Cleistogenes in *Danthonia*[1]

A. K. DOBRENZ AND
A. A. BEETLE

Assistant Professor of agronomy and Professor of Range Management, respectively, University of Wyoming, Laramie.

Highlight

Cleistogamy is the behavior of flowers which do not open but which produce fruits and seeds as a result of self-fertilization. *Danthonia californica, D. unispicata,* and *D. spicata* **were found to be cleistogamous, but** *D. intermedia* **produced no cleistogenes in Jackson Hole, Wyoming. Cleistogenes were capable of producing new plants and therefore may be a means for reproduction for cleistogamous species in Jackson Hole.**

Cleistogamy is understood to be the behavior of flowers which do not open but which produce fruits and seeds as a result of self-fertilization. Cleistogamy (literally closed marriage) results in a type of fertilization called autogamy. More simply, cleistogamy refers to florets that never open, making cross-pollination impossible. In many chasmogamous (open-pollinated) flowers self-pollination occurs, but the possibility of cross-pollination is always present.

Investigations and descriptions of cleistogamy date back to the year 1539 (according to Uphof, 1938), when Hieronymus Bock mentioned in his publication, "Neue Kreuter Buch," on barley, that some grasses were able to produce fruits without showing the various parts of the flowers. Linnaeus (1753) also was conscious of this closed flower condition as determined from his description of *Panicum clandestinum,* published in "Species Plantarum."

In the study of cleistogamy in grasses one of the most difficult problems is that of definitions. The majority of grasses in which cleistogamy occurs have both chasmogamous flowers and either one or two types of cleistogamous flowers. When the cleistogamous florets are born on the terminal panicle but show strong differences (usually in another size or loss of lodicules), the plants are called dimorphic.

According to Arber (1934), "Cleistogamic inflorescences sometimes take the minimal form of 'cleistogenes'—solitary, sessile, single flowers, with lemma and palea, but without the usual outer empty glumes." These cleistogenes occur in the lower leaf-sheaths of the flowering culms or in the axils of the lower branches. Two or three-flowered spikelets may be involved. The cleistogamous florets characteristic of *Amphicarpon* and *Chloris chloridea* are of the same order as cleistogenes, but since they are born on underground culms they would seem to need a separate term. Since none has previously been used it is suggested that they be called rhizanthogenes (or rhizanthogames). In all cases where at least two types of cleistogamous florets occur on the same plant, the plants are referred to as amphigamic.

In some cases it would appear that cleistogenes disperse with difficulty, especially when the basal sheaths are persistent and the flowering culms are not dehiscent. However, there is a tendency for an association between the presence of cleistogamous spikelets and dehiscent inflorescences (e.g., *Danthonia, Sporobolus, Scleropogon*), which sometimes aids in cleistogenic dispersal. Perhaps more important than dispersal is their formation under severe overgrazing, allowing for reproduction (cf. Dyksterhuis, 1945).

Phylogenetically, the distribution of cleistogenes is interesting. Perhaps there'is significance in the apparent absence of this character from such characteristic and well-known festucoid tribes as the Festuceae, Aveneae, Phalarideae, Agrostideae, and Hordeae. This emphasizes the mesophytic northern origin of the festucoid group in contrast to the arid southern dispersals so characteristic of the species and tribes in which cleistogenes are present, e.g., Stipeae (*Stipa leucotricha*), Sporoboleae (*Sporobolus vaginiflorus,*) Eragrosteae (*Leptochloa dubia*), Danthoneae (*Danthonia unispicata*), and Pappophoreae (*Cottea pappophoroides*).

The phylogenetic relationships among the above tribes are sufficiently diverse to leave open the question as to whether the presence of cleistogenes is an example of epharmonic development. Cleistogenes are not characteristic only of North American arid areas. They occur also in all other arid areas of the globe. They may occur in these places in the same species when it is able to bridge the gap (e.g., Parodi reported that in South America *Enneapogon desvauxii* bears cleistogenes), or sometimes is related species (e.g., Chase reported that in the Old World *Pappophorum boreale* and *P. brachystachyum* bear cleistogenes).

Cleistogene formation is, within bounds, an epharmonic development in grasses. The cases of facultative cleistogamy are probably very numerous and seldom reported. They represent an evolutionary tendency throughout the grass family. Dimorphic cleistogamy is more often reported but also shows closer association with plants occurring in warm, arid areas. Cleistogene formation is the most restricted (1) in number of tribes in which it occurs, (2) in number of species in which it occurs, and (3) in geographic area.

Danthoneae

Primitive distributions in the Gramineae are primarily tropical or subtropical, e.g., those of thc tribes

Bambuseae, Olyroideae, and Oryzeae. The groups second most primitive, at least in evolutionary origin and distribution pattern, are those which are most abundant in the southern hemisphere and are lacking at high altitudes in the northern hemisphere; e.g., Danthoneae is one of the more recently accepted tribes of the Gramineae, the recognition of which has done much for the understanding of naturally drawn borders around the remaining tribes.

Danthoneae are now more abundant in temperate regions. More species survive in the southern hemisphere than in the northern. The history of Danthoneae distribution must be presumed to be early, to have involved the same southern routes which were taken by the tropical groups, but, on the other hand, to be independent of the parallelism found in the Bambuseae, Olyroideae and Oryzeae. *Anisopogon* supplies the geographical link between South Africa and Australia. Two genera are found in India (*Danthonidium* and *Hubbardia*), *Notochloe* in Australia, and *Monostachya* occurs in the Philippines and New Guinea. However, the bulk of the genera and species of the Danthoneae are African, e.g., *Schismus* (annuals now introduced in the New World), *Plagiochloa, Asthenatherum, Pentaschistis, Pentameris, Afrachneria, Chaetobromus, Urochlaena, Lasiochloa, Prionathium, Alloechaete, Phaenanthoecium,* and *Poagrostis*. The New Zealand flora includes *Chionochloa, Notodanthonia, Erythranthera* and *Pyrrhanthera*.

Danthonia

Danthonia shows marked disjunction in range of its species. Temperature regions have species concentrations in South Africa, south Australia and New Zealand, South America, and finally North America. The Eurasian continent is the poorest in representation with one species in the Mediterranean region (*D. provincialis*) and two in the Himalaya Mountains (*D. cachemyriana* and *D. jacquemontii*). Except for occurrence of *Danthonia californica* var. *americana* on the western coastal regions of North America and South America, the species are endemic to their areas. However, in North America four centers of distribution occur: Mexico (*D. filifolia*), the Caribbean Sea (*D. domingensis*

and *D. obtorta*), the Rocky Mountains (*D. parryi, D. unispicata*), and eastern North America (*D. compressa* and *D. sericea*). *Eastern North America and the Rocky Mountains are related to each other by two similarly disjunct distributions in D. spicata and D. intermedia.*

In South America another four centers of distribution occur, the Andes (four or five species are well-known species, but 17 scientific names are based on types from here), the delta region of the Parana (two species), subtropical Brazil (about five names but little known about the species), and finally the paramos of Venezuela, Ecuador and Brazil (*D. secundiflora*).

The North and South American species are as strongly related to each other as they are to any of the Old World types. This leads to the conclusion that they arrived in the New World at one time. That the North American species were derived from the South American and dispersed across the tropics is suggested by (1) absence of Arctic and subarctic species, (2) absence of the genus from northern Europe and Asia, (3) presence of its distribution to the tip of South America, (4) its presence in the tropics of Brazil, the islands around the Caribbean Sea, and in central Mexico, (5) strong representation of a diploid chromosome number of 36 in both regions, (6) presence of cleistogamous types in both regions, (7) presence of the types with bicellular hairs and dumbbell-shaped siliceous cells as a characteristic part of the leaf anatomy in all areas.

Cleistogenes in *Danthonia*

This report contains information on *Danthonia* in the Jackson Hole area of Wyoming. It is designed to show (1) which species display a cleistogamous condition, (2) cleistogene location, attachment, and number on the cleistogamous species, (3) nodal disarticulation occurrence, and (4) germination of cleistogamic and chasmogamic seeds.

Four species of *Danthonia* occurring naturally in the flora of Jackson Hole, Teton County, Wyoming, furnished the basic materials. These species are *D. spicata, D. unispicata, D. intermedia,* and *D. californica*. In addition, *D. parryi* was collected from Pole Mountain in the Medicine Bow National Forest near Laramie,

Albany County, and transplanted on the Biological Research Station at Moran for comparative studies.

Cleistogene Location, Attachment, and Number.—Early in the growing season, cleistogenes are not readily evident. Dissection shows that these small seeds originate at the joints of the flowering culms and are wrapped by the base of the sheaths. Later in the growing season, cleistogenes appear as small bumps which can be seen plainly at joints where they occur (Fig. 1).

D. spicata is characteristically a monocleistogamous species with seldom more than one cleistogene at a joint. Each small seed, enclosed in a lemma and a palea, seems to be sessile. The prophyllum is present in the form of two indurate, wing-like structures which occur at the point of attachment.

D. californica and *D. unispicata* are termed polycleistogamous, since more than one cleistogene occurs at each joint on the flowering culm. Both of these species produce cleistogenes which are enclosed in a lemma and a palea. The cleistogenes are borne on a rachilla which arises at the base of the lowermost cleistogene and serves as a means of attachment for the others. The basal cleistogene in these two species has the characteristic indurate, wing-like structures; but cleistogenes produced on the terminal portion of the rachilla lack these appendages.

The cleistogamous condition is easiest to recognize in *D. californica*. This species produces a maximum of eight cleistogenes at each node of the flowering culm, and, late in the growing season, the terminal cleistogenes protrude from the sheath. *D. unispicata* produces 2 to 3 cleistogenes at a node, but seldom do they extend beyond the upper portion of the sheath until the flowering culm has dehisced from the plant.

A smaller number of cleistogenes is produced per node in the terminal portion of the flowering culms in the species *D. unispicata* and *D. californica*. Although there may be the same number of lemmas and paleas at each node, the cleistogenes are definitely smaller and more likely to be rudimentary.

Weatherwax (1928) compared cleistogenes and chasmogamous seeds produced in the inflorescense as follows:
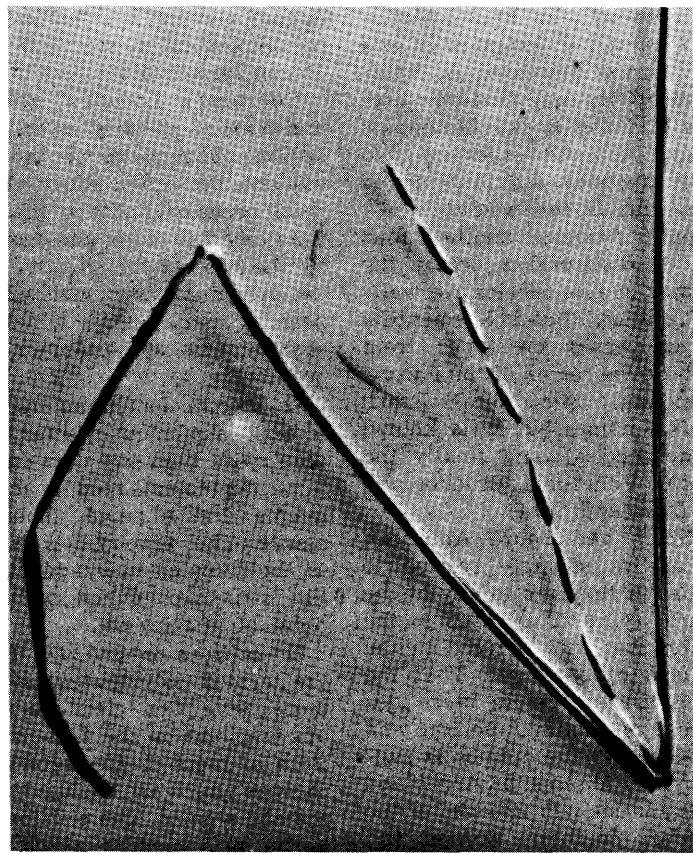
FIG. 1. Node and internode from *Danthonia californica* showing cleistogene location, attachment, and number.

three cleistogamous species of *Danthonia* at different times during the stages of growth. This breaking occurred just below each node, the basal ones being the first to fall. Actual separation of the terminal internodes occurred after the flowering culm had fallen from the plant. Each segment of the flowering culm was composed of the internode, basal node, the sheath, and the cleistogenes. At this stage of maturity the sheath was starting to loosen; thus all the cleistogenes may not have been present.

D. unispicata was the first of the cleistogamous species to begin nodal disarticulation. In late July and early August the flowering culms
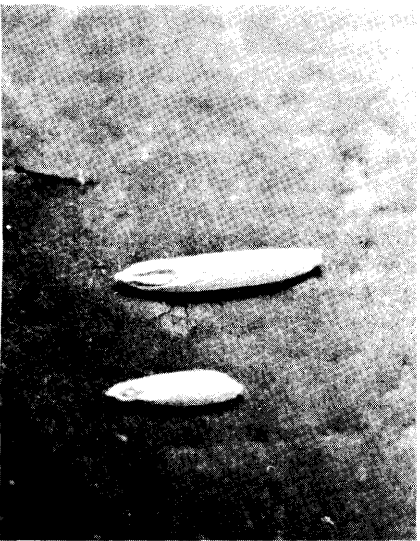

FIG. 2. A comparison in the size of seeds produced in the normal inflorescence (lower caryopsis) of *Danthonia unispicata*, and cleistogenes produced at the nodes (upper caryopsis).

"In some cases, the two types of disarticulated florets differ greatly in appearance because of the variable nature of the lemma; but there seems to be no consistent difference in the caryopsis. Seeds from both sources germinate alike; and seedling plants observed until flowering, the second season after germination, are alike in appearance and vigor." Table 1 illustrates the number of cleistogenes produced in the cleistogamous species with the number of seeds produced in these same plants. *D. unispicata* and *D. californica* produce more cleistogenes than chasmogamous seeds. Cleistogene production in *D. spicata* is relatively low compared with the chasmogamous seeds.

Cleistogenes on *D. unispicata* are larger and sometimes twice the size of chasmogamic seeds (Fig. 2).

Size differences also are characteristic of *D. californica*. Since this species produces as many as eight cleistogenes per joint, many of the terminal ones are somewhat shorter than the seeds from the inflorescence. Basal cleistogenes are longer and, in general, larger than the chasmogamic seeds. In *D. spicata*, cleistogenes and chasmogamic seeds have close resemblance, and it was difficult to determine which were produced at the joints and which from the normal inflorescence.

Nodal Disarticulation.—Disarticulation or breaking of the flowering culm at each joint occurs in the

Table 1. Comparison of chasmogamic seed production with cleistogene production among four Danthonia species.[1]

Species	D. unispicata	D. spicata	D. intermedia	D. californica
No. spikelets per flowering culm	1	5-6	7-8	3-4
No. florets per spikelet	4-5	5-6	3-4	5-6
No. nodes with cleistogenes	3-4	2	none	5-6
No. cleistogenes per node	2-3	1	none	6-7
Total no. seeds per flowering culm	4-5	27-28	25-26	21-33
Total no. cleistogenes per flowering culm	8-9	2	none	25-36

[1] Means based on 100 flowering culms of each species.

were scattered at the base of the plant. Lack of culms gave the plant a naked look because only basal leaves remained. At this time of year, the appearance of the plant is very much the same as it was in the spring before any flowering culms were produced. Just before nodal disarticulation occurred, the flowering culms turned a reddish color, which made *D. unispicata* easy to locate. Evidently, when the red color first appeared, the nutrient supply to the flowering culms had been discontinued because of the separation of the first joint from the base of the plant, and curing the grass had started.

Internodes containing only a portion of the stem and the sheath were found scattered and intermingled among the plants in the locality of *D. unispicata,* particularly when game or livestock had been present.

D. californica disarticulated in the same manner as *D. unispicata* except that the entire plant was more mature before this process began. Joints did not break into separate entities as easily in *D. californica,* and the entire culm remained united with the inflorescence until long after the flowering culm had disarticulated at the basal node. This breaking up first occurred approximately in the middle of August.

Nodal disarticulation of *D. spicata* occurred so late in the growing season (September 1 to 15) that we doubt whether such disarticulation might have any effect on the distribution and scattering of chasmogamic or cleistogamic seeds. The fact that *D. spicata* produced only a few cleistogenes in addition to the late, and only partial, nodal disarticulation of the flowering culms may indicate that it is more closely related to the two North American species, *D. intermedia* and *D. parryi.* Both of these species also occurred in Wyoming, but only *D. intermedia* was present in Jackson Hole. Neither displayed nodal disarticulation.

Germination.—The purpose of the germination tests was to determine whether cleistogenes are viable, and how their percentage germination compared with that of chasmogamic seeds which were taken from the same plant. Observations during the early part of the growing season
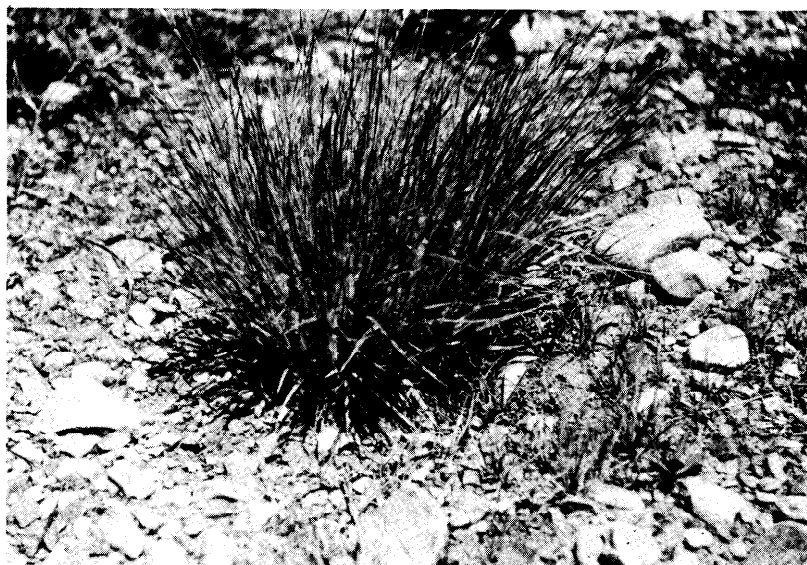

FIG. 3. Small seedlings of *Danthonia unispicata* showing their abundance and clustered distribution around the parent plant.

Table 2. Comparison of percentage germination of chasmogamic seeds and cleistogenes under various treatments.

Species	Type of seed	Treatment	Percentage germination
D. unispicata	Cleistogamic	Water and chilled	41
	Chasmogamic	Water and chilled	40
	Cleistogamic	Water and non-chilled	66
	Cleistogamic	KNO_3 and non-chilled	66
D. californica	Cleistogamic	Water and chilled	0
	Chasmogamic	Water and non-chilled	0
	Cleistogamic	Water and non-chilled	0
	Cleistogamic	KNO_3 and non-chilled	10
	Chasmogamic	KNO_3 and non-chilled	10
D. spicata	Cleistogamic	Water and chilled	70
	Chasmogamic	Water and chilled	33
D. intermedia	Chasmogamic	Water and chilled	95

showed many small seedlings clustered around the base of each parent plant of *D. unispicata* (Fig. 3). How many of these small plants were produced by cleistogenes and how many from chasmogamic seeds was impossible to determine in the field. However, seedling abundance suggests that cleistogenes are an important means of reproduction for at least this cleistogamous species of *Danthonia* in Jackson Hole.

Cleistogenes from the three species, *D. spicata, D. unispicata,* and *D. californica* proved to be viable and capable of producing new plants. There was a wide range in germination percentage of the cleistogamous species (Table 2). *D. californica* cleistogenes germinated only when the blotters had been soaked with potassium nitrate. Cleistogenes of *D. spicata* had the highest percentage (70%), with those of *D. unispicata* second (66%).

D. intermedia displayed the highest germination percentage of chasmogamic seeds while *D. californica* had the lowest percentage germination when both chasmogamic seeds and cleistogenes were compared. This

may partially explain the limited distribution of this species in the Jackson Hole area. Cleistogenes in the other two cleistogamous species of *Danthania* compared favorably with the germination of chasmogamic seeds.

The potassium nitrate treatment was the only condition under which both types of seeds from *D. californica* germinated. Therefore it is possible that certain elements in the soil can affect germination of this species.

Plants from the germinated cleistogenes and chasmogamic seeds were transplanted into pots in the greenhouse. After two months there appeared to be no difference in appearance and vigor of the two kinds of seedlings.

Summary and Conclusions

D. californica and D. unispicata were found to be polycleistogamous with more than one cleistogene produced at each joint, and all attached by an axis or rachilla. *D. spicata* was found to be monocleistogamous, producing only one cleistogene per joint and often only one joint at the base of the flowering culm had a cleistogene present. *D. intermedia* produced no cleistogenes in Jackson Hole.

Cleistogenes were more abundant per flowering culm than were the chasmogamic seeds in the two species *D. unispicata* and *D. californica*.

Nodal disarticulation occurred in the three cleistogamous species and proved to be a means by which cleistogenes and chasmogamic seeds were scattered, particularly in the localities of *D. californica* and *D. unispicata*.

Cleistogenes were found to be capable of producing new plants and therefore are described as a means of reproduction for the cleistogamous species in Jackson Hole.

LITERATURE CITED

ALLAWAY, W. H. 1957. Soil, the yearbook of agriculture. U. S. Dep. Agric., Washington, D. C. 784 p. (Especially p. 67-72).

ARBER, A. 1934. The Gramineae. Cambridge University Press, London. 480 p. (Especially p. 164-206).

BEETLE, A. A. 1961. Cleistogene formation—an example of epharmonic form and distribution pattern in the Gramineae. Wyoming Range Manage. Issue No. 154. p. 3.

BROWN, W. V. 1952. The relation of soil moisture to cleistogamy in *Stipa leucotricha*. Bot. Gaz. 113:-438-444.

CAMPBELL, J. B., K. F. BEST, AND A. C. BUDD. 1956. Ninety-nine range forage plants of the Canadian prairies. Canada Dep. Agri., Ottawa, Ontario. Publ. No. 964. 99 p. (Especially p. 26).

CHASE, A. 1918. Notes on the cleistogamy of grasses. Bot. Gaz. 5:134-136.

DYKSTERHUIS. 1965. Axillary cleistogenes in *Stipa leucotricha* and their role in nature. Ecology 26:-195-199.

HACKEL, E. 1906. "Ueber Kleistogamie bei den Gräsern." Oest. Bot. Zeit. 56:81-88, 143-154, 180-186.

HITCHCOCK, A. S. 1935. Manual of the grasses of the United States. U. S. Dep. Agric. Misc. Pub. No. 200. 1040 p.

HITCHCOCK, A. S. 1951. Manual of the grasses of the United States. 2nd. edition (Rev. by Agnes Chase), U. S. Dep. Agric. Misc. Publ. 200. 1051 p.

LINNAEUS, C. 1753. Species plantarum. W. Junk, Berlin W., Kurfürstendam, 201. 1200 p. (Especially p. 55-59).

MEYER, B. S., AND D. B. ANDERSON. 1952. Plant Physiology. D. Van Nostrand Co., Inc., Princeton, N.J. 784 p. (Especially p. 335-366).

UPHOF, J. C. 1938. Cleistogamic flowers. Bot. Rev. 4:21-49.

WEATHERWAX, P. 1928. Cleistogamy in two species of *Danthonia*. Bot. Gaz. 86:104-109.