ECOLOGY AND CONSERVATION BIOLOGY OF THE ENDANGERED PLANT SPECIES

Solidago shortii

(ASTERACEAE)

Photo by Thomas G Barnes

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Short's goldenrod (*Solidago shortii* T. & G. [Asteraceae]) is a federally-endangered plant species [Federal Register 50(172):36085–36089, 5 September 1985] endemic to a small geographic area in northcentral Kentucky. Since 1986, we have investigated various aspects of the ecology and conservation biology of this narrow endemic. Our studies have resulted in a MSc thesis (Buchele 1988), a PhD dissertation (Walck 1998), and 16 subsequent papers (Buchele and others 1989, 1991a,b, 1992a,b; Walck and others 1997a,b,c,d,e, 1998, 1999a,b,c,d, forthcoming). The purpose of this short review is to summarize briefly the results of our field, greenhouse, and laboratory studies on this rare goldenrod.

Taxonomy

Nesom (1993) placed *S. shortii* in subsection *Triplinerviae* of *Solidago*, which also includes tall goldenrod (*S. altissima* L. [Asteraceae]), one of its co-occurring congeners. No subspecific taxa have been described for *S. shortii*, and there are no synonyms for it. Both diploid ($2n = 18$; Semple and others 1993) and tetraploid ($2n = 36$; Beaudry 1963) ploidy levels have

been reported for the species. *Solidago shortii* exhibits a high level of morphological variation both within and among populations. However, enzyme profiles from 2 populations were uniform. Additional investigation is required to accurately assess genetic variation in this species (Beck and others 1999).

Abstract

We review briefly our 14 y of research results collected on the ecology and conservation biology of the narrowly-endemic, federally-endangered plant species, Short's goldenrod (*Solidago shortii* T. & G. [Asteraceae]). Of the many aspects of the ecology of *S. shortii* we investigated, low competitive ability appears to be the one that contributes most to its narrow endemism. In the long-term, *S. shortii* can survive only in early successional habitats, and this ecological characteristic, in large part, defines its management needs. We discuss methods for propagation of this rare taxon, which can be propagated easily from seeds.

KEYWORDS: ecological life history, narrow endemic, rare goldenrod, reproductive biology, plant competition, rare plant propagation

NOMENCLATURE: (plants) Gleason and Cronquist (1991); (insects) ITIS (1998)

Ecogeography

Solidago shortii is endemic to an area covering about 12 km² (4.5 mi²) in the (calcareous) Eden Shale Region (Hills of the Bluegrass; Bailey and Winsor 1964) in adjacent portions of Fleming, Nicholas, and Robertson counties, Kentucky (Figures 1 and 2), which is in the Bluegrass Section of the Interior Low Plateaus Physiographic Province of Fenneman (1938). The Eden Shale Region is in Braun's (1950) Western Mesophytic Forest Region and in Köppen's Cfa climatic-type; that is, a mild rainy climate with hot summers but without a distinct dry season (Ackerman 1941). Bedrock is Upper Ordovician.

Dr Charles W Short MD collected specimens of *S. shortii* on Rock Island at the Falls of the Ohio River in Louisville and Jefferson County, Kentucky, in 1840 and sent them to John Torrey and Asa Gray, who commemorated Dr Short with the specific epithet *shortii. Solidago shortii* apparently was extirpated from Rock Island within 20 to 30 y of its discovery; no herbarium specimens of the species collected since the 1860s are known from this site. (Rock Island virtually was destroyed during construction of McAlpine Locks and Dam in the 1920s.) In 1995, the species was reintroduced to the Falls of the Ohio area. Seven clumps of cultivated plants reared from seeds were planted in crevices of limestone bedrock within the Falls of the Ohio State Park on the Indiana side of the falls (Homoya 1996).

Solidago shortii was thought to be extinct until the 1930s when Dr E Lucy Braun discovered it in Fleming, Nicholas, and Robertson counties, Kentucky, 160 km (100 mi) east of the type locality (Braun 1941). Today, the known geographic range of *S. shortii* apparently is the same (or nearly so) as that reported by Braun, even though much effort has been expended in searching for it in various areas of Kentucky and in portions of Indiana and Ohio adjacent to Kentucky (Homoya 1996).

Buchele and others (1989) recognized 13 extant populations of *S. shortii* within its narrow geographic range (Figure 2). The number of aerial stems of the species estimated in these populations ranged from 180 (only 1 clump, population site 13) to 42,000 (population site 1); total for all 13 populations = 73,620. At least 1 additional (small) population (number 14) has been found within its 12 km² (4.5 mi²) geographic range since 1989 (Figure 2).

Populations 1, 2, and 4 are in Blue Licks Battlefield State Park; population 7, small portions of populations 8 and 10, and most of population 12 are on rights-of-way of state or US highways; and portions of population 8 not on the highway right-of-way are owned by the Kentucky Chapter of The Nature Conservancy. Populations 1 and 2 are within a designated nature preserve of the Kentucky State Nature Preserves Commission. The

Figure 1 • Plants of Solidago shortii *in population 12 (see Figure 2) on top of a ledge of the Clays Ferry Formation in the Eden Shale Region along new US 68 in Nicholas County, Kentucky.*

other populations are on privately-owned land.

The *S. shortii* population sites are in various stages of vegetational succession (Buchele and others 1989). Habitats in which the species occurs include rocky redcedar glade-like areas; rocky ledges and embankments along roads; powerline rights-of-way; rocky pastures and hay fields; redcedar *(Juniperus virginiana* L. [Cupressaceae]), redcedar-hardwood, and hardwood thickets and woodlands; and an anthropogenically-maintained (by mowing) oak (*Quercus* [Fagaceae]) "savannah." *Solidago shortii* grows on the upper, middle, and lower portions of slopes of various aspects and degrees of inclination and on several geologic formations and soil types. Elevation range of the species is 201 to 268 m (659 to 879 ft) above sea level (Buchele and others 1989).

At the 13 population sites (populations 1 to 13 in Figure 2) studied by Buchele and others (1992b), *S. shortii* was found to be associated with a total of 227 other plant species. None of these is globally rare, and most are common and geographically-widespread; 50 are non-native. Community similarities (Sörensen's index, Mueller-Dumbois and Ellenberg 1974) based on species composition ranged from 10% to 66% among the 13 sites, and only 12 species were in presence class (see Oosting 1956) 4 or 5 (present at 61% to 80% and 81% to 100% of the sites, respectively). Of the 228 taxa, 54% are hemicryptophytes, and 94.6% of them use the C_3 carbon fixation pathway; the only CAM plant is false aloe (*Agave virginica* L. [Agavaceae]).

Vegetation was sampled quantitatively only at the largest population site. Species with the highest importance values (% Importance value = [(Relative cover + Relative frequency)/2] • 100) associated with *S. shortii* (in deceasing order) were moss(es)(unidentified),

Juniperus virginiana, violet lespedeza (*Lespedeza violacea* (L.) Pers. [Fabaceae]), gray goldenrod (*Solidago nemoralis* Aiton [Asteraceae]), poverty-oatgrass (*Danthonia spicata* (L.) F. Beauv. [Poaceae]), *Solidago shortii,* sage (*Salvia lyrata* L. [Lamiaceae]), redbud (*Cercis canadenses* L. [Caesalpiniaceae]), and rough-leaved dogwood (*Cornus drummondii* C.A. Meyer [Cornaceae]). There were no species in frequency class 5, that is, occurring in 81% to 100% of the plots (Buchele and others 1992b).

Ecological Life History and Reproductive Biology

Solidago shortii is a hemicryptophyte that reproduces vegetatively by rhizomes and sexually by seeds. Shoots of *S. shortii* emerge in March, elongate vertically from March to August, and die back in mid to late autumn. Flowering stems are much taller than nonflowering ones. Flower buds form in June, and flowering occurs from August to November, peaking in September. Seeds ripen in October and November. The seed dispersal season lasts from October to March, peaking in November; seeds are dispersed by wind and by gravity and germinate mostly in March (Buchele and others 1991a; Walck and others 1997a).

Embryo sac development in *S. shortii* is of the *Polygonum*-type (Harling 1951). Plants are self-incompatible and protandrous; they are cross-pollinated by insects. The goldenrod soldier beetle, *Chauliognathus pennsylvanicus* DeGeer (Coleoptera: Cantharidae), which is known to pollinate other species of *Solidago*, is the most frequent visitor to inflorescences of *S. shortii*. Neither bumblebees, *Bombus* spp. (Hymenoptera: Apidae), nor the honeybee, *Apis mellifera* L. (Hymenoptera: Apidae), were observed visiting flowers of this species at the field population sites (Buchele and others 1992a). Bumblebees and the honeybee are important pollinators of other goldenrod species (Gross and Werner 1983).

Many stems of *S. shortii* remain vegetative in a given year. For a 3-y period (1986 to 1988), Buchele and others (1991a) reported 0% to 6.1% of the stems flowering in 27 quadrants (1 X 1 m [3.3 X 3.3 ft]) in population 1 and 2.4% to 22.7% in 20 quadrats (1 X 1 m [3.3 X 3.3 ft]) in population 2. About 20% to 25% of the flowers produce seeds in the field. However, 42% of hand-crossed flowers set seed in a greenhouse pollination study, which suggests that seed set may be pollen-limited. Number of seeds per flowering stem ranges from about 250 to 1700, and a high percentage of the seeds is viable. Predispersal seed predation varies from low to high (Buchele and others 1992a; Walck 1998). No information is available on postdispersal seed predation; however, many fewer seeds germinate than are produced at population sites.

Survivorship of seedlings to juveniles and adults is low. In the field, plants do not flower for at least 3 y after they germinate; some individuals take > 9 y to flower

(Walck and others 1999a,c). Under good growth conditions in a greenhouse, however, up to 100% of the plants flower in their first year. In the field, and also under stressful conditions (high density) in the greenhouse, plants may reproduce vegetatively before they flower (Buchele and others 1991a; Walck 1998).

Ecophysiology

Solidago shortii has non-Kranz anatomy (Baskin and Baskin 1985) and fixes carbon by the C_3 pathway, like all other goldenrods whose photosynthetic type has been determined. Neither its instantaneous rate of photosynthesis nor respiration has been measured. However, Walck and others (1999d) reported a net assimilation rate of about 0.53 mg/(cm$^2 \cdot$ d) and a relative growth rate of 0.077 g/(g $\cdot$ d) for the entire growing season. Net assimilation rate and relative growth rate values for *S. shortii* are nearly identical to those for *S. altissima*. Percentages of dry weight allocated by *S. shortii* to inflorescences, leaves, aerial stems, roots, and rhizomes were 10, 23, 11, 55, and 1, respectively (Walck and others 1999d).

In a greenhouse study, shaded plants produced much less biomass than unshaded plants. Further, only 1 of the 20 clumps (genets) of *S. shortii* transplanted into a redcedar thicket in 1989 was alive by 1994, whereas 17 of 20 clumps transplanted into an adjacent open area still were alive in 1995 (last year of study). Both number of ramets flowering and number of capitula per flowering ramet declined precipitously (to zero in 1991) for plants in the redcedar thicket, whereas throughout the 1989 to 1995 study, these 2 measures of vigor remained relatively high for plants in the open (Walck and others forthcoming).

Essentially nothing is known about the water relations (transpiration rate, stomatal conductance, water use efficiency, xylem water potential) of *S. shortii*. Established plants of this species obviously are better adapted to drought than are those of *S. altissima*, since *S. shortii* grows in a drier habitat. *Solidago shortii* allocates a higher proportion of its biomass to roots than does *S. altissima*; thus, the root to shoot ratio of *S. shortii* is considerably higher than that of *S. altissima* (Walck and others 1999d).

Solidago shortii can become nutrient limited under greenhouse conditions and apparently also under field conditions. Plants grown in soil in 1.75-l (0.5-gal) pots in a greenhouse cease to flower after a few years. Addition of nitrogen (N), phosphorus (P), and potassium (K) caused an increase in the percentage of ramets that flowered and in the number of capitula per ramet, in both field and greenhouse. However, there was a sharp decline in flowering the year following application of NPK. Thus, apparently plants are dependent on soil nutrient reserves, rather than on internal storage and recycling of nutrients. In a greenhouse experiment, the hierarchy of dry weight of *S. shortii* plants grown on 5

soil types was: phosphatic limestone > calcareous shale > sandstone > black (acid) shale > dolomite. Both plant dry weight and flowering in these experiments were related positively to P content of the soil (Walck and others forthcoming).

Using the terminology of Baskin and Baskin (1998), at maturity, seeds of *S. shortii* have nondeep physiological dormancy. Some fresh seeds are conditionally dormant (germinate only at high temperatures and mostly in light), while others are dormant (will not germinate at any temperature in light or in darkness). Both dormant and conditionally dormant seeds require several weeks of cold-moist stratification (1 to 10 °C [34 to 50 °F]) to become nondormant. Nondormant seeds germinate to high percentages over a wide range of temperature regimes (14 h light [40 μmol/(m$^2 \cdot$ s)] at 15 °C [59 °F] and 10 h dark at 6 °C [43 °F] to 14 h light [40 μmol/(m$^2 \cdot$ s)] at 35 °C [95 °F] and 10 h dark at 20 °C [68 °F]). Nondormant seeds germinate to lower percentages in constant darkness (Buchele and others 1991b; Walck and others 1997a).

Seeds buried in soil that do not germinate in spring may go through 1 or 2 conditional dormancy to nondormancy cycle(s) before they germinate (in spring), or die (Walck and others 1997b). Seeds can germinate in light with a high far-red to red photon ratio (Walck and others 1997c), under plant-leaf litter, and over a wide range of soil types of various fertilities and pHs (Walck and others 1999b). Several days of continuous moisture in late spring or summer are required for seeds to germinate on the soil surface (Walck and others 1997d). Seeds do not afterripen (come out of dormancy) well during dry storage in the laboratory, where they survive for < 4 years (Walck and others 1997e).

Solidago shortii is a facultative short-day plant and does not require vernalization (cold treatment) to flower (Walck and others 1999c).
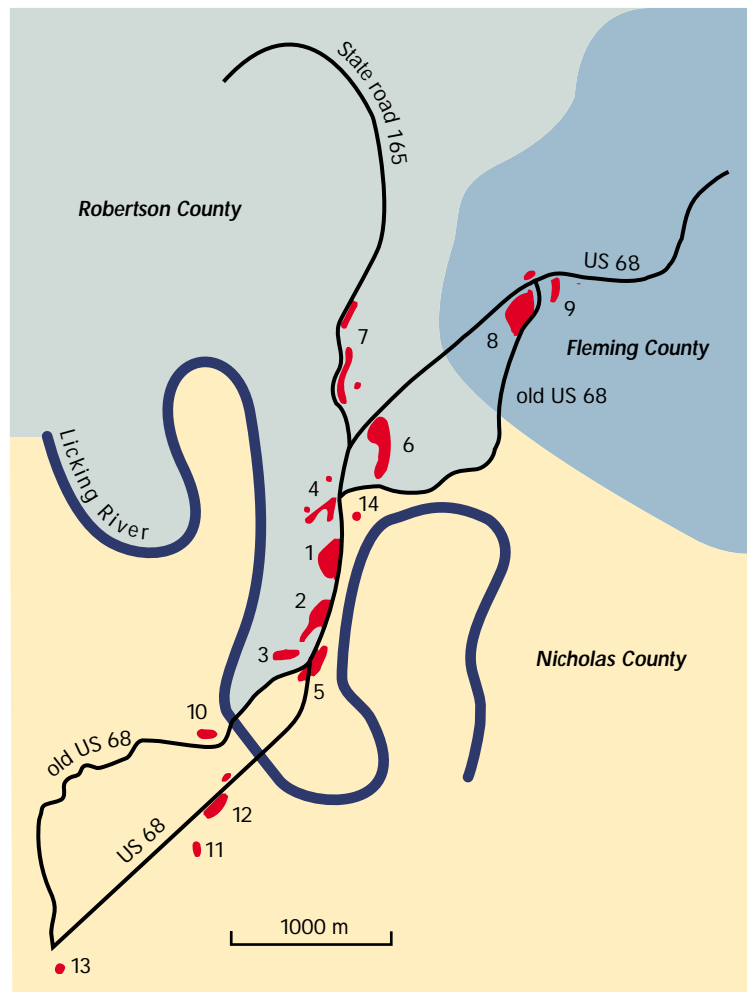

Figure 2 • Geographical distribution of the 14 known population sites of Solidago shortii. *Triangle is for the population that was extirpated from Rock Island, Louisville, and Jefferson County. Extant populations in Fleming, Nicholas, and Robertson counties are shown in detail in the bottom part of the figure. Figure is slightly modified from Buchele and others (1989) and is published with permission of The Journal of the Torrey Botanical Society (formerly* The Bulletin of the Torrey Botanical Club). *Black and white photographs of population sites 1 to 13, and to-scale line drawings showing the general distribution of* S. shortii *plants at each of the 13 sites, are contained in Buchele (1988).*

Biotic Interactions

Several taxa of phytophagous insects have been observed visiting plants of *S. shortii*; they include flower eaters, leaf and stem chewers, and sap feeders. However, amount of defoliation is consistently very low in the field. Rosette-type galls (Buchele and others 1992a) and leaf galls (personal observations) are present on a low percentage of the ramets. Plants of *S. shortii* are not eaten by cattle or horses (Walck 1998). The species is host to at least 1 parasitic fungus (same taxon on *S. altissima*, Conners 1967) and to 1 (unidentified) species of the holoparasitic angiosperm dodder (*Cuscuta* L. [Cuscutaceae])(Walck 1998). Its mycorrhizal status has yet to be determined.

Compared to *S. altissima*, *S. shortii* competed poorly. In a greenhouse study, *S. shortii* did not compete well against either *S. altissima* or tall fescue (*Festuca arundinacea* Schreber [Poaceae]) in a de Wit (1960) replacement series experiment (Walck and others 1999a,d). In a field plot experiment, removal of weedy competitors, mostly crown-vetch (*Coronilla varia* L. [Fabaceae]) and plant litter caused an increase in number of flowering ramets and in number of capitula per flowering ramet of *S. shortii*. Further, seedlings of *S. shortii* established only in treatment (removal) plots (Walck and others 1999a).

Persistence on the Landscape

We suggest that a key factor in the long-term persistence of *S. shortii* on the landscape is its adaptation to dry, rocky sites that are relatively free of competition from plants such as *S. altissima*. However, in these persistently open habitats vigor varies among population sites, apparently due to variation in amounts of available nutrients (Walck and others 1999d, forthcoming).

Solidago shortii invades disturbed sites within its narrow geographic range. The species persists on burned sites and in pastures grazed by cattle and horses. Its vigor increases with mowing and with clearing of powerline rights-of-way. The species also invades sites with relatively deep soil in old-field-like habitats adjacent to rock outcrops, but anthropogenic disturbance (for example, mowing) is needed to maintain an early successional stage and a low amount of competition. These sites may be particularly vulnerable to invasion by non-native herbaceous species, such as *Coronilla varia* or *Festuca arundinacea*. Conversely, *S. shortii* also persists for many years (usually with little or no flowering or vegetative reproduction) in moderate shade in hardwood thickets and woodlands. These plants presumably became established prior to development of the thicket or woodland. In areas subject to invasion by woody plants, periodic high intensity disturbances that result in high light, and high nutrient levels may be required to restore high vigor of the population (Buchele and others 1989; Walck and others forthcoming). Thus, metapopulation dynamics may be important in the maintenance of *S. shortii* on the landscape.

Most populations of *S. shortii* are being managed, either advertently or inadvertently, in a way that keeps each of the sites in an early stage of succession. Periodic removal (clearing) of woody vegetation in the powerline right-of-way that runs through population site 1 is done by personnel of the Kentucky State Nature Preserves Commission or of the utility company that owns the powerline. The Kentucky Chapter of The Nature Conservancy is using selective cutting and burning to create and maintain openings for *S. shortii* in the redcedar woods on their portion of population site 8.

Population sites 3, 6, and 13 and most of population site 5 have long been used as pasture for domestic livestock and hay production. Thus, these (in places rocky) sites have been maintained in the early stages of succession by grazing and mowing. Most of population site 7 and the northernmost portion of population site 8 are road rights-of-way, and these are kept in an early succession state via mowing by the Kentucky Department of Transportation.

The very rocky buffalo trace and the redcedar glade at population site 1 need little or no management to keep succession in early states. This also is true for population site 12, which is on a limestone ledge atop a steep roadside embankment (Figure 1).

All of population site 2 now is in Blue Licks Battlefield State Park. However, until recently the southern part of it was on privately-owned land. The privately-owned portion of this population site recently was purchased by the Commonwealth of Kentucky and added to the park. Over the past several years at least, the private landowner has inadvertently helped maintain the portion of this population on his land by mowing.

Possible Factors Contributing to Narrow Endemism

Of the many biological features of *S. shortii* that we have investigated, low competitive ability appears to be the one that likely contributes most to its narrow endemism. However, in addition to being a poor competitor compared to the geographically-widespread *S. altissima*, *S. shortii* has a smaller and a shorter-lived soil seed bank (Walck and others 1998) and produces fewer seeds. Thus, we suggest that low competitive ability along with its (apparent) low capacity to colonize (small, short-lived persistent soil seed bank, relatively low seed production) may help, at least in part, to account for the narrow endemism of *S. shortii*.

Propagation

Solidago shortii is easy to propagate from seeds. As described earlier, the species has no special requirement for seed dormancy break, and its germination requirements are non-exacting. For best results, seeds should be given a cold-moist treatment at 1 to 10 °C (34 to 50 °F). This could be done by placing seeds on a moist substrate (filter paper, sand, soil) in Petri dishes or other appropri-

ate containers for 10 to 12 wk in the crisper part of a refrigerator, where temperatures typically are about 3 to 5 °C [37 to 41 °F]). Following cold-moist stratification treatment, seeds should be moved to a moderate temperature (room temperature is acceptable) in a location where they are exposed to natural or artificial light for at least part of the day. A high percentage of seeds should germinate in 7 to 10 d.

Seedlings then can be transplanted to soil without taking any special precautions. We have used etridiazole plus thiophanate-methyl (Banrot), benomyl (Benlate), disulfoton (Di-Syston), and malathion (Malathion 50) to control damping-off fungi, powdery mildew, aphids, and scales, respectively.

Seedlings of *S. shortii* do best in full sun and very poorly in heavy shade. Plants grow and develop quickly under high light and summer temperature conditions in a greenhouse and will flower during their first year. Additional stems (ramets) are produced in following years by plants grown (without competition from other plants) in pots containing large amounts (for example, 4.5 l [1.2 gal]) of soil.

Six ramets were transplanted individually into an area < 1 m^2 (< 10.8 ft^2) in the Baskins' backyard in Lexington, Kentucky, in 1985. By autumn 1989, the size of this "population" had increased to > 200 stems. A few years later, there were > 600 stems in the "population," occupying an area of < 2 m^2 (< 21.6 ft^2). Apparently, this 100-fold increase in number of stems was by vegetative reproduction only; we never saw any seedlings in this "population."

Plants grown to maturity under greenhouse conditions can be transplanted easily to field or garden with good success the following spring. (This probably also is true for well-established juveniles, but we have not done it.) Transplants do best in full sun, but survive for only a few years in deep shade, where they flower only weakly, or not at all (Walck and others forthcoming).

Solidago shortii is self-incompatible, and thus plants grown in a greenhouse will need to be cross-pollinated by hand to set seeds. Those grown in the Baskins' backyard in Lexington, however, set seeds without hand pollination. As in natural populations, the goldenrod soldier beetle was a frequent visitor to flowers of *S. shortii*. Presumably, this insect was the primary pollinator, although bumblebees and honeybees were observed visiting flowers of *S. shortii* in the Baskins' backyard. *Solidago shortii* has spread (by seeds) from the site into which it was transplanted to other parts of the Baskins' backyard and also to their front yard.

Seeds of *S. shortii* retain viability for < 4 years in dry storage under ambient laboratory conditions, and rate of loss of viability varies from seed crop to seed crop. Of seeds collected in 1991, 38% were viable after 1.3 y of storage compared to 71% of 1992-collected seeds. After 3.3 y of storage, only 1% and 5% of the 1991- and 1992-collected seeds, respectively, still were viable (Walck and others 1997e). Thus, for best results we suggest storing seeds used for propagation under ambient laboratory conditions for ≤ 1 y.

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