Flower and Spikelet Morphology in Sawgrass, *Cladium jamaicense* Crantz (Cyperaceae)

JENNIFER H. RICHARDS*

Department of Biological Sciences, Florida International University, Miami, FL 33199, USA

Received: 3 January 2002 Returned for revision: 10 May 2002 Accepted: 6 June 2002 Published electronically: 5 August 2002

In recent systematic treatments of the Cyperaceae, spikelets of all but the most primitive tribes have been considered to be indeterminate, whereas historically the number of flowers, floral sex and distribution of sexes in spikelets have been important characters in suprageneric classifications. However, descriptions of these spikelet characteristics for sawgrass, *Cladium jamaicense* Crantz, vary among authors. Spikelet morphology was analysed using developmental and phenological studies of sawgrass populations in south Florida, USA. Sawgrass spikelets have two flowers that expand successively. Flowers are fundamentally hermaphroditic and protogynous. The first flower to expand (F1) terminates the spikelet axis, whereas the second flower (F2), ensheathed by an addorsed prophyll, develops in the axil of the last bract produced on the axis. In 86 % of the spikelets examined from ramets of three populations, the gynoeccium of the F1 flower aborted, so this flower was functionally male and the spikelet was protandrous. However, in 14 % of spikelets from these individuals, the F1 flower was hermaphroditic and could set seed. The F2 flower was typically hermaphroditic and matured stigmas, then anthers. Thus, spikelets in *C. jamaicense* are determinate and have two flowers that are dichogamous both within flowers and between flowers in a spikelet; spikelet sex expression can vary among plants and populations, especially in the first flower. These data for sawgrass suggest that a re-examination of spikelet development and phenology in other genera is needed to clarify the expression of these characters in the family.

**Key words:** Anemophily, *Cladium jamaicense*, determinate spikelet, Cyperaceae, dichogamy, protandry, protogyny, indeterminate spikelet, sawgrass, spikelet morphology.

INTRODUCTION

Spikelets bearing one or more reduced flowers are the basic reproductive unit in the Cyperaceae. Spikelet structure, arrangement, flower number per spikelet and floral sex have been important characters in the systematics of the family (Koyama, 1961; Eiten, 1976; Dahlgren et al., 1985; Tucker, 1987; Bruhl, 1995; Goetghebeur, 1998). Recent molecular and cladistic studies using numerous additional characters have provided suprageneric classifications and phylogenetic trees for interpretation of spikelet characters (Muasya et al., 1998, 2000). All of these studies consider cyperaceous spikelets to be indeterminate or racemose in all but the primitive tribes, in contrast to earlier workers who considered the spikelets to be determinate or cymose in at least some of the more advanced tribes (reviewed in Holttum, 1948; Mora, 1960; Eiten, 1976). Many current classifications for the family use models of spikelet structure established by Eiten (1976); yet Eiten provides only a general typology of the ultimate inflorescence units found throughout the family and does not present evidence for her conclusions other than a few verbal descriptions of mature anatomy and illustrations of dissections of mature spikelets.

Sawgrass, *Cladium jamaicense* Crantz, is the dominant macrophyte in the Everglades of south Florida, USA (Loveless, 1959; Davis et al., 1994; Gunderson, 1994).

* For correspondence. Fax +1 305 3481986, e-mail Richards@fiu.edu

The most recent molecular and cladistic phylogeny of the Cyperaceae places *Cladium* basally in the Schoeneae (Muasya et al., 2000). However, descriptions of spikelet structure for *Cladium* species vary among sources, while an understanding of spikelet phenology is lacking (Mora, 1960; Steward and Ornes, 1975; Long and Lakela, 1976; Godfrey and Wooten, 1979; Tucker, 1987). Descriptions of the spikelets as indeterminate or determinate vary amongst authors, as do the number of flowers per spikelet (two or more), and the sex of the flowers in the spikelets (male, female or hermaphrodite) (Holttum, 1948; Koyama, 1961; Eiten, 1976; Long and Lakela, 1976; Godfrey and Wooten, 1979; Dahlgren et al., 1985; Tucker, 1987; Bruhl, 1995). Studies of population structure of *C. jamaicense* in south Florida have shown that although overall genetic diversity is low, genotypic diversity is present at a local scale (Ivey and Richards, 2001a, b). These studies indicate that seed reproduction is important to the population structure of this species. Asexual plantlet production in inflorescences and seed germination has recently been studied (Miao et al., 1997, 1998; Lorenzen et al., 2000), but little is known about the details of the mating system of *C. jamaicense*. Here, I describe spikelet structure in south Florida populations of *C. jamaicense*. I use phenological observations, dissections of mature spikelets and developmental data to define spikelet flower number and sex expression, and to determine whether the spikelet is determinate or indeterminate.
Sawgrass inflorescences have clusters of spikelets [primary lateral inflorescence branches of Bruhl (1995)] distributed in the axes of bracts along an elongated inflorescence (Fig. 1A). The branching pattern of the inflorescence was analysed by dissecting the first secondary branch on the first lateral inflorescence branch under a Wild M3 dissecting microscope (Wild Heerbrugg, Ltd, Heerbrugg, Switzerland). Over 200 individual spikelets were collected from ten plants in an ex situ population at Henington Pond, Florida International University, USA (25°45-648’N, 80°30-143’W). The ten plants originated from discrete ramets collected in two south Florida sawgrass populations in 1998 and planted at Henington Pond. spikelets were dissected under a microscope to determine spikelet and flower number, and floral sex. To establish the sequence of flower maturation and carpel and stamen expansion, spikelets on primary branches 1, 4 and 7 of inflorescences on these ten plants were observed daily throughout May 2001; spikelets sampled for dissections were not taken from inflorescences that were being observed for phenology. Spikelets at different developmental stages were fixed in FAA (Ruzin, 1999), dehydrated in ethanol, CO₂-critical point dried, coated with gold–palladium and examined at 10 kV with an ISI Super IIIA scanning electron microscope (Topcon America Corporation, Paramus, NJ, USA).

Flower number, sex and position were determined for spikelets from at least 50 ramets collected from three Everglades populations: the Singeltary population (25°25-115’N, 80°28-134’W); the Taylor Slough population (25°23-950’N, 80°36-059’W); and the northeast Everglades population (25°45-648’N, 80°30-143’W). GPS coordinates of sites were recorded with a Garmin GPS 12 (Garmin International Inc., Olathe, KS, USA). Samples were taken from plants located at least 5 m apart and were sampled from the first or second secondary branch on the first or second primary branch on each inflorescence. One spikelet per plant was analysed under a dissecting microscope. Differences among populations in the distribution of spikelet sexes were tested using the log likelihood ratio $\chi^2$ in SAS (v.8.2).

To quantify variation within and among plants, measurements of spikelet length were made using MAX-CAL electronic digital callipers (Fowler Co., Inc., Newton, MA, USA) on three spikelets per plant for ten plants from each of the Singeltary, northeast Everglades and Henington Pond populations. Bract number per spikelet and the position and sex of flowers were recorded for each spikelet dissected. Details of floral structure were photographed on a Wild M3 dissecting microscope with a digital or video camera.

**RESULTS**

**Inflorescence structure**

Inflorescences were borne on stalks that raised them above the sawgrass leaves. Inflorescence height was similar throughout a sawgrass population. The inflorescence axis bore bracts that decreased in length up the axis; each bract subtended an axillary bud that produced a primary lateral inflorescence branch. The length of this branch also decreased at successive nodes along the main axis (Fig. 1A). The inflorescence terminated in a cluster of spikelets (Fig. 1A).

The axillary bud that produced the primary branch had a two-keeled (bicarinate) prophyll that remained in the axil of the subtending leaf, while the internode above the prophyll (epipodium) expanded. The branch bore a series of bracts with successively shorter internodes, and terminated in a spikelet (Fig. 1E). Buds in the axils of the bracts expanded and repeated the pattern; each had a prophyll that remained in the bract axil, a long internode, then a succession of leaves with shorter internodes and a terminal spikelet. The last axillary spikelets on any order of branching had very little intermodal elongation and thus appeared as a cluster surrounding the terminal spikelet (Fig. 1E). These axillary spikelets were subtended by a bract with a single tip and bore an addorsed prophyll that was generally bicarinate (Figs 1B and G). The terminal spikelet lacked this prophyll, as its prophyll remained at the base of the branch.

**Spikelet structure and flower sex**

Spikelets were lanceolate with an acute tip (Fig. 1B and E) and were approx. 5 mm in length (range 4.3–6.4 mm) at the time of flowering (Table 1). Spikelets produced between five and nine bracts, including the prophyll (Table 1). The
bicarinate prophyll on an axillary spikelet was much shorter than the spikelet and did not encircle it completely (Fig. 1B and G). Successive bracts on axillary and terminal spikelets increased in length and width and thus in the degree to which they enclosed the younger parts of the spikelet (Fig. 1B and G).

All of the spikelets examined in both in situ and ex situ populations produced two flowers (Fig. 1C, D, F and G; Table 1). The first flower (F1) was completely enclosed by an ensheathing bract whose edges overlapped (Fig. 1C, F and G). This flower terminated the spikelet axis (Fig. 1C). There was no prophyll associated with the F1 flower and no evidence of a remnant apex produced beyond this flower (Fig. 1C). The bract that encircled the terminal flower subtended an axillary bud with an addorsed prophyll (Fig. 1C). This prophyll ensheathed a flower (F2) that terminated the axillary bud axis (Fig. 1C, F and G). Both flowers were developmentally hermaphroditic and produced two anthers and a single gynoecium (Fig. 1D, F and G).

The anthers of both F1 and F2 were four locular and had an apiculus or sterile projection at the tip (Fig. 1E). Typically, the gynoecium of F1 had two stylar branches (Fig. 1D and F). The gynoecium of F1 flowers aborted in 86 % of samples from the three Everglades populations (Fig. 1F; Table 2). Styles on aborted carpels turned reddish-brown and the stigmatic papillae elongated. After carpel abortion, F1 matured as a male flower (Fig. 1E). However, in 14 % of the combined sample the gynoecium did not abort, and the F1 flower was hermaphroditic (Table 2) and could set fruit (Fig. 1H). When the gynoecium did not abort, F1 flowers were protogynous with the stigma maturing prior to the anthers.

The F2 flower, which developed in the axil of the bract surrounding F1, was developmentally delayed compared with F1 (Fig. 1C, D and G). In all but two plants examined, this flower matured as a hermaphrodite; in the exceptions, the carpel aborted, producing a male flower (Table 2). The F2 carpel typically had three or four style branches,
TABLE 2. Percentage of spikelets with flowers of different sexes in three south Florida populations of sawgrass, Cladium jamaicense

<table>
<thead>
<tr>
<th>Population</th>
<th>F1 M: F2 M</th>
<th>F1 M: F2 H</th>
<th>F1 H: F2 M</th>
<th>F1 H: F2 H</th>
<th>N*</th>
</tr>
</thead>
<tbody>
<tr>
<td>NE Everglades</td>
<td>0</td>
<td>97</td>
<td>0</td>
<td>3</td>
<td>61</td>
</tr>
<tr>
<td>Taylor Slough</td>
<td>0</td>
<td>64</td>
<td>0</td>
<td>36</td>
<td>50</td>
</tr>
<tr>
<td>Singeltary</td>
<td>4</td>
<td>92</td>
<td>0</td>
<td>4</td>
<td>50</td>
</tr>
<tr>
<td>Total</td>
<td>1</td>
<td>85</td>
<td>0</td>
<td>14</td>
<td>161</td>
</tr>
</tbody>
</table>

F1 and F2 are the first and second flowers to mature in the spikelet. M, Male flower; H, hermaphroditic flower.

* N, Number of ramets per population; one spikelet per ramet was sampled.

although in a few cases only two were produced. Like F1 hermaphrodites, F2 was protogynous (Fig. 1F).

Spikelets of plants observed daily at Henington Pond all had F1 male flowers and F2 hermaphroditic flowers (Table 1). All of the spikelets on these plants expanded F1 anthers first (Fig. 1E), followed 2–4 d later by F2 stigmas, then by F2 anthers 1–3 d later. Anthers of both types of flowers lasted a single day; they abscised on the day that they expanded or the day after, leaving the filaments in the spikelet (Fig. 1F). Initially, stigmas were white and papillate (Fig. 1F), but they then dried, becoming brown and shrivelled, 1 or 2 d after expansion (Fig. 1H).

Of the four arrangements of male and hermaphroditic flowers possible in two-flowered spikelets, spikelets that matured a male flower first, then a hermaphroditic flower, were most common (Tables 1 and 2). Spikelets that matured two hermaphroditic flowers were the second most frequent case. Spikelets with two male flowers were infrequent, and no spikelets that matured a hermaphroditic flower and then a male flower were observed (Table 2). The frequency of spikelet sex types varied significantly among populations (Table 2; log likelihood ratio $\chi^2 = 30.52$, $P < 0.0001$).

DISCUSSION

Determinate vs. indeterminate spikelet structure

Most recent illustrations of spikelet morphology in Cladium show an axillary male flower below an axillary hermaphroditic flower in a racemose spikelet, with sterile bracts both below and above the fertile bracts (Koyama, 1961; Eiten, 1976; Dahlgren et al., 1985). Descriptions of the spikelet depict a ‘distal’ or ‘upper’ perfect flower and a ‘subdistal’ or ‘lower’ staminate flower (Tucker, 1987; Goetghebeur, 1998). Bruhl (1995) described the spikelets of most Cyperaceae as axillary and those of Cladium as lacking a terminal flower. This current interpretation of spikelet structure differs from earlier interpretations of the spikelet of at least some Cyperaceae as a determinate, sympodial or cymose structure [Mora, 1960; Kern, 1974; see discussions in Eiten (1976) and Holttum (1948)]. The most recent developmental study (Mora, 1960) describes the spikelet of C. mariscus, as well as that of species in a number of other genera, as determinate.

The arrangement of openings of the ensheathing bracts and the position of flowers with respect to both bracts and phylls differ substantially under determinate and indeterminate interpretations of the spikelet (Fig. 2). The data presented here show that the spikelet has: (1) a typically male flower encircled by a bract with no evidence of an axis or leaves produced beyond that flower or of a remnant apex and with no associated phyll; and (2) a hermaphroditic flower that is developmentally delayed in relation to the male flower and that is produced in the axil of the bract encircling the male flower. In addition, the hermaphroditic flower is surrounded by a prophyll whose sheath opens away from the male flower, as is typical of a monocotyledonous prophyll on an axillary bud. There is no evidence for additional leaves or a remnant apex produced beyond the hermaphroditic flower. Thus, the spikelet of C. jamaicense has a terminal male flower and an axillary hermaphroditic flower subtended by the last bract produced on the spikelet axis (Fig. 2B).

An argument against this interpretation is that the F2 bract, which is in the prophyllar position, does not have the bicornate prophyll morphology typical of prophylls on spikelets (Koyama, 1961; Eiten, 1976). However, Cyperaceae prophylls can be very diverse in their form (Blaser, 1944), whereas prophylls on sylleptic branches, such as the F2 branch, often have a relatively unmodified morphology (Bell, 1991). A determinate interpretation of the spikelet is consistent with the determinate structure of the inflorescence branches and the inflorescence itself. All of these branches terminate in spikelets; the spikelets, in turn, terminate in flowers.

This description of spikelet structure in C. jamaicense contradicts current interpretations of spikelet morphology in the Cyperaceae, which recognize the odd spikelet in the primitive Hypolytreae as determinate, but consider more advanced Cyperaceae to have indeterminate spikelets (Eiten, 1976; Dahlgren et al., 1985; Bruhl, 1991, 1995; Goetghebeur, 1998). Studies of South African Carpha, Episcoenus and Schoenus species show that the spikelets in these genera are not indeterminate (Browning and Guthrie, 1994; Browning and Gordon-Gray, 1995). The data and illustrations of spikelets in these papers depict a determinate developmental pattern similar to that described here for C. jamaicense. Recent phylogenies put Carpha as a sister group to Cladium and both genera basal in the Schoeneae (Muasya et al., 2000). More intriguing is the illustration of a spikelet of Rhynchospora corymbosa (Fig. 39A, Goetghebeur, 1998). The Rhynchosporaeae are sister to the Schoeneae but are more advanced in the family (Muasya et al., 2000). This illustration shows a spikelet with a flower described as axillary to bract 4 but subsequently ensheathed by bract 5. This spikelet would be more parsimoniously interpreted as having a determinate developmental pattern in which bract 4 does not subtend a flower, and bract 5 is the last leaf on the spikelet, followed by a terminal flower; subsequent development is from a bud axillary to bract 5, similar to the pattern seen in C. jamaicense. Based on his examinations of developing spikelets, Mora (1960) included Rhynchospora among genera with determinate spikelets.
Developmental and phenological studies of living material across a broader range of species are needed to determine the distribution of spikelet types and sexes among tribes in the Cyperaceae. The data presented here raise the question of whether the determinate structure in the *C. jamaicense* spikelet is plesiomorphic, reflecting sawgrass’s basal position in the relatively primitive Schoenoeae, or whether insufficient data on spikelet development in more advanced Cyperaceae prevent us from understanding the distribution of this character in the family.

**Spikelet flower number and sex**

Previous descriptions of the number of flowers in the spikelet of *Cladium* have varied (Mora, 1960; Long and Lakela, 1976; Godfrey and Wooten, 1979), although many authors have agreed that there are two (Koyama, 1961; Tucker, 1987; Bruhl, 1995; Goetghebeur, 1998). Similarly, the description of floral sex has ranged from bisexual to male and female (Mora, 1960; Koyama, 1961; Eiten, 1976; Long and Lakela, 1976; Godfrey and Wooten, 1979; Tucker, 1987; Bruhl, 1995; Goetghebeur, 1998). All sawgrass spikelets examined in this study produced two flowers, although the timing of flower maturation differed among these flowers. Both flower primordia were bisexual, and both flowers could function as hermaphrodites and set fruit. In most spikelets, however, F1 was functionally male, while F2 was hermaphroditic. Thus, flowers in a spikelet can, but do not always, differ in sex expression. The variable expression of floral sex means that spikelet sex can vary among plants within a single population and across a geographical region. These data provide a background for interpreting the diverse descriptions of spikelet structure in this genus and emphasize the need for population studies of living material to understand floral and spikelet sex expression, which have been important systematic characters at the suprageneric level in the family (Koyama, 1961; Eiten, 1976; Dahlgren et al., 1985; Bruhl, 1995; Goetghebeur, 1998; Musaya et al., 2000).

Both flowers in the spikelet of *C. jamaicense* are protogynous, as has been attributed to the Cyperaceae generally (Goetghebeur, 1998). Abortion of the F1 gynoeicum may be an extreme expression of this protogyny, as the stigma appears to mature in the aborted carpel prior to ovary development. What controls abortion of the F1 female is unknown, but when multiple flowers from a single plant were examined, the F1 flowers were similar in their sex expression, so this character may vary at the level of the individual.

Because the two flowers in a spikelet mature at different times, spikelets, as well as flowers, are dichogamous. Male/ hermaphroditic spikelets go through a male phase (F1 anthers mature), a female phase (F2 stigma matures), then another male phase (F2 anthers mature). Thus, although *C. jamaicense* flowers are protogynous, most spikelets are functionally protandrous. Temporal separation of the sexes, or dichogamy, is common in anemophilous plants (Ackerman, 2000), where it may reduce self-pollination. The efficacy of spikelet dichogamy in preventing geitonogamy, however, depends on a number of other factors, such as the phenology of spikelets within an inflorescence, the timing of expansion of different inflorescences on a genet, the dynamics of wind pollen dispersal and the presence or absence of a self-incompatibility system. How sawgrass flower phenology and variation in flower sex expression function in relation to these other parameters should be the subject of future research.

**ACKNOWLEDGEMENTS**

I thank Drs R. L. Jones and D. W. Lee for their support and Dr T. Philipp for help with statistical analyses. This study was completed as an ancillary project to ongoing research on wetland ecosystem processes and wetland restoration at Florida International University’s Southeast Environmental Research Center (FIU SERC). Everglades plants were collected under USDA National Park Service collecting permit number 201003. This paper is SERC Contributed Paper No. 180.

**LITERATURE CITED**


Ivey CT, Richards JH. 2001b. Genotypic diversity and clonal structure of...


**Koyama T.** 1961. Classification of the family Cyperaceae (1). *Journal of the Faculty of Science, University of Tokyo, Section III, Botany* **8**: 37–148.


