TAXONOMY OF DICHANTHELIUM HIRSTII (POACEAE), A VERY RARE AND DISJUNCT WITCH-GRASS OF THE EASTERN U.S.

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ABSTRACT

After a careful range-wide study of specimens and a review of the taxonomic literature, we have determined that *Dichanthelium hirstii* (Swallen) Kartesz is taxonomically valid at the rank of species, and is a distinctive member of this complex genus. It is also one of the rarest plants in eastern North America.

RESUMEN

Después de un cuidadoso estudio de especímenes en un rango amplio y una revisión de la bibliografía taxonómica, hemos determinado que *Dichanthelium hirstii* (Swallen) Kartesz es taxonómicamente válido en el rango específico, y es un miembro distintivo de este género complejo. Es también una de las plantas más raras del este de Norte América.

TAXONOMIC HISTORY

Panicum hirstii Swallen was described as a new species by Swallen (1961). It was later transferred to the genus *Dichanthelium* as *D. hirstii* (Swallen) Kartesz (Kartesz 1999). Swallen's determination was based on collections made in 1959 from a Coastal Plain intermittent pond in Atlantic Co., New Jersey, and on two Georgia collections: from the margin of a pine-barren pond in Sumter Co. in 1900, and a cypress swamp in Calhoun Co. in 1947. The plant was later found at a Sussex Co., Delaware, pond in 1984, and at two ponds in Onslow Co., North Carolina, in 1990. It was also found at three more locations in New Jersey (two in Atlantic Co. in 1960 and 2015, and one in Burlington Co. in 2004). In 2014, it was found at the probable historical site in Sumter Co., Georgia (McAvoy et al. 2015). The probable historical site in Calhoun Co., Georgia, was surveyed for *D. hirstii* in 2014 without success. *Dichanthelium hirstii* is currently known from eight extant populations: 4 in New Jersey, 1 in Delaware, 2 in North Carolina, and 1 in Georgia. It should be noted that one of the New Jersey populations has not been seen since 1992, and should possibly be considered as "historic."

Since the 1961 Swallen protologue, Dichanthelium hirstii has, with one exception, been treated either in

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synonymy or disregarded altogether. The exception is LeBlond (2017) in Weakley's Flora of the Southern and Mid-Atlantic States, a continuously updated manual that first recognized *D. hirstii* in 1990. It has been treated as a synonym of *Panicum aciculare* Desvaux ex Poiret by Gleason and Cronquist (1991), and as a synonym of *D. dichotomum* (L.) Gould ssp. *roanokense* (Ashe) Freckmann & Lelong by Freckmann & Lelong (2003). Two previous authors have assessed its taxonomy: Kral (1983) and Schuyler (1996) (both as Panicum hirstii).

In his 1961 protologue, Swallen provides a thorough character description of the plant. Discussion is limited to comparison of the 1900 collection (*Harper 458*) from Sumter Co., Georgia, with *Panicum roanokense* Ashe, now treated as *Dichanthelium roanokense* (Ashe) LeBlond (Weakley *et al.* 2017). This is where Hitchcock & Chase (1910, p. 197) had "doubtfully referred" Harper's collection. Swallen distinguished *P. hirstii* from *P. roanokense* by the former's "very narrow panicles with relatively short-pedicelled spikelets, the shorter second glume, and the sparingly branching culms, the autumnal blades and panicles scarcely reduced."

Kral (1983) concluded that *Dichanthelium hirstii* "probably is a glabrous variant of *P. neuranthum* [Griseb.]." His description includes characters of both taxa. He describes the autumnal leaves as involute, a *neuranthum* character (*hirstii* autumnal leaves are flat), and spikelets as "smooth (or pilosulous)." *Dichanthelium hirstii* spikelets are always glabrous and smooth, while those of *D. neuranthum* (Griseb.) LeBlond are always puberulent. The panicle is described as "narrowly elliptical" with the branches "strongly ascending." Both of these characters are a better fit for *D. neuranthum*. The *D. hirstii* panicles are linear, the branches appressed, or a few slightly spreading in age or after pressing. The 8-14 cm length of large culm leaf blades given by Kral is a better fit for *D. neuranthum* culm leaf blades are mostly 5-8 cm long.

The assignment of *Panicum hirstii* to *P. roanokense* was first made by a notation in Agnes Chase's handwriting on the *Harper 458* specimen at GH. Harper himself originally annotated the specimen as *P. neuranthum*. Kral concluded *hirstii* was closer to (or inseparable from) *neuranthum* based on the narrow panicle.

Schuyler (1996) determined *Panicum hirstii* to be distinct at species rank in his summary of a status survey completed for U.S. Fish and Wildlife Service. He concluded that *P. hirstii* was "more similar" to *P. roanokense* than it was to *P. neuranthum* and *P. aciculare* Desvaux ex Poiret. He based the similarity to *P. roanokense* on spikelet size, glabrosity, venation, and presence of hyaline sterile paleas. He distinguished *P. roanokense* from *P. hirstii* by the former's "more branched and reduced axillary shoots, more open inflorescences with pedicels often twice or more as long as spikelets, and more variation in the number of nerves (7-9) in the second glumes and sterile lemmas."

Schuyler distinguished *Panicum hirstii* from *P. aciculare* and *P. neuranthum* by the former's consistently narrower inflorescence, shorter spikelet pedicels, glabrous spikelets, and more prominent leaf and spikelet veins. He also noted that *P. hirstii* differed by the second glumes and sterile lemmas having 9 veins (7 in *P. aciculare* and *P. neuranthum*) and a sterile palea (absent in *P. aciculare* and *P. neuranthum*).

Schuyler found no "apparent infraspecific variation" among specimens throughout the disjunctive range of *Panicum hirstii*. He also noted *P. hirstii*'s preference for seasonally ponded habitats, compared to the wet to dry terrestrial habitats of *P. roanokense*, *P. aciculare*, and *P. neuranthum*.

TAXONOMIC CHARACTERIZATION

Dichanthelium hirstii is one of the taller witch-grasses, its erect to spreading-ascending culms typically 55–100 cm long. Rosette leaves develop at the base of the culm and on offshoots. These leaves are shorter and broader than the culm leaves (common in the genus), measuring to 7 cm long and 10 mm wide, though usually smaller. Uncommon in the genus, the culm internodes, nodes, leaf surfaces and margins, peduncles, and inflores-cences are glabrous except for occasional puberulence at the abaxial summit of sheaths (collar), and the ciliate ligules.

Vernal phase.—leaf sheaths are usually shorter than the long internodes, with the uppermost sheath elongate, (6–)8–15 cm long. Ligules are a dense line of hairs 0.5 mm long, often with a few hairs to 1 mm mixed in. Vernal mid-culm leaf blades are stiffly erect to erect-ascending, 4.5–11.5(–14) cm long, 3–5.5 mm wide, 15–20+ x as long as wide, flat, and acuminate at the apex. The uppermost blade, sometimes called the flag, is

usually smaller, 2–6 cm long and 2–3 mm wide. Peduncles are strikingly elongate, the majority (20–)30–50 (–60) cm long. Panicles are linear at anthesis, 4.5–9(–13.5) cm long and 2–3 mm wide *in situ*. The central axis, branches, and pedicels are minutely scabrous. Panicle branches are up to 4 cm long and tightly appressed. (One to few panicle branches may spread slightly in age or pressing.) Most pedicels are less than twice as long as the spikelets, with lateral pedicels often shorter than the spikelets. The obovate to elliptic-oblong glabrous spikelets are 1.8–2.1 mm long and 1.1(–1.2) mm wide with obtuse summits. The first (lower) glume is broadly obtuse to subtruncate, (0.3–)0.4–0.7(–0.9) mm long, veinless and thinner in texture than the second (upper) glume and sterile (lower) lemma. The second glume is obtuse and 0–0.2 mm shorter than the cucullate and subacute sterile lemma. The second glume and sterile lemma are 9-veined, the veins weakly to moderately prominent. The hyaline sterile palea is about two-thirds as long as the sterile lemma. The fertile lemma is smooth and shiny at 10×, stramineous to pale yellow, about 1.5 mm long and 1.0(–1.1) mm wide.

Autumnal phase.—The autumnal phase is sparingly branched due to the few nodes and long internodes of the culm. Largely overlooked is the fact that *Dichanthelium* taxa have two autumnal branching phases with distinctive differences in leaf size and floral arrangement. Silveus (1942) describes these differences for several species, but subsequent taxonomic treatments have largely ignored these distinctions. The two branching phases are remarkably different in *D. hirstii*, which was not described until after the work of Silveus. The primary branches, or early autumnal phase, produce terminal inflorescences similar to the vernal inflorescences produced at the summit of the culm. Primary branch leaf blades are hardly reduced, and are on average wider than vernal blades, up to 9 mm wide, a condition that appears to be rare in the genus. Secondary (and subsequent) branching, or late autumnal phase, has leaf blades somewhat shorter and narrower than the primary branching phase, but the inflorescences are remarkably different, barely exsert or wholly contained within the leaf sheaths.

The timing of each floral stage—vernal, early autumnal, and late autumnal—often overlaps with the next, and primary branching can begin in summer (this too appears to be common in the genus). The early autumnal stage, with its long-exsert panicles, can be mistaken for the vernal form if not carefully examined. This could lead to an over-count of the vernal culms in a population, and a misrepresentation of leaf width between the two phases.

We hypothesize that *Dichanthelium hirstii* is a member of sect. *Angustifolia*, which includes *D. neuranthum*. Evidence supporting this hypothesis of relationship is from leaf morphology. Vernal leaf blades are stiffer and longer relative to width than those in sect. *Dichanthelium* (where *D. roanokense* is placed), often approaching or exceeding 20 × as long as wide. Vernal blades in sect. *Dichanthelium* typically are less than 15 × as long as wide and in general are more flexible. The longer autumnal blades of *D. hirstii* are also more characteristic of sect. *Angustifolia*, particularly noticeable in *D. neuranthum* and *D. pinetorum* (Swallen) LeBlond.

Dichanthelium hirstii is readily distinguished from all other taxa in the genus by the following combination of characters: terminal panicles linear, 2–3(–5) mm wide, 4.5–9(–13.5) cm long; most peduncles (20–)30– 50(–60) cm long; larger blades of primary branches wider than vernal blades, to 7(–9) mm wide; plants completely glabrous except for ligule cilia and occasional puberulence on the collar. The habit and inflorescence of *D. hirstii* superficially resemble those of *Hymenachne hemitomon* (J.A. Schultes) C.C. Hsu (*=Panicum h.*), which can grow in the same habitat. *Hymenachne hemitomon* is most readily distinguished by its larger blades (8–35 cm long by 5–15 mm wide), panicles 10–30 cm long, and acute spikelets 2.0–2.8 mm long.

Herbarium collections examined: **DELAWARE. Sussex Co.:** 10 Aug 1984, F. Hirst 110, 111, 112, 113 (DOV); 16 Jun 1985, F. Hirst 114, 115 (DOV); 26 Jul 1985, R. Naczi 875A, A. Tucker, & N. Seyfried (DOV); 17 Sep 1991, Sorrie 5913 (NCU); 8 Jun 1995, W. McAvoy 1084 (DOV); 16 Aug 1995, W. McAvoy 1232 (DOV); 19 Sep 1995, W. McAvoy 1289 (DOV); n.d., F. Hirst 116, 310 (DOV). **GEORGIA. Sumter Co.:** 23 Aug 1900, R. Harper 458 (paratype GH, NY); 7 Aug 2014, W. McAvoy 7442 & T. Patrick (GA). **NEW JERSEY. Atlantic Co.:** 29 Aug 1958, F. Hirst 12 (PH); 7 Jun 1959, F. Hirst 47 (holotype: US; isotype: MO); 7 Jun 1959, F. Hirst 27, 44A, 45, 46 (isotypes PH); 11 Aug 1959, B. Long 85320 (paratype PH); 21 Jul 1960, F. Hirst 53 (PH); 21 Jul 1960, B. Hirst s.n. (PH); 20 Jun 1964, F. Hirst s.n. & G. Cavileer (PH); 11 Sep 1964, F. Hirst s.n. (CHRB); 19 Jul 1975, V. Abraitys s.n. (CHRB); Jul 1985, K. McCarthy s.n. (CHRB); 3 Oct. 2016, K. Walz 2016-01, 02, 03, 04, 05, 06 et al. (NY). **Burlington Co.:** 21 Aug 2014, K. Walz KSW2014-01 (NY). **NORTH CAROLINA. Onslow Co.:** 20 Jun 1990, R. LeBlond 1376 (NCU); 23 Jun 1990, R. LeBlond 6644A (NCU); 13 Jul 1990, R. LeBlond 1470 (NCU); 23 Sep 1990, B. Sorrie 5273 & R. LeBlond (NCU); 13 Nov 1990, R. LeBlond 1795 (NCU); 19 Sep 1992, F. Hirst s.n. & R. LeBlond (PH).

| TABLE 1. Key characters for Dichanthelium hirstii, D. roanokense, and D. neuranthum. | | | | |
|--|-----------------------|------|--|--|
| Characters | Dichanthelium hirstii | Dich | | |

| Characters | Dichanthelium hirstii | Dichanthelium neuranthum | Dichanthelium roanokense |
|--|---------------------------------------|--|--------------------------|
| uppermost sheath length (cm) | (6–)8–15 | 3–6 | 2.5-7.5(-10.5) |
| peduncle length (cm) | (20-)30-50(-60) | 10–22 | 5–18.5 |
| panicle width at anthesis (mm) | 2-3(-5) | > 3 | > 3 |
| panicle width to length | < 1/8 | (1/8-)1/4 -> 1/2 | > 1/2-4/5 |
| panicle branch orientation | erect-appressed (-erect-ascending) | erect-ascending to ascending (-spreading) | spreading to ascending |
| spikelet indumentum | glabrous | glandular-pubescent | glabrous |
| first glume summit | broadly obtuse to subtruncate | obtuse | subacute to acute |
| first glume length (mm) | (0.3-)0.4-0.7(-0.9) | 0.8-1.0 | 0.6–0.9 |
| early autumnal to vernal blade width | at least some wider | narrower | narrower |
| larger early autumnal blade width (mm) | 5–7(–9) | < 5 | < 5 |

The following key distinguishes *Dichanthelium hirstii* from the two taxa with which it has been most confused by previous authors: *D. roanokense* and *D. neuranthum*. (The key characters are presented in tablature form in Table 1.)

| 1. Uppermost sheaths (6–)8–15 cm long; vernal peduncles mostly (20–)30–50(–60) cm long; panicles linear, 2–3(–5) mm | |
|---|------------|
| wide at anthesis, the branches erect-appressed (-erect-ascending); spikelets glabrous; first glumes broadly obtuse to | |
| subtruncate, (0.3–)0.4–0.7(–0.9) mm long; at least some early autumnal blades wider than vernal blades, 5–7(–9) mm | |
| wide | D. hirstii |
| 1. Uppermost sheaths 2.5–7.5(–10.5) cm long; vernal peduncles mostly (5–)7–19(–22) cm long; panicles > 3 mm wide to | |

| . Uppermost sheaths 2.5–7.5(–10.5) cm long; vernal peduncles mostly $(5-)7-19(-22)$ cm long; panicles > 3 mm wide | to |
|--|----------------|
| nearly as wide as long, branches erect-ascending to spreading; spikelets glabrous or pubescent; first glumes obtuse | to |
| acute, 0.6–1.0 mm long; early autumnal blades narrower than vernal blades, < 5 mm wide. | |
| 2. Mid-culm vernal blades 3-5 mm wide, usually > 15 × as long as wide; panicles usually less than 1/4 as wide as long | ng, |
| branches ascending to spreading-ascending; spikelets obovate, glandular-pubescent | _D. neuranthum |
| 2. Mid-culm vernal blades 3–8 mm wide, usually < 15 × as long as wide; panicles more than ½ to nearly as wide as long as wide; panicles more than ½ to nearly as wide as long as wide; panicles more than ½ to nearly as wide as long as well as the second se | ng, |
| branches spreading to spreading-ascending; spikelets ellipsoid, glabrous | D. roanokense |

There are also important differences in the habitat preferences and distribution of the three species. *Dichanthelium hirstii* is found in limesink depressions, pond-cypress savannas, and other seasonally ponded wetland depressions; *D. neuranthum* is found in maritime wet grasslands and wet or dry inland prairies; and *D. roanokense* is primarily a plant of wet pine savannas. *Dichanthelium hirstii* is disjunctly distributed in the Atlantic Coastal Plain from New Jersey south to Delaware, North Carolina, and Georgia. *Dichanthelium neuranthum* occurs in the Atlantic and Gulf coastal plains from North Carolina south to Florida and west to east Texas and Arkansas, with a disjunct occurrence in the North Carolina Piedmont; it is also known from Bahamas, Cuba, and Belize. *Dichanthelium roanokense* occurs in the Atlantic and Gulf coastal plains from Delaware south to Florida and west to east Texas, with a disjunct occurrence in Jamaica.

In summary, *Dichanthelium hirstii* is distinctive at species rank even by the narrowest and most classical species concept emphasizing morphology alone. By modern species concepts, with emphasis on separate evolutionary lineages, the evidence supporting species rank for *D. hirstii* becomes more profound based on its distinctive morphology, distribution, and habitat as compared with any congenors with which it could putatively be placed in synonymy. All available evidence shows that *D. hirstii* is a rare and highly imperiled species.

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