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Animal Dispersal of the North American Sedge, Cyperus plukenetii (Cyperaceae)

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ABSTRACT.—A suite of characteristics of *Cyperus plukenetii,* which facilitate zoochory (animal dispersal), is described and illustrated. Dispersal experiments with *C. plukenetii* show an average of 46.4 spikelets initially adhered to the human disperser's clothing. Of these, 38.8% were transported at least 10 m from the source, and 15.2% were dispersed at least 100 m. Data about plant height ($\bar{x}$ = 65 cm, range = 20–121) taken from living populations and from herbarium specimens indicate that a variety of mammals, and perhaps birds, may potentially function as dispersal agents of *C. plukenetii.*

INTRODUCTION

Dispersal is an important factor in determining distribution patterns of plant species. Plants have modifications to exploit various agents of dispersal, which may directly involve fruits, seeds, or other structures such as inflorescences (Ridley, 1930; Pijl, 1982). The following dispersal methods have been reported for Cyperaceae: rain wash (Ridley, 1930); transport of achenes in mud on feet of migratory waterfowl (Ridley, 1930); ingestion of fruits by migratory waterfowl (Ridley, 1930; Bend, 1937); flotation of achenes (Chermezon, 1924; Ridley, 1930; Lye, 1981); attachment of achenes of *Blysmus* sp. to animal fur (Ridley, 1930); attachment of utricles of *Uncinia* spp. to feathers (Pijl, 1982); springing perigynia in *Carex pauciflora* Lightfoot (Hutton, 1976); wind dispersal of achenes attached to a perianth of long, silky hairs in *Eriophorum* spp. (Pijl, 1982); and ant dispersal (myrmecochory) of fruits in *Carex* spp. (Handel, 1976, 1978; Gaddy, 1986).

Harper (1903) noted that *Cyperus retrofractus* (L.) Torrey "has an adaptation for dissemination by animal agencies. . . . I found many spikelets adhering to my clothes by their sharp points . . . reflexed spikelets . . . are an essential feature of this mode of dissemination." I observed this phenomenon independently in *Cyperus plukenetii* Fernald during field studies related to a revision of the North American species of *Cyperus* section *Umbellati.* Moreover, it seems likely that the observations made by Harper in Meriwether County, Georgia, were actually of the segregate species, *C. plukenetii,* which was not described until 1945. A discussion and clarification of nomenclature in this complex is found in Carter and Jarvis (1986).

Cyperus plukenetii is a widespread perennial herb endemic to the eastern United States. It occurs occasionally from southern New Jersey S to central peninsular Florida, then W through much of eastern Texas and as far inland as southern Missouri and Kentucky. *Cyperus plukenetii* inhabits sandy soils of sparse scrub woods, woods' edges, and open fields (Carter, 1984). The purpose of this study was to determine if animals may be effective dispersers of achenes in *C. plukenetii.*

MATERIALS AND METHODS

During October 1986, dispersal experiments were done on fully mature individuals of populations of *Cyperus plukenetii* from Lowndes and Brooks counties, Georgia. Voucher specimens (Lowndes County, 3.7 miles WSW of Clyattville, 19 October 1986, *Carter 5080*; Brooks County, 5.3 miles WSW of Clyattville, 19 October 1986, *Carter 5081*) have been deposited at Valdosta State College Herbarium (VSC). Individual plants were trodden over

by a human disperser wearing denim trousers and shirt. Immediately after the experimental disperser had passed over an individual plant, and was no more than 1 m from the plant, clothing was inspected and the total number of adhering spikelets was determined. Subsequently, the number of attached spikelets was determined at distances of 10 m and 100 m from the source. This procedure was done with a total of 30 different individual plants. The experimental populations were located in sparse longleaf pine–scrub oak woods with a fairly open understory.

The mean number of spikelets per spike (n = 48) and the mean number of spikes per inflorescence (n = 62) on herbarium specimens were used to estimate total spikelets per plant. These data were used to estimate the mean total spikelets produced per plant.

Stem height was measured in the field on living plants (n = 30) to determine the height of the terminal spikelets. These data were used to infer which animal species might be effective dispersers of *Cyperus plukenetii* spikelets.

RESULTS AND DISCUSSION

The single-fruited spikelets of *Cyperus plukenetii* are clustered in dense, bur-like spikes (Fig. 1A) and have indurate, subulate tips that penetrate clothing (Fig. 1D) and even bare skin. The morphology of spike and spikelet is unusual, if not unique, in the genus and has presumably evolved because of its role in dispersal by animals (zoochory). The following characteristics appear to contribute to zoochory in *Cyperus plukenetii*.

(1) Spikelets are typically small, lightweight and one-fruited.
(2) The terminal scale of the spikelet is convolute and modified into an indurate point (Fig. 1B) capable of penetrating clothing, human skin and probably the skin and fur of other animals.
(3) Typically, most spikelets of the spike are declined (Fig. 1A, B) so spikelets are oriented with their points directed at the disperser when plants are bent downward and trodden on.
(4) Personal observations indicate that spikelets are persistent on the rachis much longer than in most other *Cyperus* species; therefore, they are available for dispersal for a longer period of time. The character of persistent spikelets was first noted by Fernald (1945) in his original description of the species. In my own field work, I have occasionally observed dead scapes still bearing spikelets that matured during the previous season.
(5) Scapes, peduncles and leaves are densely covered with stiff trichomes (Fig. 1C) that cause plants to cling to clothing and hair. This feature would increase the probability of contact between animal disperser and spikelet. The type of pubescence exhibited by *Cyperus plukenetii* is unusual in the genus.
(6) Typically, primary inflorescence bracts are shorter than or equal to the inflorescence rays, which means that spikelets are more exposed to potential dispersers than in many other *Cyperus* spp.

Data from dispersal experiments show that humans are effective dispersers of *Cyperus plukenetii* spikelets. A mean of 46.4 (n = 30, SD = 33.5, range 10–151) spikelets attached initially to the human disperser's clothing. Of these, 38.8% ($\bar{x}$ = 18.0, n = 30, SD = 9.7, range 6–48) were still attached 10 m from the source, and 15.2% ($\bar{x}$ = 7.0, n = 30, SD = 6.0, range 0–27) were still embedded 100 m away.

Data from herbarium specimens indicate there are 79.33 spikelets per spike (n = 48) and 7.65 spike rays per inflorescence (n = 62). The product of these two values gives a mean of 606.7 spikelets per plant. Since most spikelets were not removed during a single pass over an individual plant (maximum of 151, $\bar{x}$ = 46.4 spikelets initially adhered) and

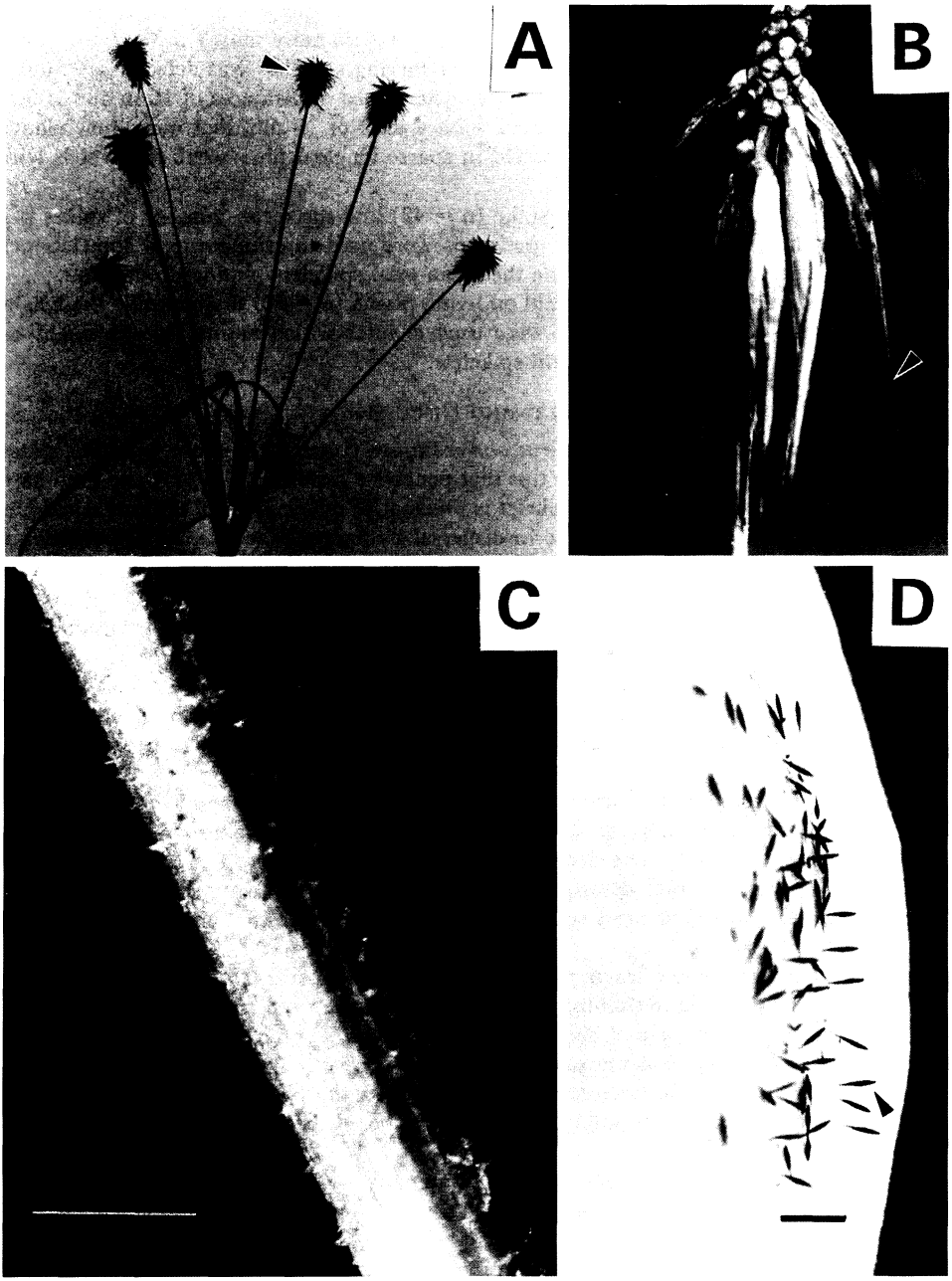

FIG. 1.—A. Inflorescence of *Cyperus plukenetii*; arrow shows spike with declined spikelets; bar = 13 mm. B. Spike with uppermost spikelets dispersed and lowermost spikelets still attached; subulate terminal scale of spikelet at arrow; bar = 1 mm. C. Peduncle pubescence; bar = 0.7 mm. D. Dispersed spikelets adhering to clothing; arrow shows spikelet embedded by its subulate tip; bar = 1 cm

TABLE 1.—A comparison of *Cyperus plukenetii, C. hystricinus* and *C. retrofractus* with regard to characteristics faciliating animal dispersal

	C. plukenetii	*C. hystricinus*	*C. retrofractus*
Number of fruits per spikelet	1(–2)	1–(2–3)	(1–)2–7
Terminal scale of spikelet	indurate subulate	indurate subulate	not indurate subulate
Posture of spikelets	divaricate to declined	divaricate to declined	divaricate to declined
Duration of spikelets	persistent	not persistent	not persistent
Pubescence	stems, foliage and peduncles pubescent	stems, foliage and peduncles glabrous	stems and foliage pubescent; peduncles glabrous to subglabrous
Length of primary inflorescence bracts	bracts generally shorter than longest inflorescence ray	bracts longer than inflorescence rays	bracts longer than inflorescence rays

since *C. plukenetii* spikelets are persistent, additional spikelets are available for dispersal during successive passes.

Mean stem height of living individuals in a Brooks County, Georgia, population was 65.6 cm (n = 30, SD = 23.4, range 20–121 cm). Perhaps the most important aspect of the stem height data is the proportion of tall individuals in the population. Spikelets borne by relatively tall plants would be available for dispersal by large quadrupeds such as white-tailed deer. Otherwise, plant height is of little importance, since even the most robust individuals of *Cyperus plukenetii* have relatively flexible herbaceous stems that are easily bent down so that attached spikelets are brought near ground level. Furthermore, aerial parts of the plant die after the end of the growing season, and lodging of upright stems eventually occurs. Because spikelets are persistent in *C. plukenetii,* long-dead, but lodged, stems may bear many spikelets at or near ground level. Thus, spikelets are available for dispersal by even rather small animals.

Observational and experimental data support the hypothesis that humans are capable of dispersing spikelets of *Cyperus plukenetii,* and it seems that spikelets would easily penetrate and adhere to the skin or fur of other animals. Furthermore, plant height data indicate that a broad range of mammals, including white-tailed deer, foxes, raccoons, opossums, skunks, squirrels, and rabbits and, perhaps, birds are potential dispersers of spikelets of *C. plukenetii.*

Cyperus plukenetii is more widely distributed and is more common throughout its range than either of its close relatives, *C. retrofractus* or *C. hystricinus* Fernald. It seems likely that the broader range and greater frequency of *C. plukenetii* are, at least in part, due to its highly specialized dispersal mechanism. Because *Cyperus hystricinus* and *C. retrofractus* exhibit certain of the modifications that occur in *C. plukenetii* (Table 1), they may be similarly, but not as effectively, animal dispersed.

Dispersal in *Cyperus plukenetii* appears analagous to that of *Stipa* (Poaceae), in which the entire spikelet is dispersed in animal fur (Pijl, 1982), and *Achyranthes* (Amaranthaceae), in which fruiting calyces are similarly dispersed (Bullock and Primack, 1977; Medley *et al.,* 1985). The morphological features of *Carex pauciflora,* which were related to a springing dispersal mechanism by Hutton (1976), seem strikingly similar to those of *C. plukenetii.* I have observed spikelet-springing in *Cyperus plukenetii*; however, the maximum dispersal distance observed was only ca. 1 m, which seems negligible by comparison with distances

observed via animal dispersal. It seems likely that, in addition to springing dispersal, *Carex pauciflora* might also be dispersed by attachment to animal fur or skin.

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