SOLIDAGO PSAMMOPHILA (ASTERACEAE: ASTEREAE), A NEW SAND DUNE ENDEMIC GOLDENROD FROM NORTHERN MICHIGAN, U.S.A.

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ABSTRACT

Solidago psammophila is described as a new species from open dune habitats along the southern shore of Lake Superior in Michigan's Upper Peninsula. Field and herbarium studies revealed that it is endemic to the state of Michigan, restricted to an approximately 100 km section of shoreline from Grand Sable Dunes in the west to Whitefish Point in the east. This goldenrod is ecologically similar to *S. gillmanii* (A. Gray) Steele in *Solidago* subsect. *Humiles* (Rydb.) Semple, sharing apparent adaptations to the sand dune environment. However, it differs from *S. gillmanii* and other members of subsect. *Humiles* in its vegetative pubescence and lack of glutinosity. It is morphologically most similar to the widespread *S. hispida* Muhl. in subsect. *Erectae* (G. Don) Semple & J.B. Beck. DNA ploidy determinations from flow cytometry revealed that this newly described species is tetraploid, whereas *S. hispida* has been shown to be uniformly diploid across its range. *Solidago psammophila* appears to be an example of the interplay of polyploidy and habitat specialization leading to ecological speciation in the recently glaciated Great Lakes region. A brief discussion of the other Great Lakes region endemic goldenrods and a revised key to all Michigan *Solidago* species are included.

KEYWORDS: endemism, goldenrod, Great Lakes region, polyploidy, *Solidago*

INTRODUCTION

The North American Great Lakes region, defined here as the area within the Great Lakes drainage basin, was completely glaciated during the most recent periods of Pleistocene glaciation (Dorr and Eschman 1970; Williams et al. 1998). In geologic terms, therefore, the contemporary flora of the region is young, having assembled only within the last 10,000 to 15,000 years. Most of the native vascular flora—ca. 2,500 species (Peirson 2010)—consists of species that migrated into the region following glaciation and that inhabit basic vegetation formations within the region. However, approximately 60 endemic vascular plant taxa have been described from the region. Unlike most widespread members of the flora, many of these endemics are restricted to ecologically specialized habitats, often along the shores of the Great Lakes (Peirson 2010).

The three best known Great Lakes shoreline endemics are *Iris lacustris* Nutt. (dwarf lake iris), *Solidago houghtonii* Torr. & A. Gray (Houghton's goldenrod), and *Cirsium pitcheri* Torr. & A. Gray (Pitcher's thistle), all of which are federally-listed threatened species. *Iris lacustris* and *S. houghtonii* both have geographic distributions that are tightly centered around the Straits of Mackinac in northern Michigan, a general distribution that is shared by a number of Great

Lakes endemics. *Iris lacustris* is restricted to calcareous shores and alvar habitats of the Niagara Escarpment from eastern Wisconsin and northern Michigan to the Bruce Peninsula in Ontario (Guire and Voss 1963; Trick and Fewless 1984), while *S. houghtonii* is likewise essentially confined to sandy and rocky shores from northern Michigan along the northern edge of Lake Huron to the Bruce Peninsula (Guire and Voss 1963; Morton 1979; Morton and Venn 2000; Laureto and Barkman 2011). The distribution of *Cirsium pitcheri*, while still encompassing the Straits of Mackinac, is broader than those of the previous two species. Pitcher's thistle inhabits beaches and active sand dunes from the southern shores of Lake Michigan north through Lake Huron, with several populations along the Lake Superior shoreline as well (Guire and Voss 1963; Voss 1996). Taken together, these three endemics illustrate the characteristic ecogeographic patterns found in a number of Great Lakes shoreline endemics (Peirson 2010).

Another striking Greats Lakes shoreline endemic is Gillman's goldenrod or dune goldenrod, treated here at the species level as *Solidago gillmanii* (A. Gray) Steele (following Semple and Peirson 2013). Like *Cirsium pitcheri*, this species is a characteristic component of sand dune vegetation along the shores of Lake Michigan and northern Lake Huron. Gray (1882) originally described this goldenrod (at the time as *S. humilis* Pursh var. *gillmanii* A. Gray), as occurring on "sand hillocks on the shores of Lakes Superior and Michigan." Voss (1996) likewise included dune goldenrods along the southern shore of Lake Superior in *S. gillmanii* (at the time as *S. simplex* Kunth var. *gillmanii* (A. Gray) Ringius), even using a photograph of a particularly robust Lake Superior plant from Chippewa County, Michigan in his Plate 7F. However, during fieldwork to sample populations of *S. gillmanii* near Deer Park, Luce County, Michigan, as part of a broader phylogeographic study of the species and other members of *Solidago* subsect. *Humiles* (Rydb.) Semple, it became apparent that these Lake Superior dune goldenrods did not fit well within *S. gillmanii* from the dunes of Lakes Michigan and Huron. While the plants shared the overall form and apparent sand dune adaptations of *S. gillmanii*, the Lake Superior plants had conspicuous pubescence on both the leaves and the stems, a characteristic not found in *S. gillmanii*. They also lacked the glutinous (sticky) leaves and capitula (flower heads) of *S. gillmanii*. It was clear that these dune goldenrods warranted a closer look.

The major objectives of this study were (1) to use field and herbarium studies to examine the Lake Superior dune goldenrod and describe its distribution and ecology; (2) to compare this dune goldenrod to other goldenrods in the Great Lakes region and to assess its taxonomic placement; (3) to use flow cytometry to determine its ploidy; and (4) to use the information thereby collected to place it more broadly in the context of the endemic flora of the region.

MATERIALS AND METHODS

Study System—*Solidago* L. (Asteraceae: Astereae) is a genus of over 130 species of perennial herbs, approximately 120 of which are native to North America (Semple and Cook 2006; Semple 2022). Michigan is home to 27 currently recognized species of goldenrod (as summarized from Voss and Reznicek 2012; Semple and Peirson 2013; Semple et al. 2017a). The most recent classifications of the genus have recognized four subgenera, 15 sections, and 12 subsections, based on morphology and a polygenomic DNA phylogeny (Semple and Beck 2021; Semple et al. 2022, submitted). To

TABLE 1. Locality and voucher information for populations of Lake Superior dune goldenrod and *S. hispida* sampled for flow cytometry analyses. All populations were in Michigan, U.S.A. Vouchers are deposited at MICH.

Taxon Population	County	Latitude	Longitude	Voucher
S. hispida var. *hispida*				
Au Train Bay	Alger	46.43	−86.83	*Peirson 853*
Superior Campground Beach	Luce	46.68	−85.75	*Peirson 856*
S. hispida var. *huronensis*				
Great Sand Bay	Keweenaw	47.45	−88.22	*Peirson 627*
Lake Superior dune goldenrod				
East of Deer Park	Luce	46.68	−85.61	*Peirson 861*
East of 3-Mile Creek	Luce	46.73	−85.32	*Peirson 833*
Superior Campground Beach	Luce	46.68	−85.75	*Peirson 855*
West of Whitefish Point	Chippewa	46.79	−84.99	*Peirson 857*

date, no comprehensive molecular phylogenetic framework has been published for *Solidago*. The genus is well known for its complex patterns of infraspecific cytogeographic variation, with approximately 46% of recognized species showing some incidence of polyploidy in their histories (Peirson et al. 2012).

Goldenrods are characteristic members of the late summer- and fall-blooming floras across much of North America. Their most commonly yellow-rayed heads are arranged into conspicuous capitulescences in many species and can be quite showy. Goldenrods are self-incompatible and are pollinated by a variety of insect pollinators (Gross and Werner 1983; Havercamp and Whitney 1983). Seed dispersal in *Solidago* species is by wind; the cypselae have a bristly pappus that aids in wind dispersal (Hood and Semple 2003).

Field Investigations—Fieldwork was conducted along the southern Lake Superior shoreline in Michigan. Sand dune and shoreline communities were surveyed from Marquette in Marquette County to Whitefish Point in Chippewa County. Populations of the Lake Superior dune goldenrod were located and sampled along a 75-km shoreline transect from Superior Campground Beach east of Grand Marais to Whitefish Point. Locality and voucher information is presented in Table 1. In addition to the target species, individuals of *S. hispida* Muhl. from the southern shore of Lake Superior were also sampled for comparison. At each site, rhizome cuttings from widely spaced individuals (clones spaced > 3 m apart) were harvested in the field and transplanted to Matthaei Botanical Gardens at the University of Michigan. The cuttings, consisting of a rosette of leaves and approximately four cm of rhizome with multiple nodes and buds, were potted in standard potting soil. Voucher specimens were harvested in the field, or taken from greenhouse-grown plants if not flowering in the field, and deposited in the University of Michigan Herbarium (MICH).

Herbarium Investigations—To determine the full geographic range of the species and to compare it to other sand dune endemic goldenrods in the Great Lakes region, *Solidago* specimens from GH, MICH, MO, MSC, MT, TEX, and UMBS were studied.

DNA Ploidy Determination—DNA ploidy (sensu Hiddeman et al. 1984) was determined by flow cytometry after the relative DNA content (from flow cytometry) was calibrated with chromosome counts and flow cytometry determinations from other studies (see below). At least one calibration/standardization was used for each recovered DNA ploidy level ($2x$ and $4x$). Similar methods have been used successfully for other species of *Solidago* (Halverson et al. 2008; Schlaepfer et al. 2008; Laureto and Pringle 2010; Peirson et al. 2012).

Methods follow those described in Peirson et al. (2012). Fresh *Solidago* leaf material was harvested from greenhouse-grown plants and stored in cool conditions for up to one week. For each sample, approximately one half of a young leaf was chopped with a clean razor blade in 0.8 ml ice-cold LB01 buffer (Doležel et al. 1989) with 50 µg/ml propidium iodide and 50 µg/ml RNAse added. An approximately equal amount of fresh leaf from *Glycine max* (L.) Merr. 'Polanka' was co-chopped as an internal DNA content standard (2.5 pg/2c; cited in Doležel et al. 1994; Doležel et al. 2007). After chopping, each sample was filtered through a 30-µm filter into a microcentrifuge tube. Filtered

samples were then centrifuged. The supernatant was subsequently removed, and the pellet was re-suspended in 50 µg/ml propidium iodide and incubated at room temperature for 20-45 minutes. Samples were run on a BD FACSCalibur flow cytometer in the Department of Integrative Biology at the University of Guelph. Samples were run at medium pressure for 90 seconds, and data were acquired using CellQuest Pro software (BD Biosciences).

Samples were analyzed using Modfit (Verity Software) to estimate peak means, CVs (coefficients of variation), and nuclei number. DNA content was calculated as:

$$\text{DNA Content} = 2.5 \times \frac{\textit{Solidago} \text{ mean}}{\textit{Glycine max} \text{ mean}}$$

where 2.5 equals the standardized mean genome size of *Glycine max* (in pg/2C) and the other mean values represent the experimentally determined values for each sample and where pg/2C is the mean nuclear DNA content in picograms expressed on a diploid basis.

RESULTS AND DISCUSSION

Study of herbarium specimens from dune systems along the southern shore of Lake Superior supported the preliminary conclusion based on initial field observations that the goldenrods there differed from *Solidago gillmanii* and likely did not belong to *Solidago* subsect. *Humiles*, to which *S. gillmanii* belongs. The Lake Superior dune goldenrods shared the overall form and apparent sand dune adaptations of *S. gillmanii* (e.g., presence of elongate vertical rhizomes that allow survival from sand burial) but differed noticeably in their pubescent stems and foliage. Vegetative pubescence (outside of the floral arrays) is not found in *S. gillmanii* or the other members of subsect. *Humiles*. Subsequent fieldwork along the southern shore of Lake Superior confirmed the earlier observations. Plants in these populations were consistently pubescent (rarely only sparsely so) and were also not noticeably glutinous. Sticky leaves, stems, and capitula have been used as defining characteristics of members of subsect. *Humiles* sensu lato and are readily apparent in *S. gillmanii* in the field.

The vegetative pubescence and virgate (wand-like) inflorescences of the Lake Superior dune goldenrods suggested a possible relationship with *Solidago hispida* Muhl. (hairy goldenrod). That species is widespread throughout eastern North America, extending as far west as the Canadian prairie provinces, in a variety of dry, often sandy or rocky habitats (Semple et al. 2017b). The typical pubescent form of *S. hispida* occurs throughout Michigan. In the Lake Superior region, it occurs along the shore in open, sandy woods, on lakeshore bluffs, and in rock outcrop habitats, but is almost never present on the open dunes (except occasionally at the margins in more stabilized areas). Examination of plants in the field and the herbarium revealed that typical *S. hispida* seems to lack the elongate vertical rhizomes that would allow for survival from sand burial in open dune habitats. While sharing vegetative pubescence and virgate inflorescences, the Lake Superior dune goldenrods differed morphologically from nearby, typical *S. hispida* in their larger stature, clump-forming habit of several to many stems, elongate vertical rhizomes, and in their larger capitula (ca 6.5 mm vs ca 4.5 mm long, respectively). These observations supported the idea that these dune goldenrods along the southern shore of Lake Superior represented an un-

TABLE 2. DNA content and DNA ploidy as determined by flow cytometry analysis of fresh leaf tissue from Solidago psammophila and S. hispida.

| Taxon | | | DNA Content (pg/2C) | | |
Population	No. Indiv.	DNA Ploidy	Mean (± SD)	Min.	Max.
S. hispida* var. *hispida					
Au Train Bay	19	$2x$	2.09 (0.03)	2.04	2.15
Superior Campground Beach	5	$2x$	2.07 (0.01)	2.06	2.09
S. hispida* var. *huronensis					
Great Sand Bay	2	$2x$	2.12 (0.01)	2.12	2.13
S. psammophila					
East of Deer Park	31	$4x$	4.37 (0.11)	4.16	4.60
East of 3-Mile Creek	5	$4x$	4.27 (0.07)	4.19	4.36
Superior Campground Beach	21	$4x$	4.36 (0.07)	4.22	4.49
West of Whitefish Point	14	$4x$	4.26 (0.08)	4.16	4.40

described species that was possibly aligned with *S. hispida* and subsect. *Erectae* (G. Don) Semple & J. B. Beck.

In some *Solidago* complexes, ecogeographic separation and/or morphological differences (e.g., the size of the capitula) have also been associated with differences in ploidy level (as discussed in Peirson et al. 2012). Given the observed habitat and morphological differences between the dune goldenrods, hereafter referred to *S. psammophila*, and nearby *S. hispida*, this study also examined if there were differences in ploidy as well. DNA ploidy determinations from flow cytometry were obtained for 71 individuals from four populations of *S. psammophila* and for 26 individuals from three populations of *S. hispida* from the Lake Superior shore (Tables 1 and 2). Flow cytometry recovered two non-overlapping DNA ploidy groups that correspond to diploid ($2x = 18$) and tetraploid ($4x = 36$) individuals (Table 2; Figure 1). All sampled individuals of *S. psammophila* were found to be tetraploid, whereas individuals of *S. hispida* were found to be uniformly diploid. The $2x$ and $4x$ DNA ploidy groupings from this study are consistent with groupings found in previous flow cytometry studies of other *Solidago* species (e.g., Halverson et al. 2008; Schlaepfer et al. 2008; Peirson et al. 2012). The diploid determination for *S. hispida* is also consistent with previous cytological studies of the species (as summarized from Semple and Cook 2006; Semple et al. 2017b). *Solidago psammophila* would be the second tetraploid in the *S. bicolor*–*S. hispida* complex, after the upper Midwest endemic *S. sciaphila* Steele (following Semple et al. 2017b). Whether *S. psammophila* formed through chromosome doubling within a single *S. hispida*-like ancestral species (autopolyploidy) or as a result of hybridization and subsequent chromosome doubling (allopolyploidy) was not examined in this study. The narrowly circumscribed distribution along a short portion of the southern shore of Lake Superior suggests a single origin of *S. psammophila*.

Given that Gray's (1882) original concept of *Solidago humilis* var. *gillmanii* was mixed and included both the Lake Michigan/Lake Huron dune plants and the Lake Superior *S. psammophila*, scrutiny of the original description and the type of *S. gillmanii* was necessary. Gray stated in his description that *S. humilis* var. *gillmanii* was "an extreme form of this variable species, with dentate even
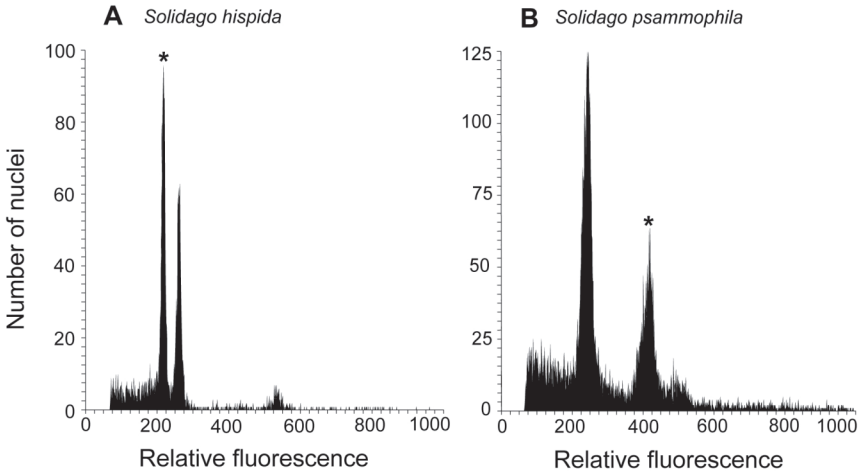
FIGURE 1. Representative fluorescence histograms of stained nuclei isolated during flow cytometry analyses of fresh tissue of *Solidago psammophila, S. hispida,* and the internal standard (*Glycine max* 'Polanka'). The *Solidago* peak is indicated by an asterisk (*). (A) diploid *S. hispida* from Superior Campground Beach, Luce County, Michigan; (B) tetraploid *S. psammophila* from Deer Park, Luce County, Michigan.

laciniate leaves and an open compound panicle; growing on sand hillocks on the shores of Lakes Superior and Michigan." Gray, however, did not cite any collections or designate a type for var. *gillmanii*. As follow-up to his biosystematic study of the "*S. spathulata–S. glutinosa* complex," which included *S. gillmanii*, Ringius (1987) reviewed the nomenclature of the group and designated a number of lectotypes, including for *S. humilis* var. *gillmanii*. Ringius' choice of lectotype, at first glance, presented a bit of a quandary. He stated that there were three collections from "the south shore of Lake Superior . . . sent to A. Gray by W. Boott" and identified by Gray as var. *gillmanii* that could serve as candidates for the lectotype (two 1875 collections (GH, NY) and a single 1879 collection (GH)). Ultimately, Ringius designated the 1879 GH collection as lectotype and stated that it matched "the protologue in having laciniate leaf margins and an open compound panicle." Examination of the 1875 and 1879 collections, however, revealed that the 1879 collection designated as lectotype by Ringius was not a plant from the Lake Superior shore.

The labels on the 1875 GH collection indicate "s. Shor l. Superior root sent by W. Boott." Examination of that collection, which consists of two sheets with portions of the same rosette (GH-00274538, GH-00274539), revealed sparse pubescence on the rosette leaves as well as capitula that did not appear glutinous. Similarly, examination of a digital image of the NY collection (NY-02369465) also appears to show pubescence on the rosette leaves and an overall lack of glutinosity. The pubescence on the foliage, the lack of glutinosity, and the label data indicating that the collections originated from the southern shore of Lake Superior confirm that the 1875 collections are *Solidago psammophila*. The label

on the lectotype, the 1879 GH collection (00012486), indicates "Roots from upper Michigan by W. Boott" and "same as 1875." Examination of the lectotype did not reveal any vegetative pubescence outside of the floral array. In addition, the capitula and leaves within the capitulescence appear to have been glutinous (e.g., they have a slightly varnished/resinous appearance). Morphologically, the 1879 collection is a characteristic, cultivated specimen of *S. gillmanii*, consistent with plants cultivated from Lake Michigan dune systems at the Matthaei Botanical Gardens during this and previous studies. Ringius (1987) stated that the 1879 GH collection was from the south shore of Lake Superior, presumably inferring that the notation on the label of "same as 1875" indicated that the specimen was from the same plant. Examination of the collections revealed that this cannot be correct, since the 1875 and 1879 collections represent *S. psammophila* and *S. gillmanii*, respectively. By "same as 1875" Gray presumably simply meant that he considered the collections to represent the same taxon. In addition, the locality information of "upper Michigan" on the label would indicate that the collection came from Michigan's Upper Peninsula, not specifically that it came from the Lake Superior shore, and Gray did include "Lake Michigan" in the original description. The lectotype of *S. gillmanii* originated from the dunes along northern Lake Michigan/Huron in Michigan's Upper Peninsula. *Solidago gillmanii* is quite common on the dunes there and absent from the Lake Superior shore, so far as is known.

TAXONOMIC TREATMENT

Solidago psammophila J.A. Peirson, sp. nov.—-TYPE: U.S.A. Michigan: Alger Co., Sect. 7, ca. 6 miles west of Grand Marais, high dunes above Lake Superior, July 26, 1948, *McVaugh 9586* (holotype: MICH!, isotypes: MT!, UMBS!).

Perennial herbs from branching vertical rhizomes or caudices. Stems 1 to ca. 15, 35–75 cm, ascending or more commonly erect (occasionally slightly decumbent at base), generally unbranched below the capitulescence, sparsely to densely hispid or short-villous proximally, occasionally appearing glabrate, especially if trichomes have been abraded by blowing sand, moderately to densely hispid to strigose in the capitulescence. Leaves alternate, simple, petiolate or sessile, sometimes stipitate glandular (but not becoming resinous or glutinous), moderately or sparsely short-pubescent to sericeous or more rarely strigose. Basal rosette and proximal stem leaves petiolate, petiole ciliate, blade ovate-oblanceolate to narrowly oblanceolate, tapering to petiole, 4–14 cm long, 0.7–3 cm wide, apex acute to obtuse or less often rounded, margin serrate. Mid and distal stem leaves sessile, lanceolate to linear, 1–4 cm long, 0.2–0.6 cm wide, reduced upward, margin entire or sparsely serrate. Capitulescence narrowly to broadly elongate-paniculiform, 7–25 cm long, 2.5–8.5 cm wide, consisting of short axillary and terminal racemiform clusters, lower branches occasionally elongated in larger plants, branches strigulose; heads few to numerous, not secund. Peduncles 3–10 mm long, strigulose; bracteoles few, linear. Involucres

FIGURE 2. *Solidago psammophila*. Holotype *McVaugh 9586* (MICH). Inset shows close-up of leaves (A), capitula (B), and cypselae (C).

campanulate, 5–8.1 mm long. Phyllaries in 3–4 graduated rows, the outer ones ovate, the inner ones linear-oblong, apex acute to obtuse or rounded, often ciliate or fringed. Ray florets 8–13, strap-shaped, 2–3 mm long, 0.6–0.9 mm wide. Disc florets 8–15, corollas 3.5–5 mm long. Cypselae narrowly obconic, antrorsestrigose, ca. 3 mm long. $2n = 36$ (from DNA ploidy determination). (Figure 2).

Etymology. The specific epithet *psammophila*, which means sand-loving, refers to the restricted ecological distribution of the species in open dune habitats.

Phenology. Plants generally begin flowering in early August and continue until late September. Cypselae mature and are dispersed from mid-September through October.

Distribution and Ecology. Solidago psammophila is restricted to active sand dunes along the southern shore of Lake Superior in Alger, Chippewa, and Luce Counties, Michigan (Figures 3 and 4). Populations of the species occur along an approximately 100 km length of shoreline from Grand Sable Dunes in the west to Whitefish Point in the east. No additional populations have been located along the Lake Superior shoreline west of Grand Sable Dunes. *Solidago psammophila* is a component of the open dune community (following Kost et al. 2007) and is commonly associated with other open dune species such as *Ammophila breviligulata* Fern., *Artemisia campestris* L., and *Arctostaphylos uva-ursi* (L.)
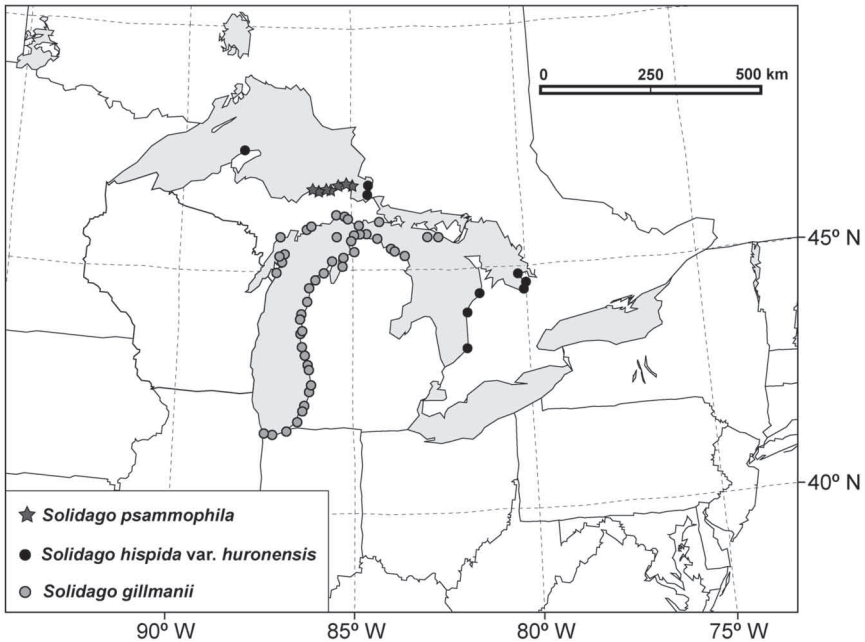

FIGURE 3. Distribution of sand dune endemic goldenrods in the North American Great Lakes region: *Solidago gillmanii* (gray circles), *S. hispida* var. *huronensis* (black circles), and *S. psammophila* (gray stars). Distributions based on the current study, Semple et al. (1999), and Peirson (2010).

FIGURE 4. Open dune habitat of *Solidago psammophila* along the southern shore of Lake Superior, east of Deer Park, Luce County, Michigan.

Spreng. It is less frequently found at the periphery of more stabilized areas like Great Lakes barrens and bluffs adjacent to open dune habitats.

Adaptation to the Dune Environment. The sand dune environment exerts strong selection on plants that grow there (e.g., through factors like nutrient deficiency, drought, and recurrent sand burial), and sand dune specialists have developed adaptations to survive the extreme environment (Maun 1994, 1998). *Solidago psammophila* produces elongate vertical rhizomes that appear to be apparent adaptations to help survive sand burial. Greenhouse germinated and grown seedlings of *S. psammophila*, as well as those of *S. gillmanii*, produce elongate vertical stems below the rosette of leaves during the first year of growth, without any exposure to burial by sand. Contrastingly, greenhouse germinated and grown seedlings of the widespread *S. glutinosa* Nutt. from northern Michigan sand barren sites (where there is little or no sand movement) do not produce elongate vertical stems. Field observations from dune systems throughout the Great Lakes region have shown that some widespread species of *Solidago* commonly occur at the margins of the open dune habitat where the sand has become stabilized. These species, which presumably lack specific adaptations, are essentially absent from the inhospitable open dune environment.

DNA Ploidy. Data from flow cytometry showed *Solidago psammophila* is uniformly tetraploid ($4x = 36$) across its range (Table 2).

Additional Specimens Examined. U.S.A., MICHIGAN: S. shore of Lake Superior, 1875, *W. Boott s.n.* (GH); ALGER COUNTY: Grand Sable Dunes west of Grand Marais, T49N R14W sec. 10, 24 Sept 1964, *R.C. Harris s.n.* (MSC);

Grand Sable Dunes, on the open dunes N of Grand Sable Lake, 5 Sept 1999, *M. Chamberland 1306* (MSC); ca. 2.5 mi W of Grand Marais, common on sand dunes just N of Grand Sable Lake, 10 Aug 1954, *E.G. Voss 2477* (MICH); open sandy area on Grand Sable Dunes, N of Grand Sable Lake, 3 Aug 1975, *D. Bach 22* (MICH); CHIPPEWA COUNTY: west of Whitefish Point, plants common on stabilized and active sand dunes, 21 Aug 2010, *J. A. Peirson 857* (MICH); Vermillion, along Lake Superior, upper beach and dunes, 9 Sept 1951, *H.H. Bartlett & C.D. Richards 320* (MICH); near Vermillion, sandy beach of Lake Superior shore, 31 Aug 1914, *C.K. Dodge s.n.* (MICH); Whitefish Point, growing on shingle beach, 1 Aug 1977, *W.T. Gillis 14073* (MSC—2 sheets); Whitefish Point, growing on shingle beach, 1 Aug 1977, *W.T. Gillis 14074* (MSC); Whitefish Point, near Lake Superior, sparsely wooded dune-marsh area, on open dune, 9 Aug 1948, *R. McVaugh 9768* (MICH, UMBS); LUCE COUNTY: ca. 1 mile east of Deer Park, active sand dunes on lake Superior, 24 Aug 2006, *J. A. Peirson 638* (MICH); ca. 1 mile E of Deer Park, on sand dunes along Lake Superior shore, active sand dunes and somewhat stabilized sand toward base of bluff, 11 Sept. 2010, *J.A. Peirson 861* (MICH); ca. 3-4 miles E of Deer Park, plants common on dunes along lake Superior, 25 Aug 2006, *J. A. Peirson 641* (MICH); mouth of Three-mile Creek east along Lake Superior shore to Crisp Point Lighthouse, off of Luce County 412, plants common on active sand dunes and in dry, stabilized, interdunal meadows, 5 Sept 2008, *J. A. Peirson 833* (MICH); east of the mouth of Three-mile Creek along Lake Superior shore, plants common on active sand dunes, 22 Aug 2021, *J. A. Peirson 923* (MICH); Lake Superior Campground Beach, off of County Road 407 between Grand Marais and Deer Park, plants common along road and on stabilized sand bluff and more active dunes, 21 Aug 2010, *J. A. Peirson 855* (MICH); near E edge of Sect. 3, T49N R10W, ca. 4 miles E of Deer Park, frequent, low dune ridge above Lake Superior, 21 Aug 1978, *E.G. Voss 15011* (MICH); County Rd. 407, at mouth of Blind Sucker River, in coastal sand dunes, 27 Aug 1993, *H.H. Schmidt & M. Merello 1074* (MO, MIN (online image), TEX).

BRIEF NOTES ON ENDEMIC *SOLIDAGO* TAXA IN THE GREAT LAKES REGION

In addition to *Solidago psammophila* and *S. gillmanii*, four other goldenrods have commonly been recognized as endemic to the glaciated North American Great Lakes region. Except for *S. hispida* var. *huronensis* Semple, which is diploid, all recognized Great Lakes endemic taxa of *Solidago* are polyploid (Table 3). Like the majority of the broader endemic flora, these *Solidago* taxa have distributions centered in the northern parts of the region. They are restricted to regionally rare, non-forested habitats that are linked to present and/or past Great Lakes shorelines (Peirson 2010).

Solidago hispida var. huronensis. This taxon, along with *Solidago psammophila* and *S. gillmanii*, constitute the three sand dune endemic goldenrods that occur in the Great Lakes region. *Solidago hispida* var. *huronensis* is most com-

TABLE 3. Distribution, habitat, and ploidy of endemic taxa of *Solidago* in the glaciated North American Great Lakes region. Data summarized from Laureto and Pringle (2010), Peirson et al. (2012), Semple et al. (1999), Semple and Cook (2006), Voss and Reznicek (2012), and the current study.

Taxon	Ploidy	Distribution	Habitats
Solidago gillmanii	$4x = 36$	Lakes Huron and Michigan shoreline	Open dunes
Solidago hispida var. *huronensis*	$2x = 18$	Lakes Huron and Superior shoreline	Open dunes
Solidago houghtonii	$6x = 54$	Lakes Huron and Michigan shoreline	Interdunal swales, sandy shores, alvars
Solidago ontarioensis	$4x = 36$	Lakes Huron, Michigan*, and Superior shoreline	Rock outcrops
Solidago psammophila	$4x = 36$	Lake Superior shoreline	Open dunes
Solidago vossii	$8x = 72$	Northern Lower Peninsula of Michigan (former postglacial shoreline)	Moist, sandy swales (inland)

*A population of *Solidago ontarioensis* on limestone bedrock at Seul Choix Point, Schoolcraft County, Michigan, is the only occurrence of the species along the Lake Michigan shoreline.

mon on active dune systems along the Canadian shores of Lake Huron, including Georgian Bay, but it also occurs along the shores of Lake Superior (both along the southeastern shore in Canada and on Michigan's Keweenaw Peninsula in western Lake Superior). Whereas *S. psammophila* and *S. gillmanii* are cohesive, morphologically well-defined tetraploid species, diploid *S. hispida* var. *huronensis* appears to intergrade with more typical *S. hispida* along the open-dune to stabilized-dune transition at some locations. Glabrous plants that are most common on sparsely vegetated open dunes tend to be replaced by sparsely pubescent plants along the back-dune, which are in turn replaced by typical *S. hispida* individuals where the dunes become stabilized (J. Peirson, personal observations from Great Sand Bay, Keweenaw County, Michigan and Pinery Provincial Park, Ontario). The evolution of this Great Lakes endemic has not been closely studied, but Semple et al. (2017b) proposed that it likely represents an ecotype adapted to local conditions (possibly including sandy habitats further east in Ontario). Given its scattered, disjunct distribution, it seems plausible that this form may have evolved multiple times in response to site-specific edaphic conditions.

Solidago houghtonii. Douglas Houghton first collected the flat-topped, large-headed *Solidago houghtonii* along the shores of northern Lake Michigan in Mackinaw Co., Michigan, on August 15, 1839 (Voss 1978). One of the best-known Great Lakes endemics, this hexaploid goldenrod is restricted to sandy and rocky shores and interdunal hollows of northern Lakes Michigan and Huron (Guire and Voss 1963; Morton 1979; Morton and Venn 2000; Laureto and Barkman 2011). A disjunct population in the Bergen Swamp, Genesee Co., New York has often been included in *S. houghtonii* (Guire and Voss 1963; Semple and Cook 2006; Laureto

and Barkman 2011); however, its relationship to populations within the main Great Lakes distribution has not been definitively studied. Morton (1979) proposed that hexaploid *S. houghtonii* is an allopolyploid derivative of a cross between *S. ohioensis* Riddell (2*n* = 18) and *S. ptarmicoides* (Torr. & A. Gray) Boivin (2*n* = 18) with a subsequent backcross to *S. ohioensis*, whereas Semple et al. (1999) proposed that *S. riddellii* Frank may be involved in its origin. Laureto and Barkman (2011) suggested, based on chloroplast DNA sequence data, that *S. gigantea* Ait. was the maternal genome donor. Extensive cpDNA haplotype sharing within *Solidago*, however, has posed challenges for elucidating relationships within the genus more generally (e.g., Peirson et al. 2013).

Solidago vossii. Inland populations of a flat-topped, large-headed goldenrod in northern Michigan (Crawford County) that had historically been included in *Solidago houghtonii* were recently described as *S. vossii* J.S. Pringle & Laureto (Laureto and Pringle 2010). The octoploid *S. vossii* is more robust and has larger involucres and ray florets than *S. houghtonii*. While its present distribution is inland, the locale lies along the shores of postglacial Lake Margrethe. The species occurs in a distinct wet sand prairie habitat that includes a mixture of plants common to mesic prairies as well as some species characteristic of Great Lakes interdunal wetlands (Laureto and Pringle 2010). Like *S. psammophila*, *S. vossii* is endemic to the state of Michigan.

Solidago ontarioensis. This tetraploid endemic, recognized at the species level by Semple and Peirson (2013), formerly *S. simplex var. ontarioensis* (Ringius) Ringius, is restricted to shoreline rock outcrop habitats in the northern Great Lakes region. Plants grown in a common garden suggest that *Solidago ontarioensis* (Ringius) Semple & Peirson comprises two phenotypically distinct sets of populations in the Great Lakes region (Peirson 2010). Large-statured plants occur on dolomite shores of northern Lake Huron and northern Lake Michigan, along the boundary of the Niagara Escarpment. Smaller-statured plants occur primarily on granite/basalt outcrops along the southern and eastern shores of Lake Superior. This distribution of phenotypes raises the possibility that *S. ontarioensis* encompasses two independently derived lineages. Phylogeographic data suggest that the two groups have separate origins (Peirson 2010; Peirson et al. 2013); however, extensive haplotype sharing has thus far precluded any concrete assessment of evolutionary relationships.

KEY TO THE SPECIES OF *SOLIDAGO* OCCURRING IN MICHIGAN, U.S.A.
(modified with permission from Voss and Reznicek 2012)

1. Heads in a terminal ± flat-topped corymbiform inflorescence.
   2. Blades of middle and upper cauline leaves ovate to elliptic (less than 3 times as long as broad), densely pubescent on both surfaces..*S. rigida*
   2. Blades of middle and upper cauline leaves linear to lanceolate or oblanceolate (over 10 times as long as broad), glabrous or nearly so.
      3. Rays 12–18, white, 4.5–8 mm long; pappus hairs slightly but clearly thickened (slenderly clavate) toward tip; upper cauline leaves slightly oblanceolate (broadest above the middle) ....*S. ptarmicoides*
      3. Rays 10 or fewer, yellow, not over 4.5 (–7) mm long; pappus hairs not thickened (or some thickening scarcely visible in *S. houghtonii*); upper cauline leaves broadest at or below the middle.

    4. Rays 1.5–3 mm long and involucre ca. 3.5–5.5 (–6.5) mm long; pedicels smooth and glabrous or rough-hispidulous.

        5. Pedicels smooth and glabrous or nearly so; leaf blades with one longitudinal vein (but often some principal lateral veins), flat ....*S. ohioensis*

        5. Pedicels and inflorescence branches densely rough-hispidulous; leaf blades with 3 or more longitudinal veins at the base, all or mostly complicate .....*S. riddellii*

    4. Rays 3–4.5 (–7) mm long and involucre ca. 5–9 mm long; pedicels scabrous-hispidulous.

        6. Larger involucres 5–7 (–8) mm long; larger plants mostly 30–60 cm tall; basal leaves entire; hexaploid; plants occurring on or near the Great Lakes shores, centered on the Straits of Mackinac ....*S. houghtonii*

        6. Larger involucres 7–9 mm long; larger plants mostly 50–80 cm tall; basal leaves sparsely serrulate; octoploid; inland in swales among *Pinus banksiana* ....*S. vossii*

1. Heads in an elongate or pyramidal inflorescence or in axillary clusters.

    7. Inflorescence terminal, often ± pyramidal (broadest toward base, about equally long, slightly nodding at top) but sometimes grading into axillary branches, and with curving, one-sided branches (the heads mostly directed upwards on well-developed branches).

        8. Cauline leaves (at least the main ones) "triple-nerved," i.e., with a pair of elongate veins arising below the middle of the midrib and distinctly stronger than other lateral veins.

            9. Leaves entire, succulent; saline habitats (e.g., edges of heavily salted roads) ....*S. sempervirens*

            9. Leaves with at least tiny and/or irregular teeth, of normal herbaceous texture; various habitats.

            10. Axis, pedicels, and branches of inflorescence glabrous; prairie and dry prairie-like habitats, blooming late in the season; lower and rosette leaves linear-lanceolate.... ....*S. missouriensis*

            10. Axis, pedicels, and branches of inflorescence at least sparsely but distinctly pubescent; or if glabrous (*S. juncea*), the lower and rosette leaves much larger than the mid-cauline leaves, ± elliptic, and the plant blooming early in the season in dry habitats.

                11. Stem glabrous all of its length below the inflorescence, rarely with a few scattered, spreading, short hairs.

                    12. Basal leaves none; cauline leaves narrowly (rarely broadly) elliptic and the lowest withered by flowering time; middle and upper cauline leaves crowded (numerous), about the same size as the lowest leaves or larger, and distinctly 3-nerved; plants blooming late (starting August–September); branches of inflorescence ± densely pubescent ....*S. gigantea*

                    12. Basal (including rosette) and lower cauline leaves with oblanceolate to elliptic blades and long petioles, persistent; middle and upper cauline leaves remote (relatively few), distinctly smaller than basal leaves, and only weakly 3-nerved; plants blooming early (starting in July); branches of inflorescence glabrous or occasionally sparsely spreading pubescent ....*S. juncea* (in part)

                11. Stem pubescent all or most of its length.

                    13. Involucres all or mostly 3.1–4.6 (–5) mm long..............................*S. altissima*

                    13. Involucres all or nearly all 2–3 mm long....................................*S. canadensis*

        8. Cauline leaves with distinct midrib but the other (weaker) veins ± pinnate.

            14. Stems ± pubescent, at least on the upper half of the plant.

                15. Cauline leaves entire or obscurely crenate-toothed; leaves and stems uniformly and densely puberulent throughout; lower and basal (including rosette) leaves oblanceolate, tapered into a winged petiole and larger than mid-cauline leaves; sandy or rocky, open and usually very dry soil....................................*S. nemoralis*

                15. Cauline leaves sharply toothed; leaves beneath (at least on main veins) and stem with mostly spreading, longer hairs (over 0.5 mm); lower and basal

leaves (none in rosettes) no larger than mid-cauline leaves (but usually absent at flowering time), all of them elliptic-lanceolate; moist or shaded ground ....*S. rugosa*

14. Stems glabrous (except sometimes just below and in the inflorescence).

    16. Lowest cauline leaves with tapering base clasping stem (encircling it for at least half its circumference); wet habitats, with leaves nearly smooth above...*S. uliginosa* (in part)

    16. Lowest cauline leaves not clasping stem; dry habitats or, if wet, the leaves very scabrous above.

        17. Stem with strongly raised angles or ribs; upper leaf surface very scabrous, with dense, tiny, stiff conical projections; swamps and other wet habitats ....*S. patula*

        17. Stem terete (may be many-ridged); upper leaf surface smooth to slightly scabrous; ± dry open or forested habitats.

            18. Basal (including rosette) and lower cauline leaves much larger than mid-cauline leaves, persistent (blades often 7–20 cm long on petioles half or more as long); branches of inflorescence glabrous or occasionally sparsely spreading-pubescent; leaves often tending to have prominent longitudinal veins, usually glabrous beneath but occasionally with some hairs on midrib; throughout Michigan, beginning to bloom in July (before other goldenrods) ....*S. juncea* (in part)

            18. Basal and lower leaves often withered by flowering time or, if present, not much larger than mid-cauline leaves; branches of inflorescence rather densely pubescent; leaves clearly pinnate-veined, with midrib and principal veins beneath spreading-pubescent (as in *S. rugosa*); southern Lower Peninsula, blooming late ....*S. ulmifolia*

7. Inflorescence axillary or terminal, but even if pyramidal the branches not one-sided and the top not nodding.

    19. Leaves decreasing in size from middle of stem to the base, the mid- to upper cauline leaves sharply toothed, much exceeding the distinctly axillary inflorescences (not necessarily any branches) they subtend; stems glabrous (except rarely on upper internodes), the lowest leaves usually withered by flowering time; achenes ± densely pubescent.

        20. Leaf blades narrowly elliptic, sessile; stem terete, glaucous when fresh, not (or scarcely) zigzag; leaves glabrous (except for short-ciliate margin); cespitose ...*S. caesia*

        20. Leaf blades broadly ovate-elliptic, abruptly contracted to a winged petiole; stem ribbed or angled throughout, ± zigzag from node to node; leaves (at least the midrib beneath and petiole margins) ± sparsely pubescent; colonial from creeping rhizomes..*S. flexicaulis*

    19. Leaves increasing in size from middle of stem to the base, the mid-cauline leaves usually entire to crenate-toothed and usually not subtending inflorescences (these more clearly terminal); stems glabrous or pubescent, the lowest leaves usually persistent; achenes glabrous or glabrate (except in *S. psammophila* and the *S. glutinosa* group).

        21. Stem sparsely to densely pubescent its entire length and leaves pubescent, at least abaxially.

            22. Rays white or cream when fresh...*S. bicolor*

            22. Rays yellow

                23. Stems usually numerous (5–8), from deep vertical rhizomes; involucres 5–8 mm long; achenes antrorse-strigose; tetraploid; active coastal sand dunes of Lake Superior..*S. psammophila*

                23. Stems solitary or few (1–3), from shallow caudices; involucres 3–4.5 mm long; achenes glabrous or glabrate; diploid; usually dry habitats, including margins of coastal sand dunes..*S. hispida* (in part)

        21. Stem glabrous at least below the middle and leaves generally glabrous.

            24. Lower cauline leaves ca. 6–18 times as long as broad, the petiole clasping the stem for half or more of its circumference; plants occurring in wet habitats (including rock crevices on Lake Superior) ....*S. uliginosa* (in part)

24. Lower cauline leaves ca. 3–8 times as long as broad, not clasping (leaves of basal rosettes sometimes as much as 11 times as long as broad); plants occurring mostly in dry habitats.

    25 Achenes antrorse-strigose; involucres and leaves resinous (more easily determined when fresh, but usually appearing varnished, shiny or glandular when dry).

        26. Plants robust; stems from deep vertical rhizomes; petiole ciliate; plants flowering mid August to October; active coastal sand dunes of Lakes Huron and Michigan ....*S. gillmanii*

        26. Plants relatively small; stems from shallow caudices; petiole usually not ciliate; plants flowering late June to mid August; coastal rock outcrops of Lakes Michigan and Superior or inland sand barrens.

            27. Involucres 4.5–6.2 mm long; plants flowering mid July to mid August; tetraploid; coastal rock outcrops of the Upper Peninsula ....*S. ontarioensis*

            27. Involucres 3.4–4.3 mm long; diploid; plants flowering late June to late July; inland sand barrens of the Lower Peninsula........*S. glutinosa*

    25. Achenes glabrous or glabrate; involucres and leaves not resinous.

        28. Cauline leaves (3–) 5–15 (–17) below inflorescence; margins of lower and middle leaves crenulate; plants occurring on rock outcrops and dunes on Lake Superior and northern lake Huron ....*S. hispida* (in part)

        28. Cauline leaves ca. (11–) 15–30 below inflorescence; margins of lower and middle leaves entire to sparsely toothed in the upper half; plants occurring in prairies, jack pine plains, and oak barrens, sandy fields and rock outcrops (inland).

            29. Basal rosette and lower stem leaves present at flowering; plants flowering from early July to late August; jack pine plains, sandy fields, and rock outcrops of the northern Lower Peninsula and western Upper Peninsula..*S. jejunifolia*

            29. Basal rosette and lower stem leaves absent at flowering; plants flowering September and October; prairies, sandy fields, and oak barrens of the southern half of the Lower Peninsula......*S. rigidiuscula*

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