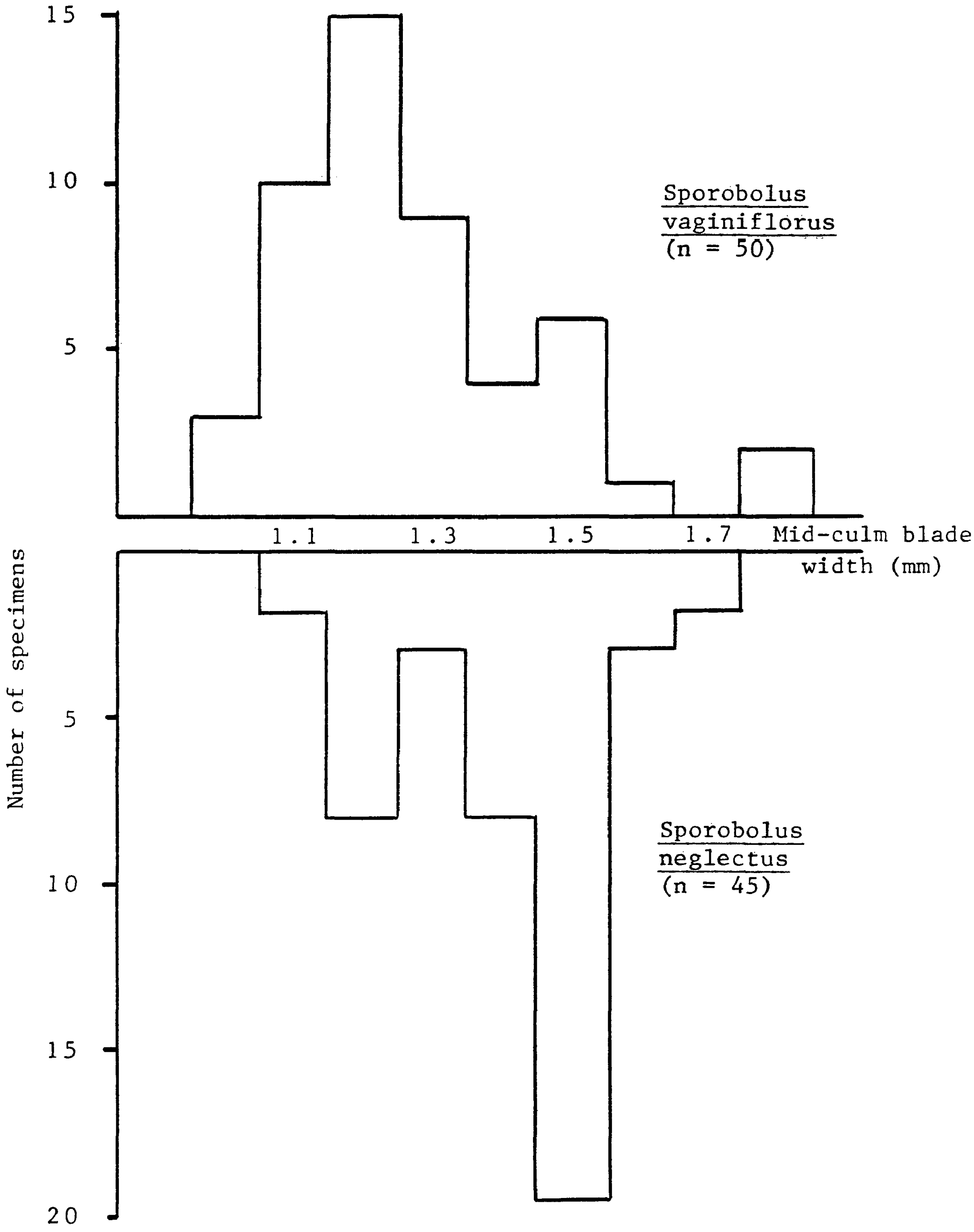


Figure 4. Mid-culm blade width in *S. vaginiflorus* and *S. neglectus*.

six florets for each of 65 specimens (Table IV). This difference was due to the three florets from the terminal panicle since there were no chasmogamous florets on the mid-culm panicle. Based on the examination of three florets per panicle the frequency of cleistogamy in the terminal panicle of S. neglectus was 86.5%, of S. vaginiflorus 65.7%. Examination of all florets of the terminal panicle of 63 specimens gave similar results (S. neglectus 86.4%, S.E. = 4.96; S. vaginiflorus 51.9%, S.E. = 5.21). There was a highly significant difference in percent cleistogamy associated with floret position in the terminal panicle for both species (Table IV).

Anthers fell into three size categories in both species (Figs. 5, 6, and 7): (1) Large anthers (S. neglectus > 0.8 mm, S. vaginiflorus > 1.4 mm), if present, were found only in terminal florets and in most cases appeared to be associated with chasmogamous reproduction; only rarely were maturing ovaries associated with large anthers in unopened florets. (2) Mid-sized anthers (S. neglectus 0.5 mm, S. vaginiflorus 0.7-1.0 mm), were normally tangled in the stigma atop the developing ovary and occurred only in the terminal panicle. (3) Small anthers (S. neglectus < 0.3 mm, S. vaginiflorus < 0.5 mm), found beside the developing ovary and apparently not associated with the stigma, were the most common size observed. Although florets with these small anthers were often sheath-enclosed, they were sometimes found in portions of the terminal panicles which were exerted from the sheaths. All three size classes of anthers occurred in terminal florets of terminal panicles (Fig. 8), but

Table IV. Frequency of cleistogamous florets by culm and panicle position

Location	*Sporobolus neglectus* (n = 32)	*Sporobolus vaginiflorus* (n = 33)	χ^2-value [a]
Terminal panicle			
Terminal floret	65.6	27.3	
Mid-panicle floret	93.8	75.8	
Lowest floret	100.0	93.9	
χ^2-value [a]	18.33**	34.76**	
Mid-culm panicle			
Terminal floret	100.0	100.0	
Mid-panicle floret	100.0	100.0	
Lowest floret	100.0	100.0	
Estimated percent cleistogamy for all locations	93.2	82.8	9.95**

[a] The significance of the χ^2-tests is as follows: $p < 0.01$, **.

Figures 5-7. Large anthers exerted from spikelet (Fig. 5), mid-sized anthers tangled in stigma atop the ovary (Fig. 6), and small anthers beside maturing ovary (Fig. 7). All figures are 10X. *Sporobolus vaginiflorus* on the left, *S. neglectus* on the right in all figures. (a = anther, g1 = first glume, g2 = second glume, l = lemma, o = ovary, p = palea and s = stigma)

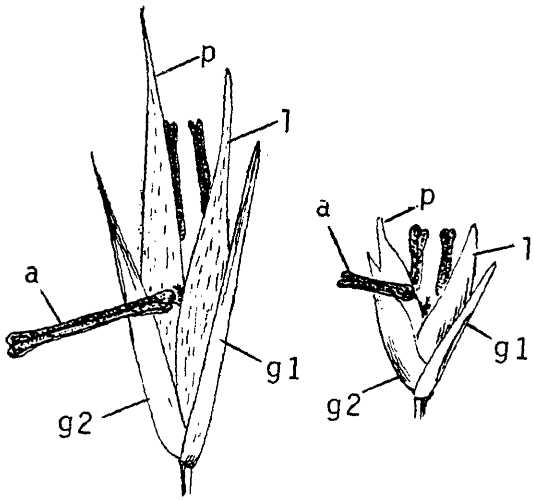
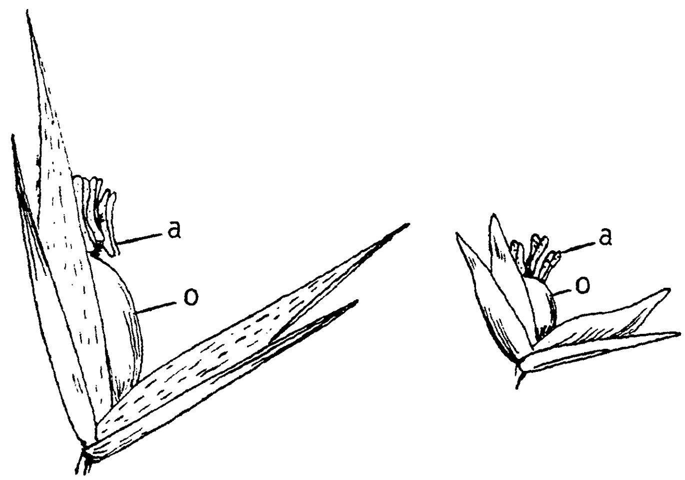


Figure 5.

Figure 6.



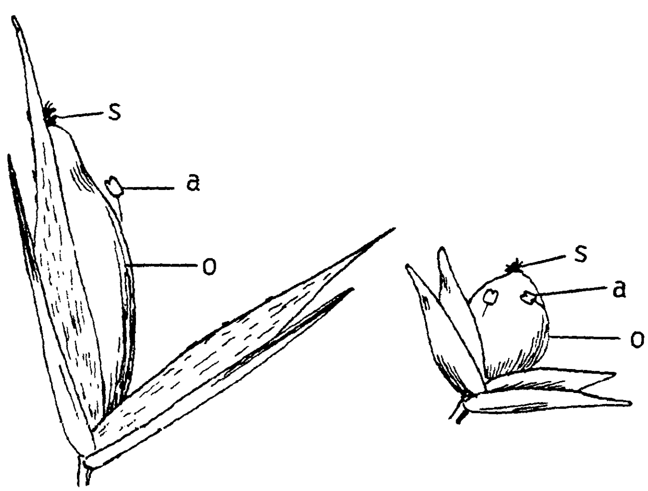


Figure 7.

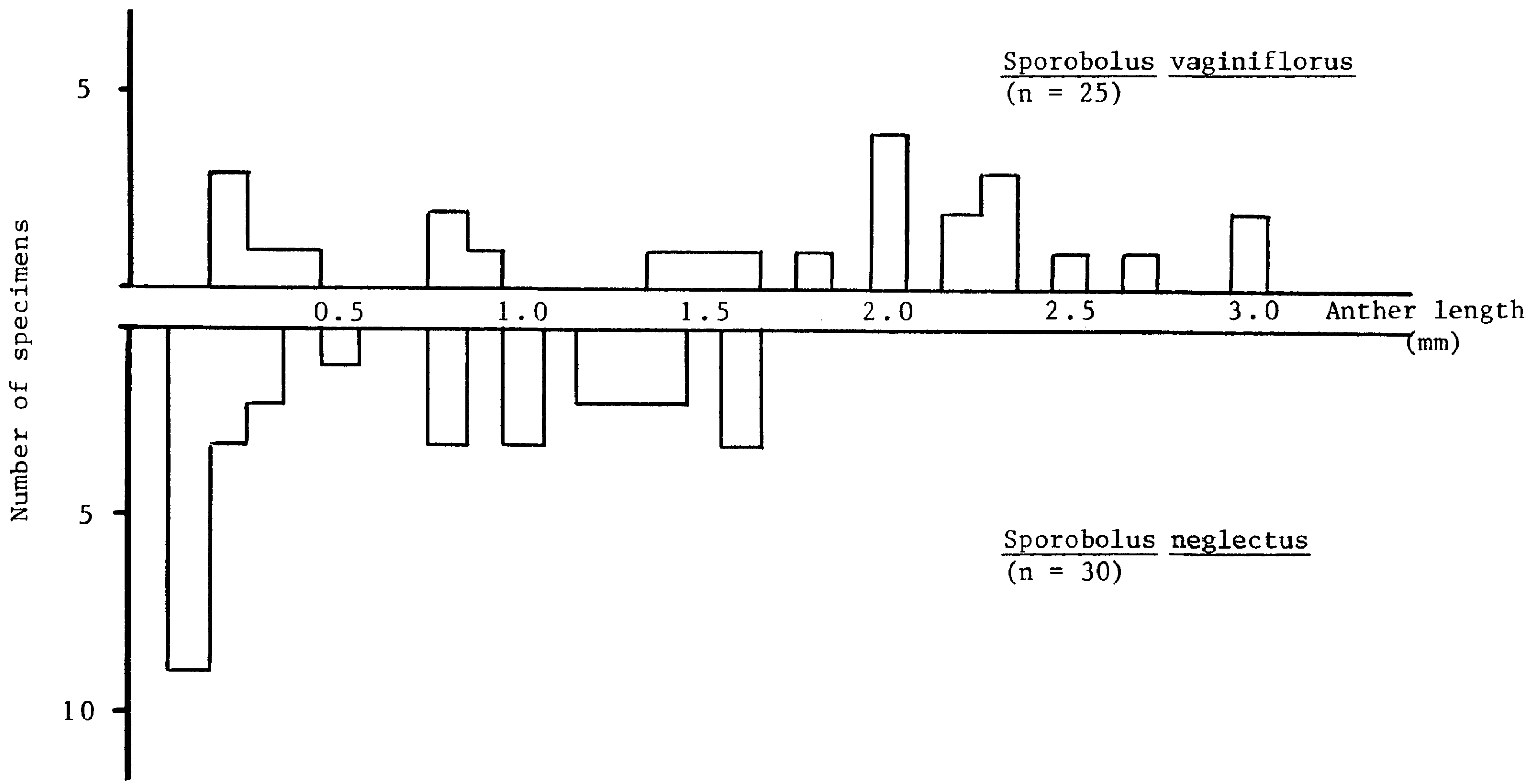


Figure 8. Frequency distribution of anther length in terminal floret of terminal panicle.

terminal florets of mid-culm panicles had only the smallest anther size class (Fig. 9).

There was a reduction in anther number (Fig. 10) associated with the reduction in anther size. The difference in mean anther size and mean anther number associated with the terminal floret of the mid-culm panicle as compared to the terminal floret of the terminal panicle was highly significant in both species (Table V).

The significant reductions in the measurements of the terminal spikelets of the mid-culm panicle compared to the terminal spikelets of the terminal panicle (Table II), were not necessarily related to the increased occurrence of cleistogamy at the mid-culm position. Using lemma length as an indicator of spikelet size, there was a significant difference in mean size of chasmogamous and cleistogamous spikelets in the terminal panicle of S. neglectus, but not of S. vaginiflorus (Table VI). Furthermore, there was a highly significant reduction in mean size of cleistogamous spikelets of the mid-culm panicle when compared to the cleistogamous spikelets of the terminal panicle in both species.

The combined data for terminal spikelets of the terminal and the mid-culm panicle, showed positive correlations between anther number, anther length, lemma length and the presence of chasmogamy for both species (Table VII). The weak correlations between lemma length and other characters in S. vaginiflorus reflect the lack of size differences in cleistogamous and chasmogamous spikelets shown in Table VI. The low correlations with chasmogamy in S. neglectus may be

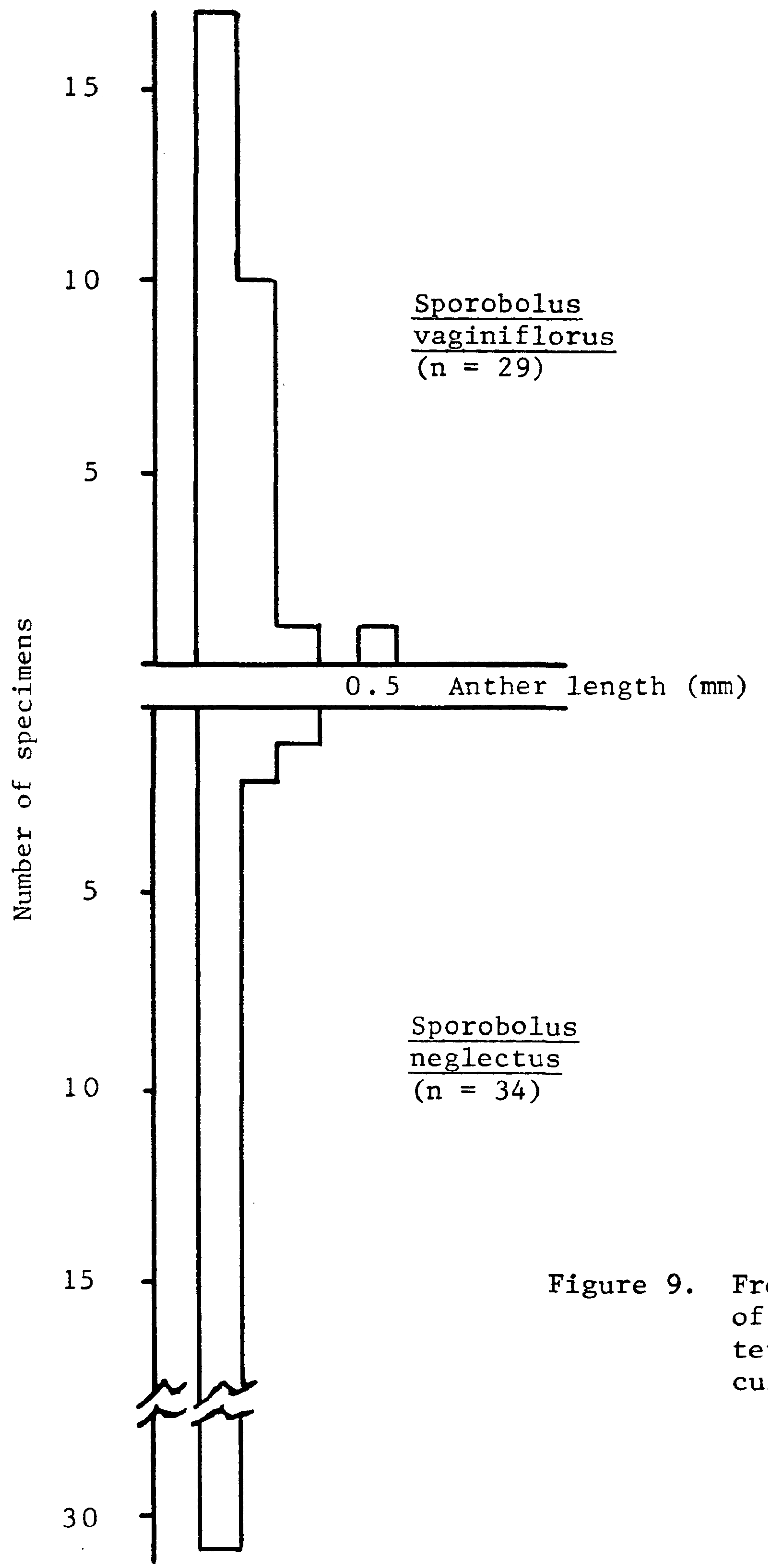


Figure 9. Frequency distribution of anther length in terminal floret of mid-culm panicle.

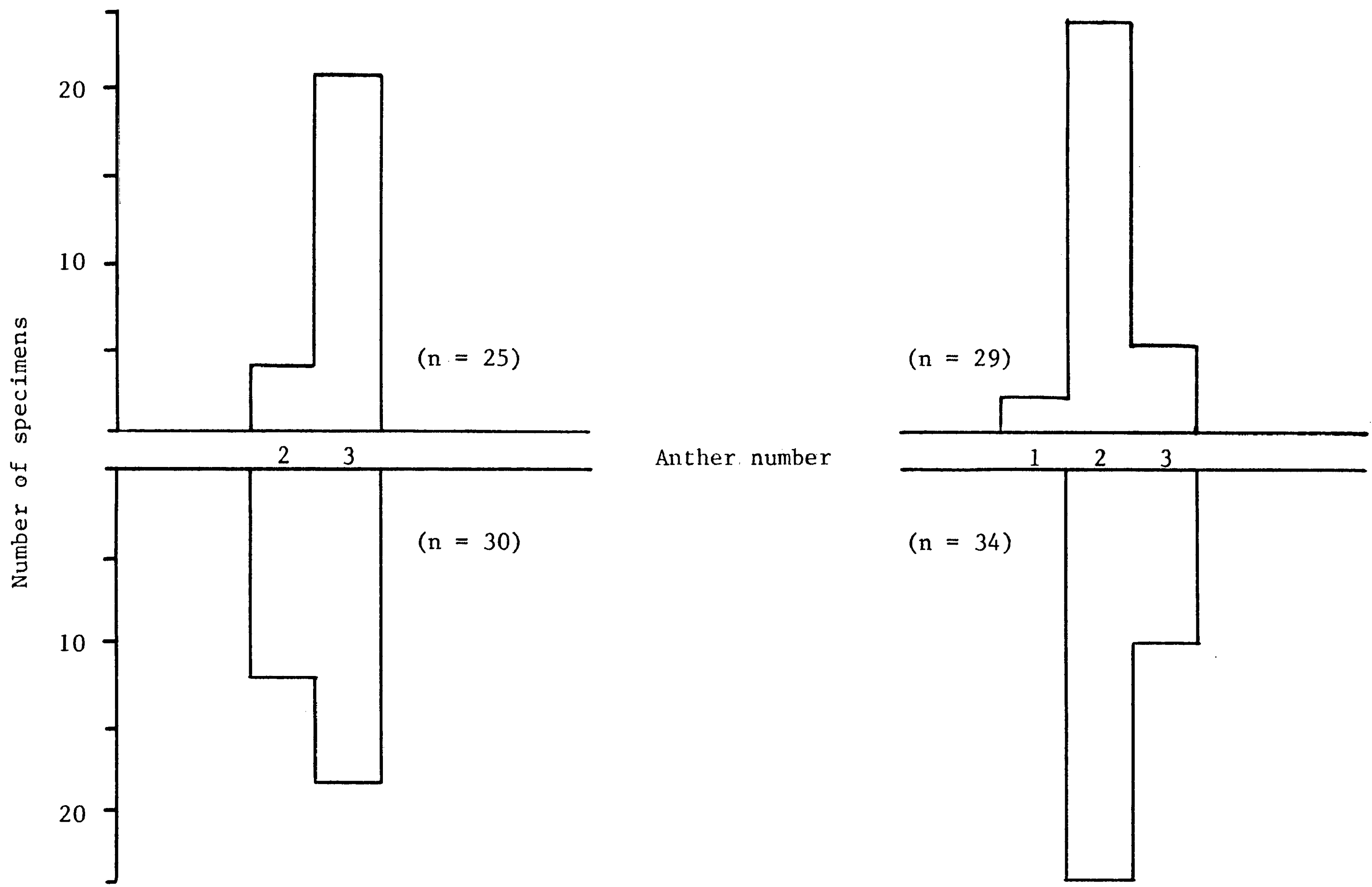


Figure 10. Frequency distribution of anther number in terminal florets of terminal and mid-culm panicles. Terminal florets of terminal panicle on the left; terminal florets of mid-culm panicle on the right. Upper bars are _S. vaginiflorus_, lower bars are _S. neglectus_.

Table V. Differences in anther length and anther number by location [a]

	n	Anther length (mm)	Anther Number
Sporobolus neglectus			
Terminal panicle, terminal floret	30	0.69 ± 0.10	2.6 ± 0.09
Mid-culm panicle, terminal floret	34	0.11 ± 0.01	2.3 ± 0.08
t-value [b]		5.56**	2.53**
Sporobolus vaginiflorus			
Terminal panicle, terminal floret	25	1.62 ± 0.18	2.8 ± 0.07
Mid-culm panicle, terminal floret	29	0.16 ± 0.02	2.1 ± 0.09
t-value		8.09**	6.26**

[a] Value represent mean ± one S.E.

[b] The significance of the t-tests is as follows: $p < 0.01$,**.

Table VI. Lemma length of cleistogamous (CL) and chasmogamous (CH) spikelets as a function of position [a]

Species	Terminal CH spikelet	Terminal CL spikelet	Mid-culm CL spikelet
Sporobolus neglectus	2.48 ± 0.07 (14)	2.21 ± 0.05 (31)	1.96 ± 0.04 (45)
t-value [b]		$- 3.18^{**}$	3.88^{**}
Sporobolus vaginiflorus	4.67 ± 0.09 (34)	4.58 ± 0.13 (16)	3.96 ± 0.10 (50)
t-value		$- 0.52$	3.76^{**}

[a] Values represent mean $\pm$ one S.E. Sample sizes are given in parentheses.

[b] The significance of the t-test is as follows: $p < 0.01$, **.

Table VII. Correlation among anther length, anther number, lemma length and chasmogamy [a]

Species	Anther length	Anther number	Lemma length
Sporobolus neglectus (n = 64)			
Anther number	0.457		
Lemma length	0.622	0.409	
Chasmogamy	0.346	0.023	0.213
Sporobolus vaginiflorus (n = 54)			
Anther number	0.645		
Lemma length	0.329	0.137	
Chasmogamy	0.668	0.496	0.209

[a] Values are Pearson-r correlation coefficients.

attributable to sampling error due to its low degree of chasmogamy.

In a sample of anthers ranging from 0.1 mm to 2.4 mm in length, taken from 11 different plants of _S. vaginiflorus_, the number of pollen grains ranged from 0 to 2826. The number of anthers per ovule ranged from 2 to 3 giving estimated pollen-ovule ratios between 0 and 8478. In a similar sample from _S. neglectus_, anthers ranged in length from 0.1 mm to 1.5 mm, the number of pollen grains ranged from 0 to 1564 and the number of anthers per ovule was 2 or 3, giving estimated pollen-ovule ratios between 0 and 4592. The number of pollen grains showed strong correlation with the anther length (_S. neglectus_, r = 0.926; _S. vaginiflorus_, r = 0.969) (Fig. 11). Although not quantified, there was frequently an observed decrease in stainability of pollen from small anthers with low pollen counts suggesting decreased viability. Other characters related to reproduction which showed significant differences between the species were mean pollen diameter, fruit length, and potential seed production (number of spikelets per culm) (Table VIII).

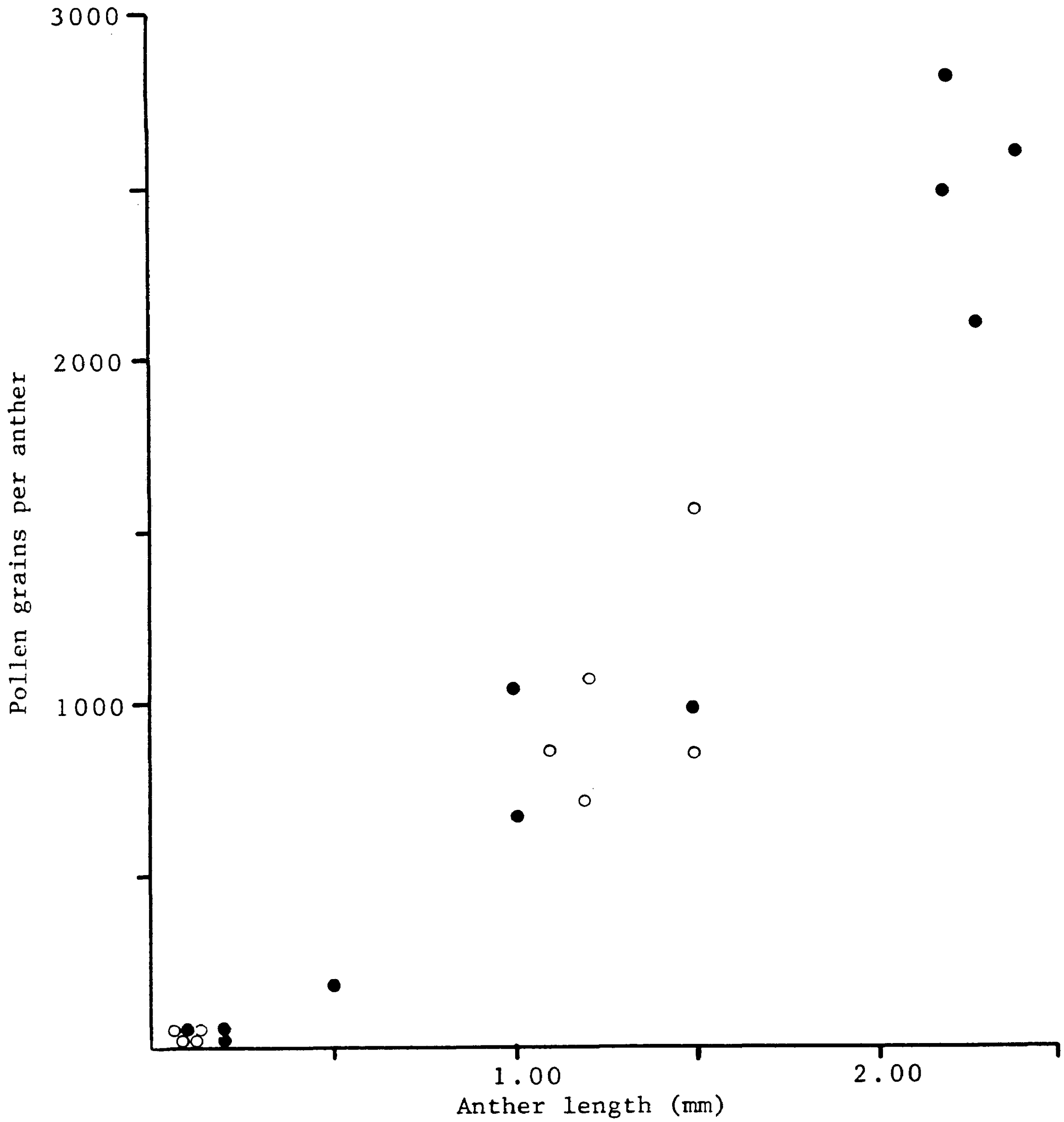


Figure 11. Relationship of number of pollen grains per anther to anther length. Closed circles are S. vaginiflorus, open circles are S. neglectus.

Table VIII. Differences in other reproductive characters [a]

Species	Pollen diam. (μm)	Fruit length (mm)	Spikelets per culm
Sporobolus neglectus	25.4 ± 0.24 (37)	1.2 ± 0.05 (35)	72.1 ± 4.76 (20)
Sporobolus vaginiflorus	26.2 ± 0.21 (37)	2.1 ± 0.03 (35)	35.7 ± 3.59 (15)
t-value [b]	2.67**	13.30**	6.10**

[a] Values represent mean $\pm$ one S.E. Sample sizes are given in parentheses.

[b] The significance of the t-tests is as follows: $p < 0.01$, **.

DISCUSSION

Sporobolus neglectus and S. vaginiflorus have similar life histories (Fig. 1) characterized by a relatively long period of vegetative growth, a short period of flowering and fruiting, and death following seed set. This phenological pattern could be advantageous in habitats which are subject to mowing during the early and middle parts of the growing season, when the growth rate of many plants common to disturbance habitats is highest. Small size during this early part of the growing season, with flowering and fruiting postponed until later helps to ensure survival and fruit production. Such recurrent, early season disturbance is probably needed for the maintenance of these species. Their absence in unmowed and other infrequently disturbed habitats which are populated by larger weedy species suggests an inability to compete successfully with such species without recurrent disturbance. They may be limited in distribution to areas of early succession, at least in part, by their small size.

Although the similarity of the life histories of the species was striking, there appeared to be quantitative differences in their life-cycle strategies. Sporobolus neglectus had a higher percent cleistogamy, smaller fruits, a greater potential seed production and a lower germination rate than did S. vaginiflorus.

The percent cleistogamy reported here probably underestimates the proportion of fruits produced by cleistogamy in 1982, since developing fruits were rarely seen in chasmogamous florets. The lack of chasmogamous fruits precluded the inclusion in this study of a comparison of chasmogamous and cleistogamous fruits and the seedlings they produced. Studies of energy allocation to cleistogamous and chasmogamous seed production and of relative competitive abilities of the species are needed to determine the significance of the reproductive differences seen in this study.

Nearly all reproduction was cleistogamous in 1982; however, using pollen-ovule ratio as an indicator of breeding system (Cruden, 1977), S. neglectus and S. vaginiflorus potentially cover the entire range of systems from cleistogamy to xenogamy. Despite the high percent cleistogamy in the species, the presence of chasmogamous florets in the terminal panicles maintains xenogamy within the populations studied. Longer term study is needed to determine the importance of chasmogamy in the species.

Histologic study is needed to determine the mechanism of pollination in those cleistogamous florets whose reduced anthers did not appear to have been in contact with the stigma. The absence of pollen in some of these anthers and the decreased pollen stainability associated with them may suggest agamospermy as part of the breeding system, in spite of its reported absence in S. vaginiflorus (Brown and Emery, 1958). Study of embryo sacs would help to answer this question.

Reductions in anther size and number and their correlations with cleistogamy verify the observations of earlier workers (Fernald, 1950; Hackel, 1906; Ritzerow, 1908). Although there was an apparent reduction in cleistogamous spikelet size, this may not be directly related to cleistogamy since there were also significant differences in size between cleistogamous spikelets related to their culm position (Table VI).

The spatial separation of cleistogamous and chasmogamous florets (Table IV) in these species supports the suggestion that position in the inflorescence as well as environment and genetic makeup determine the occurrence of cleistogamy (Lord, 1980). Early maturation of cleistogamous florets in these species suggests a temporal as well as a spatial separation of cleistogamous and chasmogamous reproduction. Such early maturation of cleistogamous florets, known as precocious development, has been reported in other grasses and has been attributed to a shortened meiotic stage (Brown, 1952; Campbell, 1980; Harlan, 1945).

This study quantified the lack of vegetative differences between *S. neglectus* and *S. vaginiflorus* (Sutherland, 1975). Although there was a significant difference in the mean mid-culm blade width (Table III), the small size difference and the overlapping ranges (Fig. 4) limit the usefulness of this character, particularly for field identification.

The mid-culm spikelets of some specimens (Fig. 3) corresponded to Shinners' (1954) description of *S. vaginiflorus* var. *neglectus* (i.e., pubescent lemmas and spikelets lengths of 2.0-2.6 mm). These spikelets had lengths within 2 S.D. (0.54 mm) of the mean mid-culm lemma length of S. neglectus ($\bar{x}$ = 1.96 mm, S.E. = 0.04). However, the terminal spikelets of these specimens had lemma lengths within 1 S.D. (0.51) of the mean terminal lemma length of *S. vaginiflorus* ($\bar{x}$ = 4.46 mm, S.E. = 0.07). The small size of these mid-culm spikelets appears to be related to their development or their position of the culm (Table II). These specimens should, therefore, be classified as *S. vaginiflorus*, not as intermediate forms of *S. neglectus* and *S. vaginiflorus*.

The highly significant differences in spikelet morphology (Table I) indicate the distinctiveness of the taxa in the area studied, despite the co-occurrence of the species, their common phenology and their vegetative similarity. This distinctiveness may be attributable to the high degree of cleistogamy in the populations studied.

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APPENDIX

Study Site Locations, all in Douglas County, Nebraska

1. Allwine Prairie Preserve (SE¼S23 T16N R11E) * †
    a. Inside main gate, east of drive
    b. Road to ponds
2. Stolley Prairie (SW¼S15 T15N R11E), road to lower field *
3. 72nd St. and Hartman Ave., Omaha (NW¼S36 T16N R12E), NE corner of intersection
4. Benson Park, 72nd St. and Military Ave., Omaha (SW¼S1 T15N R12E), abandoned asphalt road SW of pavilion
5. HWY. N36 and 84th St. (SE¼S10 T16N R12E), NW corner of intersection
6. Hwy. US275 and W. Dodge Rd. (SE¼S15 T15N R10E), west of south-bound Hwy. US275
7. Rainwood Rd. entrance to Lake Cunningham campground (SE¼S14 T16N R12E), north of road
8. Dodge St. near 60th st., Omaha (NW¼S19 T15N R13E), Elmwood Park near pedestrian overpass

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* Primary collection site, no disturbance during study period.

† *Sporobolus neglectus* only.