

REINSTATEMENT OF *SAGITTARIA MACROCARPA* (ALISMATACEAE)

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ABSTRACT

Sagittaria macrocarpa J.G. Sm. is here restored to full species status. A narrow distribution, the rarity of specimens available for study, and morphological similarity to closely related taxa has contributed to this species being overlooked or misidentified for a century. Recent research in population genetics, molecular sequencing, and morphology support the hypothesis that *Sagittaria macrocarpa* is distinct from congeners. In addition, the taxon occupies a unique range of habitats and apparently a limited distribution.

RESUMEN

Se restaura aquí a *Sagittaria macrocarpa* J.G. Sm. al status de especie. Una distribución restringida, la rareza de los especímenes disponibles para su estudio, y la semejanza morfológica con taxa relativamente próximos ha contribuido a que esta especie sea pasada por alto o se identifique erróneamente durante un siglo. Investigaciones recientes en genética de poblaciones, secuenciación molecular, y morfología apoyan la hipótesis que *Sagittaria macrocarpa* es diferente de sus congéneres. Además, el taxon ocupa un único rango de hábitats y aparentemente una distribución limitada.

INTRODUCTION

Recent field and herbarium studies have documented specimens referable to *Sagittaria macrocarpa* J.G. Sm., a name long misapplied and in synonymy under *S. graminea* Michx. Morphological and molecular studies lend significant support for designating *S. macrocarpa* a distinct taxon. In this paper we provide evidence for reinstating *S. macrocarpa* to specific status. *Sagittaria macrocarpa* J.G. Sm. was described in 1894 (Smith 1894). He cited only the holotype, a specimen collected by M.A. Curtis from “margin of ponds” in South Carolina (undated, Curtis s.n. MO!). Bogin (1955) cited an isotype of *S. macrocarpa* at GH; while correctly identified, this specimen is almost certainly not an isotype (see discussion ahead). Until now, these two are the only specimens known of *S. macrocarpa* sensu J.G. Sm.

Small (1909) misapplied the name *S. macrocarpa* to plants that were later to be named *S. fasciculata* by Beal (1960). This misapplication was apparently based on the large achenes of *S. macrocarpa* and *S. fasciculata*, which are markedly larger than other taxa of the *S. graminea* complex. In a later publication, Small (1933) again included *S. macrocarpa* in his text and provided habitat and range statements that are consistent with *S. macrocarpa* of J.G. Sm. However, Small’s description does not exclude plants later to be named *S. fasciculata* Beal, particularly those with 3–5 whorls of flowers.

Bogin (1955) reduced *S. macrocarpa* to varietal status, as *S. graminea* Michx. var. *macrocarpa* (J.G. Sm.) Bogin. At the same time, Bogin misapplied the name *macrocarpa* to plants that later were named *S. fasciculata* Beal.

Beal (1960) correctly recognized plants of North Carolina montane bogs and sluggish streams as *S. fasciculata* Beal, based on spatulate emersed leaves, broad basal phyllodia, and narrow distribution. He placed *S. macrocarpa* in synonymy with *S. graminea* var. *graminea*, stating that *S. macrocarpa* “differs from

typical *S. graminea* var. *graminea* in no way except the size of achenes which are as much as 3 mm in length in contrast to the usual length of 1.5–2.0 mm of var. *graminea*. However, specimens of var. *graminea* collected by the author [Beal] in the coastal plain of North Carolina exhibit a range in achene size including 3 mm. Therefore, *S. macrocarpa* J.G. Sm. must be relegated to synonymy.” During our research, however, we have not seen any *S. graminea* with achenes approaching 3 mm. Wooten (1973) and Haynes and Hellquist (2000) followed Beal (1960) in placing *S. macrocarpa* in synonymy under *S. graminea*. In their treatment for Flora of North America, Haynes and Hellquist (2000) use subspecies rather than variety to designate infraspecific rank within *Sagittaria graminea*; we will do so henceforth.

REDISCOVERY AND SPECIMENS

During a botanical inventory of Fort Bragg Military Reservation, North Carolina, specimens initially determined as *Sagittaria isoetiformis* J.G. Sm. were collected and discussed by Sorrie et al. (1997). These plants possess leaves with slender distal blades and/or bladeless (phyllodial) leaves; they have since been annotated to *S. macrocarpa* based on achene and floral morphology. Other plants collected on Fort Bragg possess somewhat wider blades and were originally determined to be *S. graminea*, but based on achene and floral morphology these specimens also belong to *S. macrocarpa*. All of these plants occur in blackwater stream-heads, beaver ponds, and artificial impoundments; none occur in natural depression ponds or Carolina bays, habitats occupied by *S. isoetiformis*.

Once the salient characters of *S. macrocarpa* were determined, the senior author found additional populations and historical specimens elsewhere in the Sandhills region of North and South Carolina. The following list represents all known vouchers. ITAM stands for the herbarium at the office of Integrated Training and Management on Fort Bragg, North Carolina; WEWO stands for the herbarium at Weymouth Woods State Nature Preserve, North Carolina; the other acronyms follow Index Herbariorum (2006).

NORTH CAROLINA. Hoke Co.: Fort Bragg, Field Branch, boggy portion of formerly impounded blackwater stream, S of firebreak 11 and west of Turkey Road, 18 Sep 1993, Sorrie 7558 (NCU, pers. herb.); Fort Bragg, Calf Branch at Southern Pines Road, open streamside disturbed by siltation, 11 Aug 1993, Sorrie 7545 with B. Van Eerden and R. Kral (pers. herb.); Fort Bragg, Gum Branch at Chicken Road, margin of blackwater stream, sandy bottom with some mud and clay, 20 Jul 1993, Sorrie 7566 (NCU, pers. herb.); same location, 16 Sep 1981, J. Carter III 1497 (WEWO); Fort Bragg, Puppy Creek at Plank Road Cutoff, with *Scirpus etuberculatus*, *Spartanium americanum*, *Potamogeton diversifolius*, 2 Jun 1995, T. Crawford and P. Crutchfield B1329 (ITAM); Fort Bragg, NE shore of McArthur Lake, with *Mayaca aubletii*, *Eleocharis flavescens*, *Nymphaea odorata*, 29 Sep 1992, P. Crutchfield and M. Jones B652 (ITAM). **Hoke/Moore Cos.:** Fort Bragg, Johnsons Millpond, a large beaver pond dotted with peat islets, locally common in shallow pools and where inlet streams enter, with *Sagittaria engelmanniana*, *Eleocharis robbinsii*, 9 Oct 1991, Sorrie 5969 with A. Weakley, J. Carter III (NCU, pers. herb.); same location, sandy substrate at east shore, 18 Aug 1993, Sorrie 7557 (DUKE, GH, NCU, pers. herb.); same location, peaty-sandy shore, 16 Aug 2002, Sorrie 10981 with J. Gray (US, pers. herb.). **Moore Co.:** Aberdeen Recreation Lake, 4 mi NE of Pinebluff, Chloride 1.6 ppm, 16 Jun 1960, E. Beal 5592 (DUKE, NCU); same location, southern shores, 30 May 2004, Sorrie 11262 (GH, UNA, NCU); Pinebluff Lake, impounded blackwater stream with stressed *Nyssa biflora* at head end, with *Panicum hemitomon*, *Juncus debilis*, 28 May 1997, Sorrie 9252 (NCU, pers. herb.); same location, 21 Jul 2000, Sorrie 10571 (pers. herb.); margin of Powell's Pond at intersection of Fort Bragg-Aberdeen Hwy. and Saunders Blvd., 28 Jun 1979, T. Howard s.n. (WEWO); submerged just below beaver dam, Weymouth Woods State Nature Preserve, 23 Oct 1965, H. Ahles 63085 (WEWO); Weymouth Woods, partially submerged in old beaver pond, 9 Aug 1976, J. Carter III s.n. (NCU, WEWO); Weymouth Woods, along Pine Island Trail near crossing of James Creek, 28 Sep 2002, Sorrie 11016 (pers. herb.); Moore County without location, 27–28 Jun 1897, W. Ashe s.n. (NCU). **SOUTH CAROLINA. Aiken Co.:** infrequent in wet portion of herb-dominated sandhills seepage bogs in high voltage powerline clearing between Vaulcluse and Graniteville above Flatrock Pond, Horse Creek, 26 Jun 2001, P. McMillan 5447 with R. McCartney, H. Shealy (CLEMS). **Chesterfield Co.:** just above hot water discharge of power plant, W margin of Lake Robinson, 1/2 mi S of Hwy. 346 bridge, 15 Sep 1986, C. Aulbach-Smith 4200 (USCH), 4192 (NCU, USCH). **County unknown:** “margin of ponds S. Car.,” undated, M.A. Curtis s.n. (MO)–TYPE; “S. Carolina,” undated, M.A. Curtis s.n. (GH).

STATUS OF CITED ISOTYPE

A second Curtis specimen was cited by Bogin (1955) as an isotype of *S. macrocarpa*: “S. Carolina,” undated, M.A. Curtis s.n. (GH). On the sheet J.G. Smith wrote “This plant...is intermediate between *S. teres* and *S. macrocarpa*.” In all respects this specimen matches *S. macrocarpa*, except for the achenes, which are 2.0 mm long and 1.5 mm wide. However, the achenes appear to be immature and apparently not fully developed. The labeling of this specimen differs from the type collection in several particulars and we believe it not to

be an isotype. First, the lettering is printed by machine, not in longhand as on the MO type label. Second, the paper used for the label is different from that of the MO label. Third, there is no mention of habitat (“margin of ponds”) as on the MO label. For these reasons, we suggest that Curtis collected the GH specimen at a different place and date than the type at MO. Based on evidence and discussion above, we believe this specimen is not an isotype of *S. macrocarpa*.

GENETIC STUDIES

Edwards and Sharitz (2000) investigated the genetic structure of *S. isoetiformis* and *S. teres* S. Wats. One population in their study gave divergent results: “We were surprised to discover a population (NCJM) [Johnsons Millpond, Fort Bragg, North Carolina] that was monomorphic at two loci for alleles not found in any other population of either *S. isoetiformis* or *S. teres*. There are several possible explanations for this phenomenon: (1) we did not sample enough populations to detect the alleles elsewhere; (2) the NCJM population has been repeatedly misidentified as *S. isoetiformis*, but actually represents a known species in the *Gramineae* section of the genus; (3) the NCJM population represents a cryptic species that has not been morphologically distinguished from *S. isoetiformis*, or (4) the NCJM population is *S. isoetiformis*, but contains remnant genetic input from past introgression with another species.” As a result of our research, all specimens at Johnsons Millpond previously assigned to *S. isoetiformis* have now been correctly assigned to *S. macrocarpa*; therefore, choices 2 and 3 of Edwards and Sharitz apply to the present situation.

Keener (2006) investigated most of the genus utilizing sequences of the nuclear ribosomal DNA non-transcribed spacer (5S-NTS) in a systematic analysis. His findings indicated a rather strong sister relationship of *S. macrocarpa* with *S. cristata* Engelmann, a taxon of the extreme north central United States and south central Canada. A reasonable hypothesis is yet to be formed as to how these sister taxa came to have such a large disjunct gap in their distributions.

MORPHOLOGICAL CHARACTERS

The following is a description of *S. macrocarpa*, expanded on Smith (1894). **Plant:** perennial, monoecious herbs, glabrous, emerged from shallow water or stranded during flowering and fruiting, to 40 cm tall. Rhizomes absent; **corms present**; stolons often extending from **corms** but usually broken or lost during collecting; tubers unknown; roots septate. **Leaves:** narrowly bladed and petiolate, or phyllodial. Leaves ascending to erect, (6.5–)8.0–22.2(–28.2) cm long, slender, when petiolate dilated distally into linear blades (0.8–)1.0–3.1(–4.0) mm wide, lacking sagittate processes; margins entire; apex acute. **Scapes:** often 1 but range up to 4, erect, (11.4–)14.3–27.2(–33.8) cm long, exceeding leaves; inflorescences racemose, bearing 1–3 nodes; lowest node bearing 1–2 carpellate flowers and 1–2 staminate flowers; upper nodes bearing staminate flowers; nodal bracts scarious, connate at base for more than 1/4 to 1/3 total length, ovate, tips blunt or acute, (1.9–)2.1–2.7(–3.0) mm long. **Flowers:** pedicels ascending; receptacles convex; sepals spreading to recurved, 3.0–3.5 mm long, translucent, shorter than petals; petals 3, white, (4.2–)4.6–6.4(–7.3) mm long, entire. Carpellate flowers: carpels numerous, apocarpous, ovules 1, styles terminal. Staminate flowers: stamens 8–10, filaments distinct, moderately dilated basally, sparsely to fairly densely short-pubescent, 0.4–0.7 mm long, anthers 0.9–1.0 mm long, yellow. **Fruiting heads:** 8–10 mm in diameter; achenes obovate, 2.0–2.7 mm × 1.3–2.0 mm, compressed, beaked, adaxially keeled, keel margin entire to scalloped; abaxially slightly keeled, keel margin entire; faces ridged, ridges horseshoe shaped, margins scalloped to entire; resin canal 1, rarely 2; beak laterally attached, obliquely emerging, 0.5–1.0 mm long. Figure 1 depicts the salient features.

Table 1 compares several key characters among *Sagittaria macrocarpa*, *S. isoetiformis*, *S. graminea* ssp. *graminea*, and *S. fasciculata*. Although no single character uniquely identifies any one of the four taxa, a number of combinations will do so effectively. The thick rhizome of *S. graminea* ssp. *graminea*, when present, will positively distinguish that entity from the others; however, Godfrey & Wooten (1979) state that in young plants (through the first year or so of blooming) the rhizome is not yet well developed.

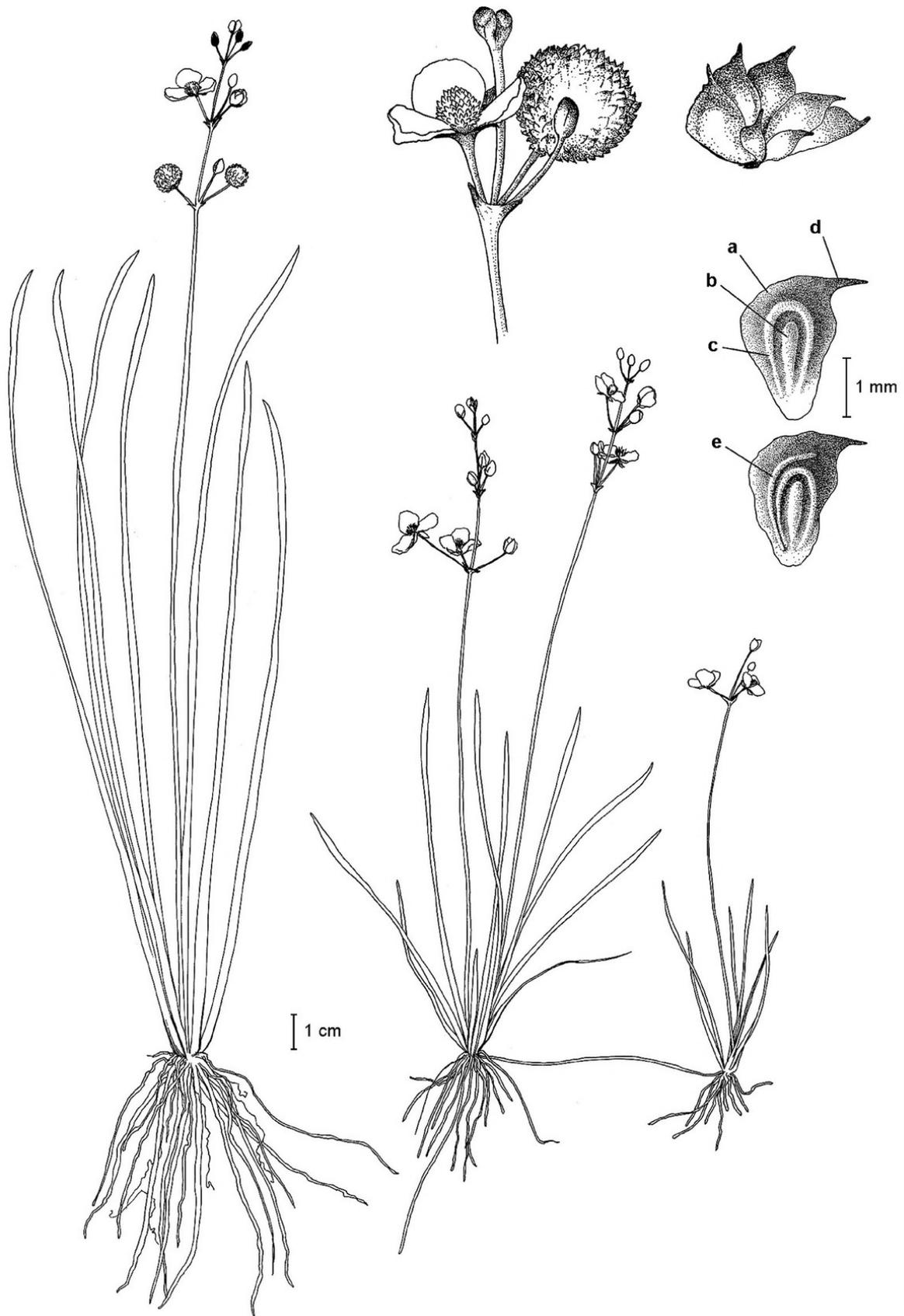


FIG. 1. Two plants of *Sagittaria macrocarpa* (one with offshoot from stolon), with detail of inflorescence and achenes. a. achene keel. b. resin canal. c. facial ridge. d. beak. e. secondary facial ridge.

TABLE 1. Comparison of selected morphological characters of *Sagittaria macrocarpa*, *S. isoetiformis*, *S. graminea* ssp. *graminea*, and *S. fasciculata*. Measurements in millimeters. FNA refers to Haynes & Hellquist (2000); Beal refers to Beal (1960); otherwise, measurements are from original work. * = A. Edwards unpublished data.

| | <i>macrocarpa</i> | <i>isoetiformis</i> | <i>graminea</i> | <i>fasciculata</i> |
|--------------------------------------|--|--|--|--|
| Achene length | (2.2–)2.4–3.0 | 1.5–2.0(–2.5) | 1.4–2.0 | 2.5–3.0 FNA 2.5–3.5 Beal |
| Achene width | 1.3–2.1 | 0.9–1.2(–1.5) | 0.9–1.2(–1.5) | 1.2–1.5 FNA 1.3–2.0 Beal |
| Beak length | 0.5–0.9 | 0.2–0.6 | 0.2–0.4 | ca. 0.5 |
| Achene face | resin canal 1(–2), flanked by 2(–3) low ridges | resin canal 2–3, flanked by 2–3 low ridges | resin canal 1, surrounded by 2 high ridges | resin canal 1, flanked by 2 low ridges |
| No. of inflorescence whorls | 1–3 | 1–5 | 1–7 | 2–5 |
| Bracts connate | up to 2/5 of length | at least 1/2 | 1/3–2/3 | 1/4 |
| Leaf blade width | 1.0–4.3 | <1–2.2 | 3.0–15.0 | 5.0–21.0 |
| Rhizome present and thickness | no or very slender | no or very slender | yes, thick | no |
| Corms produced | no | yes* | no | yes |
| Stolons present | yes or no | yes, but usually not collected | no | yes |

A KEY TO THE NARROW-LEAVED MEMBERS
OF THE *SAGITTARIA GRAMINEA* COMPLEX

The following key will serve to identify narrow-leaved members of the *Sagittaria graminea* group occurring in the southern Atlantic region of the United States. *Sagittaria graminea* ssp. *weatherbiana* (Fernald) R.R. Haynes & Hellquist is a much coarser plant with blunt-tipped leaves at least 1 cm wide.

1. Leaves phyllodial.
 2. Achenes 1.5–2.0(–2.5) mm long; achene with 3 or more facial ridges and 2 or more resin canals; inflorescence bracts connate for more than half of entire length _____ **S. isoetiformis**
 2. Achenes (2.2–)2.4–3.0 mm long; achene with 2–3 facial ridges and 1–2 resin canals; inflorescence bracts connate for less than 40% of entire length _____ **S. macrocarpa**
1. Leaves petiolate.
 3. Carpellate pedicels distinctly thicker in cross section than staminate pedicels, recurved in fruit _____ **S. platyphylla**
 3. Carpellate pedicels more-or-less equal to staminate pedicels in diameter, ascending in fruit.
 4. Rhizomes coarse; achene with markedly raised facial ridges, forming an elliptical bowl-like structure.
 5. Inflorescence racemose _____ **S. graminea** ssp. **graminea**
 5. Inflorescence paniculate _____ **S. graminea** ssp. **chapmanii**
 4. Rhizomes absent or slender; achene with slightly raised facial ridges (markedly raised in *S. graminea*).
 6. Leaf blades at least 5 mm wide and anthers about 0.6–0.7 mm long _____ **S. fasciculata**
 6. Leaf blades less than 4.5 mm wide and anthers about 0.9–1.1 mm long.
 7. Achenes (2.2–)2.4–3.0 mm long, beaks 0.5–0.9 mm long _____ **S. macrocarpa**
 7. Achenes 1.4–2.0(–2.5) mm long, beaks 0.2–0.6 mm long.
 8. Achenes with markedly raised facial ridges, forming an elliptical bowl-like structure; leaf blades at least 3.0 mm wide _____ **S. graminea** ssp. **graminea**
 8. Achenes with slightly raised facial ridges; leaf blades less than 2.3 mm wide _____ **S. isoetiformis**

HABITAT AND DISTRIBUTION

Sagittaria macrocarpa inhabits very shallow water of beaver ponds, impoundments, slow-moving streamhead creeks, and occasionally in adjacent wet seepage slopes, all within the longleaf pine (*Pinus palustris* P. Miller)

ecosystem. These are blackwater drainages with dark tannin-stained water, low pH, and low nutrient content. Substrates are sands or clayey sands of the Middendorf Formation (Upper Cretaceous). Peat mosses (*Sphagnum* spp.) are common associates, along with members of *Juncus*, *Eleocharis*, *Scirpus*, *Panicum*, *Dichanthelium*, *Lachnanthes*, *Nymphoides*, *Nymphaea*, *Sparganium*, *Potamogeton*, and *Mayaca*. Ericaceous shrubs are often prominent around the margins of these wetlands. Within the genus *Sagittaria*, only *S. engelmanniana* J.G. Sm. and *S. graminea* (rarely) have been found growing with *S. macrocarpa*, based on personal observations.

To date, all populations occur in the rolling Sandhills Region (inner coastal plain) of North and South Carolina. Although documented from only four counties in two states, there is abundant potential habitat in the region as beaver continue to reclaim former range and as humans continue to create streamhead impoundments.

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