



Why is *Solidago shortii* narrowly endemic and *S. altissima* geographically widespread? A comprehensive comparative study of biological traits

Jeffrey L. Walck¹, Jerry M. Baskin² and Carol C. Baskin^{2,3} ¹*Department of Biology, PO Box 60, Middle Tennessee State University, Murfreesboro, TN 37132, USA,* ²*School of Biological Sciences, University of Kentucky, Lexington, KY 40506, USA, and* ³*Department of Agronomy, University of Kentucky, Lexington, KY 40546, USA*

Abstract

Aim and location *Solidago shortii* T. and G. occurs in a small area of north-central Kentucky (USA), whereas *S. altissima* L. is geographically widespread in North America and is naturalized in Europe, Asia and Australia. *Solidago shortii* grows in a variety of habitats, but primarily in rocky/shallow soil areas, and *S. altissima* occurs in adjacent old fields/pastures. The purpose of this study was to identify differences in the biology of these two species that might contribute to an explanation for differences in their geographical distribution and habitat.

Methods Results of an extensive literature review and of original research by the authors were used in a detailed comparison of the two species. The most ecologically relevant aspects of the biology investigated were morphology, genetics, geography, life cycle, life history, reproductive biology, physiology, biotic interactions and response to disturbance.

Results Although *S. shortii* and *S. altissima* are quite similar in many aspects of their biology, there are some important differences. *Solidago altissima* is a better competitor than *S. shortii* via its greater height, larger leaf area and more extensive clonal growth. On the other hand, *S. shortii* is a better drought-stress tolerator than *S. altissima* via allocation of a higher percentage of biomass to roots, higher root/shoot ratio and (seemingly) greater capacity to maintain leaf turgor (i.e. not wilt as readily) under xeric conditions. Moreover, higher seed production in *S. altissima* and its capacity to form a larger- and longer-lived soil seed bank than *S. shortii* probably contribute to differences in colonization abilities. Landscape disturbances and metapopulation dynamics are important factors in maintenance of the species population of *S. shortii*, and in prevention of its extinction.

Main conclusions *Solidago shortii* probably is a relatively young species that as had insufficient time to expand its range. Furthermore, it is not well suited for migration to, or colonization of, habitats outside its range due to poor competitive and colonization abilities.

Keywords

Conservation biology, plant geography, rarity, *Solidago shortii*, *Solidago altissima*.

INTRODUCTION

Comparison is one of the most fundamental methods of study used in plant ecology (Bradshaw, 1987; Grime *et al.*, 1988). In particular, it has been used extensively to understand the cause(s) of plant rarity, especially of narrow endemism (*sensu* Kruckeberg & Rabinowitz, 1985). In these studies, the autecology of a rare species is compared with that of one or more of its geographically widespread congeners in an attempt to 'unearth "susceptibilities"' (cf. Grime, 1965). The susceptibilities lead to low survival, yield and/or reproduction, that may explain the narrow habitat and/or geographical distribution of the endemic (Baskin *et al.*, 1997; Bevill & Louda, 1999). Detection of unusual features between taxa is facilitated by the common species serving as a control against which to compare data from the rare species (Fiedler, 1987). Moreover, comparisons of closely related congeners minimize confounding effects of disparate phylogenetic histories (Silvertown & Dodd, 1996; Gitzendanner & Soltis, 2000).

In their review on aspects of endemism, Kruckeberg & Rabinowitz (1985) concluded that 'More comparative studies to contrast the biologies of rare taxa with those of related common ones would be particularly valuable.' Since that time, many comparative studies have been published. These studies can be placed generally in two categories. The first approach contrasts traits among multiple species (e.g. Kunin & Gaston, 1993; Kelly & Woodward, 1996; Hegde & Ellstrand, 1999), whereas the second one contrasts traits among a small set (usually a pair) of species (e.g. Baskin *et al.*, 1997; Witkowski & Lamont, 1997; Bevill & Louda, 1999; Gitzendanner & Soltis, 2000). The benefit of a multiple-species approach is that general patterns of rarity can be elucidated from a broad spectrum of life forms, life cycles, taxonomic categories, etc., whereas that of a pairwise approach allows detailed studies of carefully-selected species to control phylogenetic relatedness. Results of the latter set of studies can be surveyed for general patterns as well (Kunin & Gaston, 1993; Bevill & Louda, 1999).

On the other hand, a major constraint for both comparative approaches is the number of factors examined. The investigation of a limited number of factors impedes a thorough identification of processes and causes of rarity. Generally, only one or a few aspect(s) is(are) examined in comparative studies on rare vs. common species. The limited scope of studies contrasts with the ideas of Stebbins (1980) and Fiedler (1986). In his gene pool–niche interaction theory, Stebbins (1980) called for a synthetic approach to understand rarity, i.e. rarity is caused by an interaction of historical, ecological and genetic factors. Stebbins' idea was significant in that it made clear, for the first time, that a species was unlikely to be rare for any singular reason (Fiedler, 1995). Moreover, as pointed out by Fiedler (1986) '...it is the synthesis of as much data as possible which provides an integrated explanation of why a certain taxon may be rare....' The difficulty of an indepth comparison is that a great amount of information is required on the biology of the study species. No single person could collect

all the necessary data in their lifetime. Thus, the comparative biologist might need to rely on research published by many authors.

Baskin *et al.* (1997) and Witkowski & Lamont (1997) synthesized a considerable amount of information on the biology of a narrow endemic and a closely related, geographically widespread congener in an attempt to explain the cause(s) of rarity. Baskin *et al.* (1997) compared the geography, ecology, morphology, physiology, cytology and life history characteristics of *Echinacea tenesseeensis*, endemic to cedar glades of middle Tennessee (USA), and *E. angustifolia*, which grows in the prairies of central North America. They relied on its recent origin and on certain ecological characteristics that limit its colonization abilities to account for endemism in *E. tenesseeensis*. Witkowski & Lamont (1997) compared the vegetative, reproductive and ecological attributes of the rare *Banksia goodii* and widespread *B. gardneri*, both of which occur in south-western Australian scrub-heath and woodland. They concluded that the rarity of *B. goodii* may be the result of its recent origin, its habitat specialization and impacts of habitat fragmentation.

Comparative studies that utilize the synthetic (comprehensive) approach (*sensu* Stebbins, 1980; Fiedler, 1986) contribute greatly to our understanding of the various ideas regarding the causes of rarity, and in particular, the relative importance and relationships between them. The main ideas presented over the years concerning rarity can be summarized in three categories: history (rare species are new or they are old), ecology (rare species are habitat specialists and/or poor competitors) and genetics (rare species have low genetic variation) (Fiedler, 1995). Two previous comprehensive studies (Baskin *et al.*, 1997; Witkowski & Lamont, 1997) found that history (youthfulness) coupled with ecological traits (poor colonization ability, habitat specialization) contributed to the narrow habitat and geographical range of the rare species. Interestingly, genetic variation and other ecological traits (e.g. competitiveness) were not suggested to be important factors in these two studies. In contrast, studies that used a limited number of traits report that narrow endemics may have low genetic variation (cf. Gitzendanner & Soltis, 2000) or be poor competitors (cf. Baskin & Baskin, 1988). Does this indicate that our ideas on rarity differ between studies that are comprehensive vs. those that are limited in scope? Clearly, general patterns of rarity will not emerge until additional comprehensive data sets are examined to provide the necessary framework to understand the complexity of rarity. On the other hand, the possibility exists that no general pattern may emerge because each species has its own history and constraints.

In the present study, a comprehensive comparison was carried out on two closely-related, co-occurring congeners to identify differences in their biology that might contribute to an explanation for the great differences in their habitats and geographical distribution. The species are the narrow-endemic *Solidago shortii* T. and G. and the geographically-widespread *S. altissima* L. (Asteraceae). An advantage of

selecting these taxa was that a great amount of information was available on their biology. The results of a literature review and of original research by the authors were used to compare various aspects of the biology of *S. shortii* and *S. altissima*. Categories of aspects compared were morphology, genetics, ecogeography, ecological life cycle, life history, reproductive biology, ecophysiology, biotic interactions and response to disturbance.

Study species

Solidago shortii is a federally endangered species endemic to adjoining portions of Fleming, Nicholas and Robertson counties, Kentucky (USA). The type locality for the species occurs at the Falls of the Ohio River, Louisville, Jefferson County, Kentucky, approximately 160 km west of its present-day distribution; however, it was apparently extirpated from this site over 100 years ago. The species occurs in a variety of habitats: powerline right-of-ways, ledges and rocky embankments of roadsides, pastures and old-field-like areas, cedar glade-like areas, and red cedar (*Juniperus virginiana*) and/or hardwood thickets/woodlands (Buchele *et al.*, 1989).

Solidago altissima (*S. canadensis* L. var. *scabra* T. and G.) is native from Nova Scotia to north-eastern Ontario and Montana south to Florida, eastern Texas, New Mexico and Arizona (USA), and from Nuevo León and Tamaulipas to Oaxaco, Mexico (Croat, 1972; Scoggan, 1979; Melville & Morton, 1982; Nesom, 1989). It is naturalized in Europe (Weber, 1997; 2000), Trans-Caucasia and Siberia (cf. Weber, 2000), Japan (Numata & Asano, 1969), Taiwan (Li, 1978), Australia (Auld & Medd, 1987) and western North America (Semple, 1993). The species is a component of the vegetation of prairies and of sites undergoing secondary succession, such as old fields, abandoned pastures and non-managed roadsides (Werner *et al.*, 1980).

MATERIALS AND METHODS

Approximately 510 references on *S. altissima* (or *S. canadensis* s.l.) published between 1895 and 2000, and 35 on *S. shortii* between 1842 and 2001, were examined. Many ecological works do not make clear which variant(s) of *S. canadensis* was(were) studied. All references were screened and information collected from those in which it could be established that *S. altissima* was included. In some instances, information on an aspect of another variety of *S. canadensis* was used as it was lacking for *S. altissima*.

To shorten the list of references for publication purposes, one paper might be cited in place of several papers that studied and reported on the same aspect. The choice of which paper(s) to cite was decided based on the number of previous studies included in a particular paper and on the amount of information overlap. If one paper could be cited in the place of several other ones, especially if the paper cited referred to the other ones, it was carried out. Indices of published information, such as those for chromosome numbers (Bolkhovskikh *et al.*, 1969) or for fungal pathogens

(Farr *et al.*, 1989), were particularly useful. For example, chromosome counts of *S. shortii* published before 1969 are included in Bolkhovskikh *et al.* (1969). Although all counts reported in Bolkhovskikh *et al.* were examined, only those published after 1969 are cited in the present study. For the most part, a complete list of publications examined are in Walck (1998).

We strived to include as many aspects of the biology of the two *Solidago* species as possible. However, some aspects (e.g. biomass) were too variable to include for a meaningful comparison. In addition, information overlap was reduced as much as possible without deletion of details. For example, not all growth parameters in the literature (e.g. leaf area duration) are included in our study, because other descriptive parameters (e.g. leaf area) could be substituted without reduction of information. Many parameters are reported to describe the morphology or physiology of the two *Solidago* species during an experiment (e.g. biomass, density, frequency, net photosynthetic rate, relative growth rate). Thus, the term 'vigour' was used to characterize the overall growth condition of the plants based on the various parameters. In some instances, the reaction of one (or some) parameter(s) may have been positive to a particular treatment, but that of others may have been negative or have had no response. In such circumstances, the interpretation of the results of the experiment(s) was judged on the researcher's assessment of the experimental outcome.

Statistical comparisons between the species for particular aspects were possible only in those experiments in which both *Solidago* species were included. The statistical results are not given in the present study because the original paper is cited. In other cases, the species were studied separately and no statistical comparisons are possible. Thus, a conservative assessment was made to summarize the information for a particular aspect and to evaluate the differences between the species. Studies in which an interaction of factors were investigated (e.g. addition of fertilizer and levels of herbivory) are cited only under one factor.

RESULTS

Morphology and genetics

Solidago shortii and *S. altissima* are hemicryptophytes that reproduce vegetatively by rhizomes and sexually by seeds (achenes) (Table 1). Compared with *S. shortii*, rhizomes of *S. altissima* are longer, stems taller, leaf area larger and genets (clones) spread over more area. On the other hand, *S. shortii* has higher root/shoot and (root + rhizome)/shoot ratios than *S. altissima*, and its seeds are considerably larger. Maximum depth of root penetration has not been determined for *S. shortii*, but it appears to be much greater than 0.5 m.

Although both species exhibit high levels of morphological variation within and between populations, the cause(s) of this variation in *S. shortii* is(are) unknown. Moreover, subspecific taxa are recognized in *S. altissima* but not in *S. shortii*. Alternatively, *S. altissima* can be placed as a

Table 1 Comparison of the morphology and genetics of the two *Solidago* species

	<i>Solidago altissima</i>	<i>Solidago shortii</i>
<i>Morphology</i>		
Life form	Hemicryptophyte ¹	Hemicryptophyte ²
Roots	Fibrous, descend vertically to 3.3 m ³	Descend > 0.5 m ⁴
Rhizomes	Length ≤ 60 cm, diameter up to 10 mm ⁵	Length at least 18 cm, diameter 2 mm ⁶
Stems	Height 75–220 cm, diameter 3–13 mm ⁷	Height 140 cm (most < 50), diameter 3 mm ⁶
<i>Leaves</i>		
Area (cm ²) per ramet	Up to <i>c.</i> 400 ⁸	Up to <i>c.</i> 250 ⁹
Specific leaf area (cm ² g ⁻¹)	<i>c.</i> 150 (adult plants) ¹⁰	<i>c.</i> 150 (adult plants) ⁹
Leaf area ratio (cm ² g ⁻¹)	<i>c.</i> 60 (adult plants) ⁹	<i>c.</i> 60 (adult plants) ⁹
Achenes	Mostly 60–70 µg, 1.8 mm long × 0.4 mm wide ¹¹	370 µg, 2.3 mm long × 0.6 mm wide ¹²
Root/shoot ratio	<i>c.</i> 0.1–0.6 (adult plants) ¹³	<i>c.</i> 0.8–1.2 (adult plants) ⁹
(Root + rhizome)/shoot ratio	<i>c.</i> 0.2–1.0 (adult plants) ¹³	<i>c.</i> 0.8–1.2 (adult plants) ⁹
Genet structure	Compact to widely spreading ¹⁴	Compact ²
Phenotypic variation factors	Genetic, environmental, maternal and clinal ¹⁵	Not studied, but high variability exists ¹⁶
Species complex	Two subspecific taxa (7 in <i>S. canadensis</i> complex) ¹⁷	No subspecific taxa ¹⁸
<i>Genetics</i>		
Ploidy level (2 <i>n</i>)	Diploid (18), tetraploid (36) or hexaploid (54) ¹⁹	Diploid (18) or tetraploid (36) ²⁰
Allozyme variation	Substantial ²¹	Substantial ²²

References: ¹Numata & Asano (1969); ²Buchele *et al.* (1991); ³Weaver (1919), Jastrow & Miller (1993); ⁴Buchele *et al.* (1989), Baskin & Baskin (personal observation); ⁵Weaver (1919), Cain (1990); ⁶Buchele *et al.* (1991), J.L. Walck (unpublished data); ⁷Iwaki *et al.* (1969), Croat (1972), Weber (1997), Meyer (1998); ⁸Walck *et al.* (1999a), Potvin & Werner (1983); ⁹Walck *et al.* (1999a); ¹⁰Schmid *et al.* (1988), DeLucia *et al.* (1991), Walck *et al.* (1999a); ¹¹Hartnett & Abrahamson (1979), Semple & Ringius (1983), Meyer & Root (1993), Walck *et al.* (1997a), Meyer & Schmid (1999a); ¹²Buchele *et al.* (1991), Walck *et al.* (1997a); ¹³Abrahamson & Caswell (1982), Gross *et al.* (1983), Abrahamson *et al.* (1988), Cornelius (1990a), Schmid & Bazzaz (1992), Martel (1998), Walck *et al.* (1999a); ¹⁴Werner *et al.* (1980), Maddox *et al.* (1989); ¹⁵Schmid & Dolt (1994), Weber & Schmid (1998); ¹⁶Beck *et al.* (2001); ¹⁷Semple *et al.* (1984); ¹⁸Beck *et al.* (1999); ¹⁹Nesom (1989), Turner & Zhao (1992), Semple *et al.* (1993), Weber (1997); ²⁰Bolkhovskikh *et al.* (1969), Semple *et al.* (1993); ²¹Maddox *et al.* (1989); ²²Calie *et al.* (2001), P.J. Calie (personal communication).

subspecific taxon (var. *scabra*) in the highly variable *S. canadensis* complex. Different ploidy levels are recorded in both species. Substantial allozyme variation is reported in both *S. altissima* and *S. shortii*.

Ecogeography

Because the geographical range of *S. altissima* is much broader than that of *S. shortii*, *S. altissima* obviously occurs in more physiographic regions, climatic provinces, hardiness zones and regional climax (potential) vegetation types, and grows over a wider altitudinal range and in soils belonging to more orders than *S. shortii* (Table 2). Further, *S. altissima* occurs both south and north of the glacial boundary in North America, whereas *S. shortii* naturally occurs only south of it. On the other hand, *S. shortii* has been cultivated out-of-doors in Ontario (Canada), Massachusetts, Pennsylvania and Missouri (USA), considerably north and west of its present-day distribution, and thus in other physical and biotic regions. Both species grow over a wide range of soil fertilities, textural classes and moisture-retaining capacities in the field. Although *S. altissima* occurs on soils that vary widely in pH in the field, *S. shortii* does not. However, *S. shortii* grew in a greenhouse on five types of soil that represented those in the major physiographic regions of Kentucky and adjacent states and had a broad range of pH.

Ecological life cycle

Phenology differs little between the two species (Table 3). Shoot elongation begins in March, and shoots continue to elongate until August/September. Flower buds are formed during summer, flowering peaks in August/September, seeds disperse mostly in November and seeds germinate mostly in March. Senescence of shoots occurs in autumn, and winter rosettes may, or may not, be formed. Both species produce new rhizomes and roots during the summer.

Life history and reproductive biology

Solidago altissima and *S. shortii* are self-incompatible and cross-pollinated by insects (Table 4). In contrast to *S. altissima*, soldier beetles are the primary pollinators of *S. shortii* at field sites and neither honeybees nor bumblebees have been observed visiting flowers of *S. shortii* in the field. However, honeybees and bumblebees were present on flowers of *S. shortii* in a garden. The two species apparently are reproductively isolated, although a specimen of *S. shortii* × *S. altissima* was reported. Hybridization between the two species needs to be confirmed.

Compared with *S. altissima*, percentage of stems flowering in populations of *S. shortii* is lower and fewer seeds are produced per flowering ramet. However, a broad range of

Table 2 Comparison of the ecogeography of the two *Solidago* species

	<i>Solidago altissima</i>	<i>Solidago shortii</i>
Geographic range		
Native	> 5,000,000 km ² area of North America ¹	12.2 km ² area of nc Ky. ¹
Non-native	Naturalized in many regions of the world ¹	Grown in gardens in se Ont., ec Mass., sc Pa., c Ky. and ec Mo. ²
Physiographic regions ^a	c. 16 ³	1 (cultivated in four other regions) ³
Soil orders ^b	9 ⁴	1 (cultivated in 2–3 other orders) ⁴
Glacial boundary ^a	Occurs north and south of it (ditto Europe) ³	Occurs south of it, but cultivated north of it ³
Elevation (m)	c. 20–2800 ⁵	201–268 (cultivated at 10–300) ⁶
Climatic provinces ^b	c. 11 (naturalized in six other provinces) ⁷	1 (cultivated in 1 other province) ⁷
Hardiness zones ^a	2a–9b, 10 ⁸	6a (cultivated in 4a and 6b) ⁸
Regional climax vegetation types ^a	c. 26 ⁹	1 (cultivated in 2 other types) ⁹
Soil		
Fertility	Wide range ^{10,c}	Wide range ^{11,c}
pH	4.8–7.8 ^{12,13,c}	7.2–8.0 ^{11,c}
Textural classes	Clayey, loamy, sandy ^{13,c}	Clayey, loamy ^{11,c}

^aNorth America or United States distribution.

^bWorld-wide distribution.

^c*Solidago altissima* and *S. shortii* grew in a greenhouse on five types of soils, broadly representative of those in the major physiographic regions of Kentucky and adjacent states. These soils exhibited a wide range of nutrients and organic matter, pH (4.2–7.0) and textural classes (loam, sand, silty clay, silty clay loam) (Walck *et al.*, 1999b, J.L. Walck, unpublished data).

References: ¹see study species section; ²Conners (1967), Buchele *et al.* (1991), Walck (1998), Beck *et al.* (1999), P.J. Calie, K. Havens (personal communication); ³cf. Hunt (1974); ⁴cf. Brady (1990); ⁵Harrington (1954), Semple (1993), Yura (1997); ⁶Buchele *et al.* (1989), Walck (1998), J.L. Walck (unpublished data); ⁷cf. Thornthwaite (1933); ⁸cf. Cathey (1990); ⁹cf. Küchler (1964); ¹⁰Bostick (1967), Abrahamson *et al.* (1983), Cornelius (1990a), Weber (2000); ¹¹Buchele *et al.* (1989); ¹²Bostick (1967); ¹³Kelley (1922), Turner (1928), Rebele (1992), Weber (2000).

Table 3 Comparison of the ecological life cycle of the two *Solidago* species

	<i>Solidago altissima</i>	<i>Solidago shortii</i>
Life cycle	Polycarpic perennial ¹	Polycarpic perennial ²
<i>Phenology</i>		
Shoot emergence	March–April ³	March ²
Shoot elongation	March–August/September ³	March–August ²
Flower buds	Presumably mostly June–August ⁴	Mostly June–July ²
Flowering	July–November, peaks in August/September ⁴	August–November, peaks in September ^{2,5}
Seed dispersal	October–April, mostly October/November ^{5,6}	October–March, mostly November ²
Seed germination	Mostly March–April ⁷	Mostly March ⁷
Senescence	September–November ³	September–November ²
Winter rosette	Mostly absent, formed in October ^{3,8}	Mostly absent, formed in October ²
Rhizomes initiated	June–July ^{3,9}	July ²
New roots initiated	June–July ¹⁰	Presumably July

References: ¹Cain (1990); ²Buchele *et al.* (1991); ³Iwaki *et al.* (1969), Hirose (1971), Cain (1990); ⁴Ginsberg (1983), Abrahamson & Weis (1997); ⁵J.L. Walck, J.M. Baskin and C.C. Baskin (personal observation); ⁶Meyer & Schmid (1999a), ⁷Walck *et al.* (1997a, b, 1998); ⁸Hartnett & Bazzaz (1985a); ⁹Bradbury & Hofstra (1976); ¹⁰Iwaki *et al.* (1969), Hirose (1971), Bradbury & Hofstra (1976).

overlap occurs in the percentage of flowers that set seed, which probably is pollen limited, in both species. Wind is the primary dispersal agent for seeds of both species. By inference from size and dispersal distance of seeds in *S. rigida*,

it appears that seeds of *S. shortii* probably could be dispersed as far from the mother plant as those of *S. altissima*. Levels of seed viability and amount of pre-dispersal seed predation are nearly identical for the two species. Although the amount

Table 4 Comparison of the life history and reproductive biology of the two *Solidago* species

	<i>Solidago altissima</i>	<i>Solidago shortii</i>
Embryo sac development	Polygonum type ¹	Polygonum type ²
Breeding system	Self-incompatible ³	Self-incompatible ⁴
Pollinators/flower visitors	Primarily honeybees (<i>Apis mellifera</i>), bumblebees (<i>Bombus</i> spp.), soldier beetles (<i>Chauliognathus pennsylvanicus</i>) and syrphid flies, many visitors ⁵	Primarily soldier beetles, several visitors ⁴
Ability to hybridize with other taxa	Low, honeybee foraging species specific ⁶	Perhaps with <i>S. altissima</i> in nature ⁷
Flowering ramets in population (%)	50–80 ⁸	0–23 ⁹
Pollen limitation	Yes ³	Perhaps ⁴
Seed set (%)	13–33 ³	22–25 ⁴
Seeds per flowering ramet	c. 10,000–20,000 ¹⁰	c. 250–1700 ¹¹
Seed dispersal		
Disseminule	Achene with pappus ⁶	Achene with pappus ⁹
Agents	Wind, water ¹²	Wind ¹³
Distance (m)	Up to 2.4 or 14.9 in 8–10 km h ⁻¹ wind ¹⁴	Probably up to at least 15 in 10–15 km h ⁻¹ wind* ¹⁶
Seed viability	Low–high ¹⁵	Moderate ¹⁶
Seed predation		
Pre-dispersal	Low–high, varies yearly ^{13,17}	Low–high, varies yearly ¹³
Post-dispersal	Low by ants, high by fungi ¹⁸	Unknown
Soil seed bank (relative)	Large and long-lived ¹⁹	Small and short-lived ¹⁹
Seedling establishment/recruitment	Usually low, but can be high ²⁰	Usually low, but can be high ²¹
Survivorship		
Seedling to juvenile/adult	Deevey-type II, III and combination of I/II curves ²²	Deevey-type I, II, III and combinations of I/II, I/III and II/III curves ²¹
Vegetatively produced ramets	Low–moderate during a growing season ²³	Appears to be high during a growing season ¹³
Sexual reproduction		
Age threshold	Mostly > 1st year in field, 1st year in greenhouse ²²	≥ 3rd year in field, 1st year in greenhouse ²¹
Size threshold	Yes ²⁴	Probably ⁹
Effort (%)	mostly c. 10–25 (of shoot), 5–20 (of total) ²⁵	c. 24 (of shoot), 10 (of total) ²⁶
Vegetative reproduction		
Method(s)	Rhizomes, root buds ²⁷	Rhizomes ⁹
Age threshold	First year in field and greenhouse ²⁸	> 1st year in field, 1st year in greenhouse ²⁹
Size threshold	No, but can produce rhizomes before flowering ³⁰	Can produce rhizomes before flowering ⁹
Effort	c. 5–35 ³¹	c. 1 ²⁶

*Seeds of *S. rigida*, which are slightly larger (weight and dimension) and have a longer pappus than those of *S. shortii*, are dispersed up to 15 m (Platt & Weis, 1977).

References: ¹Beaudry (1958); ²Harling (1951); ³Gross & Werner (1983); Weber (2000); ⁴Buchele et al. (1992a); ⁵Robertson (1928), Parrish & Bazzaz (1979), Werner et al. (1980), Melville & Morton (1982), Gross & Werner (1983), Schmid & Dolt (1994); ⁶Werner et al. (1980), Melville & Morton (1982), Gross & Werner (1983); ⁷Medley (1993), Beck et al. (2001); ⁸Meyer & Schmid (1999b); Uriarte (2000), ⁹Buchele et al. (1991); ¹⁰Hartnett and Abrahamson (1976), Werner & Platt (1976), Meyer & Schmid (1999a); ¹¹Walck (1998); ¹²Numata & Asano (1969), Kelley & Bruns (1975), Meyer & Schmid (1999a); ¹³J.L. Walck, J.M. Baskin and C.C. Baskin (personal observation); ¹⁴Werner et al. (1980), Matlack (1987); ¹⁵Hartnett & Abrahamson (1976), Walck et al. (1997c); ¹⁶Walck et al. (1997c); ¹⁷Werner et al. (1980), Weber (2000); ¹⁸Reader (1993), Meyer & Schmid (1999a); ¹⁹Walck et al. (1998); ²⁰Hartnett & Bazzaz (1985b), Cain (1990), Meyer & Schmid (1999a); ²¹Walck et al. (1999c, d); ²²Walck et al. (1999c), Meyer & Schmid (1999a); ²³Iwaki et al. (1969), Cain (1990); ²⁴Hartnett (1990), Schmid & Weiner (1993); ²⁵Abrahamson & Gadgil (1973), Platt (1975), Abrahamson & Caswell (1982), Gross et al. (1983), Abrahamson et al. (1988), Walck et al. (1999a); ²⁶Walck et al. (1999a); ²⁷Raju et al. (1966), Cain (1990); ²⁸Hartnett & Bazzaz (1985b), Walck et al. (1999a); ²⁹Buchele et al. (1991), Walck et al. (1999a); ³⁰Hartnett & Bazzaz (1985b), Schmid et al. (1995); ³¹Abrahamson & Caswell (1982), Gross et al. (1983), Abrahamson et al. (1988), Schmid et al. (1988), Walck et al. (1999a).

of post-dispersal seed predation is unknown in *S. shortii*, fewer seeds germinate than are produced at population sites. *Solidago altissima* forms a larger and longer-lived soil seed bank than does *S. shortii*.

Seedling establishment/recruitment and survivorship of plants marked as seedlings are highly variable for both

species. In the field, *S. shortii* flowers and produces rhizomes at a later age than does *S. altissima*. On the other hand, under greenhouse conditions both species flower vigorously and produce rhizomes in their first year. The difference in age of first flowering between the species in the field is apparently because of the relatively more stressful habitat of

Table 5 Comparison of the ecophysiology of the two *Solidago* species

	<i>Solidago altissima</i>	<i>Solidago shortii</i>
<i>Carbon</i>		
Photosynthetic pathway	C ₃ ¹	C ₃ ²
Net (maximum) photosynthesis	c. 12–20 ³ μmol CO ₂ m ⁻² s ⁻¹	Unknown
Dark respiration	c. 3 ¹ μmol CO ₂ m ⁻² s ⁻¹	Unknown
Light saturation	c. 1000 ⁴ μmol m ⁻² s ⁻¹ PPFD	Presumably full sun ⁵
Light compensation point	c. 30–50 ⁴ μmol m ⁻² s ⁻¹ PPFD	Unknown
Quantum yield	c. 0.05 ⁶ mol O ₂ /mol absorbed photons	Unknown
Shade tolerant	No ⁷	No ⁵
Net assimilation rate (mg cm ⁻² d ⁻¹)	0.54 (entire growing season)*	0.53 (entire growing season)*
Relative growth rate (g g ⁻¹ d ⁻¹)	0.074 (entire growing season)*	0.077 (entire growing season)*
<i>Carbohydrate</i>		
Storage	Inulin, in roots and rhizomes (for 2–3 years) ⁸	Inulin, in roots and rhizomes ⁹
Distribution	Seasonally typical of herbaceous perennials ⁸	Presumably typical of herbaceous perennials
Dry weight allocation (%)	Roots: 37, rhizomes: 7, stems: 18, leaves: 31, inflorescences: 7*	Roots: 55, rhizomes: 1, stems: 11, leaves: 23, inflorescences: 10*
<i>Water</i>		
Water stress	Vigor decreases, some physiological adjustments, wilts readily in field and in pots ¹⁰	Wilting rarely observed in field and does not wilt as readily as <i>S. altissima</i> in pots ¹¹
Salt tolerant	No ¹²	Unknown
Stomatal conductance	Mostly c. 300–600 ¹³ mmol H ₂ O m ⁻² s ⁻¹	Unknown
Transpiration	c. 7.5 ¹⁴ mmol m ⁻² s ⁻¹	Unknown
Water use efficiency	c. 1.5–2.0 ¹⁵ μmol CO ₂ /mmol H ₂ O	Unknown
Leaf water potential	c. –0.2 to –0.6 MPa (predawn), stomates can close at –1.6 to –2.0 MPa ¹⁶	Unknown
<i>Nutrients</i>		
Concentration in plant	Consistent among sites, but highly variable ¹⁷	Unknown
Distribution in plant	Seasonally typical of herbaceous perennials ¹⁸	Presumably typical of herbaceous perennials
Source	Mostly dependent on soil reserves rather than on internal storage or recycling ¹⁸	Mostly dependent on soil reserves rather than on internal storage or recycling ⁵
<i>Clonal integration</i>		
Ramets share resources	Yes (nutrients and photoassimilates) ¹⁹	Presumably
Rhizome connections	Persist for 4–5 years, but usually 1 year ²⁰	Unknown
<i>Seed dormancy/germination</i>		
Type of dormancy	Non-deep physiological ²¹	Non-deep physiological ²¹
Requirement to break dormancy	Cold stratification ²²	Cold stratification ²²
Dormancy cycling in buried seeds	Yes ²³	Yes ²³
Photoecology	Germination low in darkness and moderate in far-red light ²⁴	Germination moderate–high in darkness and far-red light ²⁴
Substrate conditions	Germinates well on wide range of soil types, fertilities and pHs, but poor under litter and plant cover, high moisture needed ²⁵	Germinates well on wide range of soil types, fertilities and pHs and under litter, but best on bare (open) ground, high moisture needed ²⁶
<i>Flowering</i>		
Photoperiod	Facultative short day ²⁷	Facultative short day ²⁸
Vernalization	Not required ²⁷	Not required ²⁸

*Values based on plants of both species grown under uniform conditions in a greenhouse (Walck *et al.*, 1999a).

References: ¹DeLucia *et al.* (1991), Egli & Schmid (1999); ²Baskin & Baskin (1985); ³Potvin & Werner (1983), Hirose & Werger (1987), Schmid *et al.* (1988), DeLucia *et al.* (1991), Turner *et al.* (1995), Meyer (1998); ⁴Hirose & Werger (1987), Cornelius (1990a), DeLucia *et al.* (1991), Turner & Knapp (1996); ⁵Walck *et al.* (1999b); ⁶DeLucia *et al.* (1991), Schieving *et al.* (1992); ⁷Hartnett & Bazzaz (1983), Cornelius (1990a); ⁸Houston & Burrell (1948), Bradbury & Hofstra (1977); ⁹Pollard & Amuti (1981); ¹⁰Weaver *et al.* (1935), Potvin & Werner (1984), Cornelius (1990a), Martin *et al.* (1991), Pilson (1992a), Horner & Abrahamson (1999), Walck *et al.* (1999a); ¹¹Buchele *et al.* (1989), Walck *et al.* (1999a); ¹²Yura (1997), Martel (1998); ¹³Potvin & Werner (1983, 1984), Schmid *et al.* (1988), Martin *et al.* (1991), Turner *et al.* (1995); ¹⁴Schmid *et al.* (1988); ¹⁵Cornelius (1990a), Turner *et al.* (1995); ¹⁶Potvin & Werner (1983, 1984), Turner & Knapp (1996), Martin *et al.* (1991); ¹⁷Nordstrom (1984), Abrahamson & McCrea (1985), Weber (2000); ¹⁸Hirose (1971, 1974), Abrahamson & McCrea (1985); ¹⁹Abrahamson *et al.* (1991); ²⁰Cain (1990), Abrahamson *et al.* (1991); ²¹Walck *et al.* (1997c); ²²Walck *et al.* (1997a); ²³Walck *et al.* (1997d); ²⁴Walck *et al.* (1997a, d, e); ²⁵Goldberg & Werner (1983), Cornelius (1990b), Reader (1993), Meyer & Schmid (1999a), Walck *et al.* (1997b), J.L. Walck (unpublished data); ²⁶Walck *et al.* (1997b, 1999d, e); ²⁷Schwabe (1986); ²⁸Walck *et al.* (1999c).

S. shortii, and not to inherent differences in growth and development between them. A minimum size probably is required for flowering in *S. shortii*, as in *S. altissima*, but its relationship to plant age is unknown for both species. Sexual reproductive effort in *S. shortii* is within the (broad) range of that reported for *S. altissima*, but vegetative reproductive effort is higher in *S. altissima* than in *S. shortii*. Both species can reproduce vegetatively by rhizomes before flowering.

Ecophysiology

Solidago shortii and *S. altissima* have non-Kranz anatomy and thus utilize the C₃ photosynthetic pathway (Table 5). Maximum net photosynthesis, dark respiration, light saturation, light compensation point and quantum yield for *S. altissima* are similar to those reported for herbaceous sun plants (cf. Larcher, 1995). None of these ecophysiological parameters has been measured for *S. shortii*. However, like *S. altissima*, *S. shortii* grows best in full sun and persists (but rarely flowers) in moderate shade. Moreover, net assimilation rates and relative growth rates for the two species are nearly identical. Thus, it seems reasonable that their photosynthetic characteristics are similar.

Levels of carbohydrates in roots and rhizomes of *S. altissima* decrease as new leaves, stems, and (later) inflorescences develop in spring and summer, and then increase gradually near the end of the growing season. Seasonal distribution of carbohydrates has not been studied in *S. shortii*, but it is presumably similar to that in other herbaceous perennials. Both species allocate similar percentages of dry biomass to inflorescences and leaves. However, *S. shortii* allocates proportionately less dry biomass to stems and rhizomes and more to roots than does *S. altissima*.

Stomatal conductance to water vapour, transpiration rate, leaf water potential and water use efficiency of *S. altissima* are similar to those reported for herbaceous sun plants (cf. Larcher, 1995). Moreover, *S. altissima* is not tolerant of salt (NaCl)-stress conditions. None of these ecophysiological parameters has been measured for *S. shortii*. However, observations indicate that *S. shortii* does not wilt as readily as *S. altissima* in the field or in pots in the greenhouse, and thus apparently it has a greater capacity to maintain leaf turgor than does *S. altissima*.

Nutrient levels in roots and rhizomes of *S. altissima* increase in autumn (from soil reserves) and remain stable over winter. Concentrations of nutrients in new rhizomes and shoots increase in spring, and then decrease as stems elongate. Leaves and stems are sources of nutrients during inflorescence development. Seasonal distribution of nutrients has not been studied in *S. shortii*, but it is presumably similar to other herbaceous perennials. Both species depend mostly on the supply of reserves in the soil, internal storage and nutrient recycling within the plant does not seem to be important.

Ramets of *S. altissima* share resources, and it seems reasonable to assume those of *S. shortii* do so as well. However, the length of time that rhizome connections between ramets persist has not been determined for *S. shortii*.

Seeds of both species have non-deep physiological dormancy at maturity. They come out of dormancy during winter (cold stratification), and thus are non-dormant by early spring. Seeds of the two species in a persistent seed bank cycle between conditional dormancy and non-dormancy. However, *S. shortii* seeds are less dependent on light to germinate than *S. altissima* seeds, which may explain the greater capacity of *S. altissima* to form a persistent seed bank. Both species germinate to moderate percentages under simulated plant-canopy light (high FR/R ratio) and over a wide range of physicochemical edaphic conditions.

Solidago shortii and *S. altissima* are facultative short-day plants, and neither species requires vernalization to flower.

Biotic interactions

More taxa of parasitic fungi and phytophagous insects, more guilds of phytophagous insects and more types of galls have been recorded on *S. altissima* than on *S. shortii* (Table 6). However, these differences probably are related more to the wider distribution of *S. altissima* than to inherent differences *per se* between the two species. Amounts of insect herbivory and of gall infestation on *S. altissima* are highly variable, but are consistently low on *S. shortii*. However, leaves of *S. shortii* sustain relatively high damage by cicadellids (leaf hoppers) (T. Carr, personal communication). Parasitic fungi and phytophagous insects decrease the vigour of *S. altissima*, and probably also that of *S. shortii*. Although plants of *S. altissima* have resistance to attack by parasitic fungi and phytophagous insects, those of *S. shortii* contain diterpenes, secondary compounds shown to be herbivore toxins and feeding deterrents (cf. Larcher, 1995).

Besides parasitic fungi and phytophagous insects, several additional parasitic, mutualistic or herbivory interactions can be noted. The holoparasitic angiosperm *Cuscuta* grows on both species. Severe damage by snails to plants of *S. altissima* has been reported, whereas snail herbivory has never been observed on *S. shortii*. *Solidago shortii* retains its vigour in pastures grazed by cattle and horses, whereas *S. altissima* decreases under grazing. Presence or absence of mycorrhizal fungi and of root nematodes and palatability have not been determined for *S. shortii*.

Solidago altissima is competitively superior to *S. shortii* and to many other species. Although chemicals isolated from *S. altissima* have been shown to have allelopathic effects under laboratory conditions, they have little activity under field conditions. It is unknown whether *S. shortii* produces allelopathic chemicals.

Response to disturbance

Vigor of *S. shortii* increases with mowing and the species persists on sites after fire (Table 7). In contrast, vigour of *S. altissima* decreases with mowing and fire, especially following frequent episodes of both factors. Vigor of both species increases with fertilization. At its type locality at the Falls of the Ohio River, *S. shortii* grew in a rocky (limestone) habitat that was swept-over by water. Herbarium specimens

Table 6 Comparison of the biotic interactions of the two *Solidago* species

	<i>Solidago altissima</i>	<i>Solidago shortii</i>
Fungi		
Parasitic	Host 36 taxa ¹ , vigor decreases ²	Host at least 1 taxon ³
Mycorrhizal	Present ⁴	Unknown
<i>Cuscuta</i>	Present ⁵	Present ⁶
Nematodes	Present ⁷	Unknown
Phytophagous insects		
Number	c. 100 taxa (generalists and specialists) present ⁸	at least 12 taxa present ⁹
Guilds	Root feeders; stem borers; leaf chewers, miners and rollers; sap feeders; flower feeders ⁸	Leaf chewers and miners, sap feeders, flower feeders ⁹
Gall types	Flower, stem, rosette, leaf, rhizome ¹⁰	Rosette, leaf ⁹
Defoliation and gall infestation	Low–high with spatial and temporal variations ¹¹	Consistently low ^{6,9}
Effects	Vigor decreases, but stands not eliminated; compensatory responses may occur ¹²	Presumably vigor decreases
Snail herbivory	Occasional to severe damage ¹³	None observed ⁶
Grazing	Vigor decreases ¹⁴	Persists in cattle and horse pastures ⁶
Insect and fungal resistance	Genetic and chemical ¹⁵	Probably at least chemical ¹⁶
Palatability		
Insects, slugs	Plant preferred as food ¹⁷	Unknown
Mammals	Plant eaten very little, toxic to mice ¹⁸	Not eaten by cattle and horses ⁶
Interspecific competition		
Relative	Superior ¹⁹	Inferior ¹⁹
General	Mostly superior, but neighbours decrease vigor ²⁰	Inferior ²¹
Intraspecific competition	Growth density dependent, may not conform to self-thinning rule ²²	Growth density dependent ²³ , presumably may not conform to self-thinning rule
Allelopathic effects	Probably little ²⁴	Unknown

References: ¹Farr *et al.* (1989); ²Schmid (1994); ³Connors (1967); ⁴Dhillion & Friese (1994), Nakatsubo *et al.* (1994); ⁵US Department of Agriculture (1960), Weber (2000); ⁶J.L. Walck, J.M. Baskin and C.C. Baskin (personal observation); ⁷US Department of Agriculture (1960); ⁸Werner *et al.* (1980), Root & Cappuccino (1992), Fontes *et al.* (1994), Jobin *et al.* (1996), R.B. Root (personal communication); ⁹Buchele *et al.* (1992a), T. Carr (personal communication); ¹⁰McEvoy (1988); ¹¹Hartnett & Abrahamson (1979), Sholes (1981), Root & Cappuccino (1992), Carson & Root (2000), Weber (2000); ¹²Sholes (1981), Schmid *et al.* (1990), Cain *et al.* (1991), Root (1996), Abrahamson & Weis (1997), Meyer (1998), Carson & Root (2000); ¹³Jobin *et al.* (1996), Weber (2000); ¹⁴Weaver & Hansen (1941), Hartnett *et al.* (1996); ¹⁵Maddox & Root (1990), Seaman *et al.* (1990), Heath (1992), Pilson (1992b), Schmid (1994), Abrahamson & Weis (1997); ¹⁶Seaman *et al.* (1990); ¹⁷Gangwere (1961), Cates & Orians (1975), Messina (1982); ¹⁸Worthley *et al.* (1967), Irwin (1985), Root (1996), Weber (2000); ¹⁹Walck *et al.* (1999a); ²⁰Zimmerman & Kucera (1977), Armesto & Pickett (1986), Hartnett & Bazzaz (1985c), Goldberg (1987, 1988), Cornelius & Faensen-Thiebes (1990), Burton & Bazzaz (1995), Meyer & Schmid (1999b), Weber (2000); ²¹Walck *et al.* (1999d); ²²Hartnett & Bazzaz (1985a); ²³J.L. Walck (unpublished data); ²⁴Werner *et al.* (1980), Hanson & Dixon (1985), Ito *et al.* (1998).

indicate that plants at the type locality had high vigor. *Solidago altissima* also may be subjected to seasonal flooding, because it grows along waterways. Soil compaction, prolonged flooding and some herbicides have detrimental effects on *S. altissima*; their effects on *S. shortii* have not been determined. Both species can invade sites following disturbances, albeit *S. shortii* colonizes such areas only within its very narrow geographical range.

DISCUSSION

Remarkably, *S. shortii* is similar to *S. altissima* in many aspects of its biology (Tables 1–7). Of the approximately 125 aspects compared in the present study, the majority (c. 70%) of them were identical, or differed only slightly, between the two species. An in-depth comparison of various characteristics of the rare *E. tenesseeensis* and the widespread *E. angustifolia* did not reveal any outstanding

differences in their general biologies (Baskin *et al.*, 1997). Likewise Witkowski & Lamont (1997) remarked that ‘...there are few grounds for regarding [the widespread] *B. gardneri* as biologically different from [the rare] *B. goodii*.’ Unlike the previous two studies, however, there are some important differences between *S. shortii* and *S. altissima*.

Of the numerous features of the biology of *S. shortii* and *S. altissima* compared in this study, competitive ability appears to be the single most important factor responsible for the great difference in their geographical distribution and habitat. *Solidago altissima* is competitively superior to *S. shortii* (Table 6) because of its larger size and more extensive lateral (clonal) growth (Table 1). In general, size of plants has an important influence on competitive ability (Hills & Murphy, 1996; Rösch *et al.*, 1997), and thus on distribution patterns, relative abundance and diversity of plant species (Goldberg & Barton, 1992). Recently, Carson

	<i>Solidago altissima</i>	<i>Solidago shortii</i>
Fire	Vigor mostly decreases ¹	Persists on sites after burning ²
Mowing	Vigor decreases ³	Vigor increases ²
Soil compaction	Vigor decreases ⁴	Unknown
Flooding		
Short-term	Grows along waterways ⁵	Had high vigor at Falls of the Ohio River ⁶
Prolonged	Eliminated ⁷	Unknown
Herbicides	Mostly susceptible ⁸	Unknown
Fertilization	Vigor increases ⁹	Vigor increases ⁶
Ability to invade	Increased rapidly (741 km ² year ⁻¹) after naturalization ¹⁰	Can invade new sites ¹¹

Table 7 Comparison of the response to disturbance of the two *Solidago* species

References: ¹Schwegman & Anderson (1986), Gibson (1989), Hartnett (1990), Gibson *et al.* (1993), Howe (1994), Johnson & Knapp (1995); ²J.L. Walck, J.M. Baskin and C.C. Baskin (personal observation); ³Kline (1986), Gibson *et al.* (1993), Stoll *et al.* (1998), Weber (2000); ⁴Schmid & Bazzaz (1990); ⁵Numata & Asano (1969), Croat (1972), Weber (1997); ⁶Walck *et al.* (1999b); ⁷Noble & Murphy (1975), Weber (2000); ⁸Tomkins & Grant (1974); ⁹Abrahamson *et al.* (1988), Cornelius (1990a, b), Schmid *et al.* (1990), Meyer & Root (1993), Collins & Wein (1998), Stoll *et al.* (1998); ¹⁰Yura (1997), Weber (1998); ¹¹Buchele *et al.* (1989).

& Root (2000) proposed that *S. altissima* is the dominant herb over a broad geographical range because, more so than other herbs, it can decrease understory light levels that displace other herbs and resist invasion. Hills & Murphy (1996) classified *S. canadensis* (probably *S. altissima*, cf. Weber, 1997) as a competitor strategist (*sensu* Grime, 1979).

On the other hand, *S. shortii* apparently is better adapted to (xeric) rocky/shallow soil areas in various types of habitats, i.e. a better drought-stress tolerator (*sensu* Grime, 1979), than *S. altissima* because of its proportionately larger allocation of biomass to roots, larger root/shoot ratio, smaller and more compact growth form and (seemingly) greater capacity to maintain leaf turgor (Tables 1 and 5). These features of *S. shortii*, along with its relatively large seed size, are consistent with those reported for other stress-tolerant plants (Hills *et al.*, 1994; Larcher, 1995). Likewise, the endemic taxa of south-eastern France and of Corsica primarily are stress-tolerators, stress-tolerant ruderals, or stress-tolerant competitors (Médail & Verlaque, 1997). Although *S. shortii* invades relatively deep soil in old-field-like habitats, it is easily overtopped by other species, such as *S. altissima*. *Solidago shortii* can be maintained in old fields if anthropogenic disturbance keeps the site in an early-successional stage. On the other hand, *S. altissima* occurs only sparingly with *S. shortii*, in the rocky sites (Buchele *et al.*, 1989, 1992b; J.L. Walck, J.M. Baskin & C.C. Baskin, personal observations). Low competitive ability of other narrowly endemic (rare) plants of rocky habitats has been implicated as the primary (proximal) cause of their narrow geographical range (Baskin & Baskin, 1988).

The relatively low seed production and small, short-lived soil seed bank of *S. shortii* probably are important in contributing to differences in colonization ability between it and *S. altissima* (Table 4). Several studies have found that rare species have lower seed (or fruit) production than their widespread congeners (Meagher *et al.*, 1978; Fiedler, 1987;

Pavlik *et al.*, 1993; Byers & Meagher, 1997). Byers & Meagher (1997) remark that '...lower seed production may make it difficult for [the narrow-endemic] *Eupatorium resinsum* to colonize new habitats as frequently as [the widespread] *E. perfoliatum*.' Moreover, soil seed banks can buffer populations of rare species from loss of genetic diversity and against extinction (Fischer & Matthies, 1998; McCue & Holtsford, 1998). Although *S. shortii* invades new sites within its geographical range (Table 7), the chances of colonizing new areas and of maintaining its population via a soil seed bank are much smaller than those of *S. altissima*.

The rapid geographical expansion of *S. altissima* in Europe following naturalization has been explained by its high competitive and colonization abilities (Zwölfer, 1976). Initial colonization of a site by *S. altissima* involves establishment of genets from seeds, but subsequent development occurs mostly by production of ramets by clonal growth (Hartnett & Bazzaz, 1985a). *Solidago altissima* was first introduced to Europe as an ornamental plant around 1735, and the first observation of naturalization was about 1850. By 1950, a large portion of Europe was colonized by the species (Weber, 1998). Like many rare plants, *S. shortii* grows well and is vigorous in cultivation outside its native range (Table 2). The oldest record for cultivation of *S. shortii* is 1845 in Massachusetts (Beck *et al.*, 1999). In contrast to *S. shortii*, *S. altissima* was widely distributed and used by gardeners in Europe but no evidence implies multiple introductions at a large intensity or scale (Weber & Schmid, 1998). Nevertheless, there is no indication that *S. shortii* has become naturalized in Massachusetts or at any other site of cultivation.

Plants of *S. shortii* possess more morphological variation than those of *S. altissima* growing within the geographical range of *S. shortii* (Beck *et al.*, 2001). Measuring morphological or phenotypic variation of a plant species is one

method of assessing genetic variation. The advantage of studying morphological variation is that the phenotypic characters are often ecologically adaptive (Schaal *et al.*, 1991). Moreover, *S. shortii* has substantial allozyme variation (Calie *et al.*, 2001; P.J. Calie, personal communication). While there may be a slight reduction in allozyme variation in other rare species relative to their widespread congeners, it is not the case that rare species are confined to low levels of diversity (Gitzendanner & Soltis, 2000). The high morphological and allozyme variation of *S. shortii* excludes genetic variation as a major influence in the rarity of this species.

Habitat specificity, particularly edaphic and climatic factors, has been implicated as a cause of rarity (Mason, 1946; Prober & Austin, 1991). However, *S. shortii* (1) grows in a variety of habitat types (Buchele *et al.*, 1989), (2) does not occur with a coherent group of plant species (Buchele *et al.*, 1992b), (3) germinates and grows over a broad range of soil and light conditions (Table 2) and (4) can be cultivated in climates and in edaphic and topographic situations different from those in its native range (Table 2). The environmental conditions in which *S. shortii* has been germinated and grown occur throughout eastern North America, and especially within the range of *S. altissima*.

Recently, Bruelheide & Scheidel (1999) reported a case in which herbivory played a major role in limiting the distribution of the rare plant *Arnica montana* in Germany. This species is restricted to high elevations because the impact of slug herbivory increases with decreasing altitude. In the case of *S. shortii*, herbivory (by insects and snails) does not appear to be important in restricting the range because levels of it are consistently low (Table 6). In contrast, levels of herbivory by insects and by snails on *S. altissima* plants can be high, especially during outbreaks of insects. Insect herbivory can dramatically limit the abundance of *S. altissima* over many years (Carson & Root, 2000). Moreover, herbivory decreases the size of *S. altissima*, which can delay or prevent the species from reducing understory light levels, and thus reduces its competitive effects. Low herbivory on *S. shortii* would be consistent with the hypothesis that rarity may offer an escape from attack by making the species less 'apparent' to be found by a herbivore (*sensu* Feeny, 1976).

Solidago shortii is maintained on the landscape in space and time via its adaptation to xeric sites that are relatively free of competition. However, many of the population sites of *S. shortii* are subject to invasion by woody plants, and thus require disturbance to maintain an early successional stage. *Solidago shortii* tolerates various types of disturbances, but the frequency by which disturbances can occur without declines in population vigor is unclear (Table 7). Médail & Verlaque (1997) reported that endemic taxa of south-eastern France and of Corsica also could tolerate disturbances (fires, erosion, grazing) as long as the disturbances reduced competition and did not occur too frequently. Other studies, as well, have found that populations of rare species occur in habitats subjected to disturbance (Pavlovic, 1994; Byers & Meagher, 1997; Holderegger, 1997). Like other successional

plants, *S. altissima* requires disturbance for establishment and maintenance of its populations, but too frequent disturbance decreases vigor (Table 7). Disturbance of the landscape and metapopulation dynamics undoubtedly are important factors in the establishment and maintenance of *S. shortii* populations, and in preventing it from going extinct in the wild.

Solidago shortii belongs to the same subsection of the genus as *S. altissima* (Nesom, 1993; J.C. Semple, personal communication). However, the evolutionary relationship between *S. shortii* and *S. altissima*, or other members of the *S. canadensis* complex, is unclear. Whether *S. shortii* is a neo- or palaeo-endemic needs to be investigated in a phylogenetic framework. It seems reasonable to assume that *S. shortii* is a neoendemic because (1) the species has a highly localized distribution, and (2) many other species endemic to cedar glades, or to glade-like (rocky/shallow soil) habitats, in south-eastern United States are relatively young (Baskin & Baskin, 1986; Delcourt *et al.*, 1986; J.C. Semple, personal communication). Thus, *S. shortii* probably has had insufficient time to expand its range. On the other hand, *S. shortii* is not well suited for migration to, or colonization of, habitats outside its present-day range, because it has poor competitive and colonization abilities.

ACKNOWLEDGMENTS

We thank Pat Calie, Tim Carr, Kayri Havens, Richard Root and John Semple for providing information used in our paper and/or for reviewing portions of the manuscript.

REFERENCES

- Abrahamson, W.G., Anderson, S.S. & McCrea, K.D. (1988) Effects of manipulation of plant carbon nutrient balance on tall goldenrod resistance to a gallmaking herbivore. *Oecologia*, **77**, 302–306.
- Abrahamson, W.G., Anderson, S.S. & McCrea, K.D. (1991) Clonal integration: nutrient sharing between sister ramets of *Solidago altissima* (Compositae). *American Journal of Botany*, **78**, 1508–1514.
- Abrahamson, W.G., Armbruster, P.O. & Maddox, G.D. (1983) Numerical relationships of the *Solidago altissima* stem gall insect-parasitoid guild food chain. *Oecologia*, **58**, 351–357.
- Abrahamson, W.G. & Caswell, H. (1982) On the comparative allocation of biomass, energy, and nutrients in plants. *Ecology*, **63**, 982–991.
- Abrahamson, W.G. & Gadgil, M. (1973) Growth form and reproductive effort in goldenrods (*Solidago*, Compositae). *American Naturalist*, **107**, 651–661.
- Abrahamson, W.G. & McCrea, K.D. (1985) Seasonal nutrient dynamics of *Solidago altissima* (Compositae). *Bulletin of the Torrey Botanical Club*, **112**, 414–420.
- Abrahamson, W.G. & Weis, A.E. (1997) *Evolutionary ecology across three trophic levels: goldenrods, gallmakers, and natural enemies*. Princeton University Press, Princeton, NJ.
- Armesto, J.J. & Pickett, S.T.A. (1986) Removal experiments to test mechanisms of plant succession in oldfields. *Vegetatio*, **66**, 85–93.

- Auld, B.A. & Medd, R.W. (1987) *Weeds: an illustrated botanical guide to the weeds of Australia*. Inkata Press, Melbourne.
- Baskin, J.M. & Baskin, C.C. (1985) Photosynthetic pathway in 14 southeastern cedar glade endemics, as revealed by leaf anatomy. *American Midland Naturalist*, **114**, 205–208.
- Baskin, J.M. & Baskin, C.C. (1986) Distribution and geographical/evolutionary relationships of cedar glade endemics in southeastern United States. *Association of Southeastern Biologists Bulletin*, **33**, 138–154.
- Baskin, J.M. & Baskin, C.C. (1988) Endemism in rock outcrop plant communities of unglaciated eastern United States: an evaluation of the roles of the edaphic, genetic and light factors. *Journal of Biogeography*, **15**, 829–840.
- Baskin, J.M., Snyder, K.M., Walck, J.L. & Baskin, C.C. (1997) The comparative autecology of endemic, globally-rare and geographically-widespread, common plant species: three case studies. *Southwestern Naturalist*, **42**, 384–399.
- Beaudry, J.R. (1958) Studies on *Solidago* L.-III. Megasporengesis, development of the megagametophyte and mode of reproduction in *Solidago altissima* L. *Proceedings of the Genetics Society of Canada*, **3**, 7–14.
- Beck, J.B., Naczi, R.F.C. & Calie, P.J. (1999) Lectotypification of *Solidago shortii* (Asteraceae), with considerations of the historical and intellectual circumstances surrounding the original species description in Torrey and Gray's *Flora of North America*. *Harvard Papers in Botany*, **4**, 417–427.
- Beck, J.B., Naczi, R.F.C. & Calie, P.J. (2001) Insights into the species delineation and population structure of *Solidago shortii* (Asteraceae) through morphometric analysis. *Rhodora*, **103**, 151–171.
- Bevill, R.L. & Louda, M. (1999) Comparisons of related rare and common species in the study of plant rarity. *Conservation Biology*, **13**, 499–508.
- Bolkhovskikh, Z., Grif, V., Matvejeva, T. & Zakharyeva, O. (1969) *Chromosome numbers of flowering plants*. Academy of Sciences of the USSR, V.L. Komarov Botanical Institute, 'Nauka', Leningrad.
- Bostick, P.E. (1967) A geobotanical investigation of Chandler Mountain, St Clair Co., Alabama. *Castanea*, **32**, 133–154.
- Bradbury, I.K. & Hofstra, G. (1976) The partitioning of net energy resources in two populations of *Solidago canadensis* during a single developmental cycle in southern Ontario. *Canadian Journal of Botany*, **54**, 2449–2456.
- Bradbury, I.K. & Hofstra, G. (1977) Assimilate distribution patterns and carbohydrate concentration changes in organs of *Solidago canadensis* during an annual developmental cycle. *Canadian Journal of Botany*, **55**, 1121–1127.
- Bradshaw, A.D. (1987) Comparison – its scope and limits. *New Phytologist*, **106** (Suppl.), 3–21.
- Brady, N.C. (1990) *The nature and properties of soils*, 10th edn. Macmillan, New York.
- Bruelheide, H. & Scheidel, U. (1999) Slug herbivory as a limiting factor for the geographical range of *Arnica montana*. *Journal of Ecology*, **87**, 839–848.
- Buchele, D.E., Baskin, J.M. & Baskin, C.C. (1989) Ecology of the endangered species *Solidago shortii*. I. Geography, populations, and physical habitat. *Bulletin of the Torrey Botanical Club*, **116**, 344–355.
- Buchele, D.E., Baskin, J.M. & Baskin, C.C. (1991) Ecology of the endangered species *Solidago shortii*. II. Ecological life cycle. *Bulletin of the Torrey Botanical Club*, **118**, 281–287.
- Buchele, D.E., Baskin, J.M. & Baskin, C.C. (1992a) Ecology of the endangered species *Solidago shortii*. IV. Pollination ecology. *Bulletin of the Torrey Botanical Club*, **119**, 137–141.
- Buchele, D.E., Baskin, J.M. & Baskin, C.C. (1992b) Ecology of the endangered species *Solidago shortii*. V. Plant associates. *Bulletin of the Torrey Botanical Club*, **119**, 208–213.
- Burton, P.J. & Bazzaz, F.A. (1995) Ecophysiological responses of tree seedlings invading different patches of old-field vegetation. *Journal of Ecology*, **83**, 99–112.
- Byers, D.L. & Meagher, T.R. (1997) A comparison of demographic characteristics in a rare and a common species of *Eupatorium*. *Ecological Applications*, **7**, 519–530.
- Cain, M.L. (1990) Patterns of *Solidago altissima* ramet growth and mortality: the role of below-ground ramet connections. *Oecologia*, **82**, 201–209.
- Cain, M.L., Carson, W.P. & Root, R.B. (1991) Long-term suppression of insect herbivores increases the production and growth of *Solidago altissima* rhizomes. *Oecologia*, **88**, 251–257.
- Calie, P.J., Seltsam, N., Denham, A.T. & Ford, B.A. (2001) Genetic diversity present in the restricted endemic *Solidago shortii* (Asteraceae). *Abstracts of the Botanical Society of America, Botany 2001 Meeting Held 12–16 August 2001, Albuquerque, New Mexico*, p. 52.
- Carson, W.P. & Root, R.B. (2000) Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecological Monographs*, **70**, 73–99.
- Cates, R.G. & Orians, G.H. (1975) Successional status and the palatability of plants to generalized herbivores. *Ecology*, **56**, 410–418.
- Cathey, H.M. (1990) *Plant hardiness zone map*. US Department of Agriculture, Agricultural Research Service Miscellaneous Publication no. 1475.
- Collins, B. & Wein, G. (1998) Soil resource heterogeneity effects on early succession. *Oikos*, **82**, 238–245.
- Connors, I.L. (1967) *An annotated index of plant diseases in Canada and fungi recorded on plants in Alaska, Canada and Greenland*. Publication no. 1251, Canada Department of Agriculture, Queen's Printer, Ottawa, Canada.
- Cornelius, R. (1990a) The strategies of *Solidago canadensis* L. in relation to urban habitats. I. Resource requirements. *Acta Oecologica*, **11**, 19–34.
- Cornelius, R. (1990b) The strategies of *Solidago canadensis* L. in relation to urban habitats. III. Conformity to habitat dynamics. *Acta Oecologica*, **11**, 301–310.
- Cornelius, R. & Faensen-Thiebes, A. (1990) The strategies of *Solidago canadensis* L. in relation to urban habitats. II. Competitive ability. *Acta Oecologica*, **11**, 145–153.
- Croat, T. (1972) *Solidago canadensis* complex of the Great Plains. *Brittonia*, **24**, 317–326.
- Delcourt, H.R., Delcourt, P.A., Wilkins, G.R. & Smith, E.N. Jr (1986) Vegetational history of the cedar glades regions of Tennessee, Kentucky, and Missouri during the past 30,000 years. *Association of Southeastern Biologists Bulletin*, **33**, 128–137.

- DeLucia, E.H., Sheno, H.D., Naidu, S.L. & Day, T.A. (1991) Photosynthetic symmetry of sun and shade leaves of different orientations. *Oecologia*, **87**, 51–57.
- Dhillon, S.S. & Friese, C.F. (1994) The occurrence of mycorrhizas in prairies: application to ecological restoration. *Spirit of the Land, Our prairie legacy. Proceedings of the 13th North American Prairie Conference* (eds R.G. Wickett, P.D. Lewis, A. Woodliffe and P. Pratt), pp. 103–114. Department of Parks and Recreation, Windsor, Ontario.
- Egli, P. & Schmid, B. (1999) Relationships between leaf nitrogen and limitations of photosynthesis in canopies of *Solidago altissima*. *Acta Oecologica*, **20**, 559–570.
- Farr, D.F., Bills, G.F., Chamuris, G.P. & Rossman, A.Y. (1989) *Fungi on plants and plant products in the United States*. APS Press, St Paul, MN.
- Feeny, P. (1976) Plant apparency and chemical defense. *Recent Advances in Phytochemistry*, **10**, 1–40.
- Fiedler, P.L. (1986) Concepts of rarity in vascular plant species, with special reference to the genus *Calochortus* Pursh (Liliaceae). *Taxon*, **35**, 502–518.
- Fiedler, P.L. (1987) Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). *Journal of Ecology*, **75**, 977–995.
- Fiedler, P.L. (1995) Rarity in the California flora: new thoughts on old ideas. *Madroño*, **42**, 127–141.
- Fischer, M. & Matthies, D. (1998) Experimental demography of the rare *Gentianella germanica*: seed bank formation and microsite effects on seedling establishment. *Ecography*, **21**, 269–278.
- Fontes, E.M.G., Habeck, D.H. & Slansky, F. Jr (1994) Phytophagous insects associated with goldenrods (*Solidago* spp.) in Gainesville, Florida. *Florida Entomologist*, **77**, 209–221.
- Gangwere, S.K. (1961) A monograph on food selection in Orthoptera. *Transactions of the American Entomological Society*, **87**, 67–230.
- Gibson, D.J. (1989) Hulbert's study of factors effecting botanical composition of tallgrass prairie. *Prairie pioneers: ecology, history and culture. Proceedings of the 11th North American Prairie Conference* (eds T.B. Bragg and J. Stubbendieck), pp. 115–133. University of Nebraska Printing, Lincoln.
- Gibson, D.J., Seastedt, T.R. & Briggs, J.M. (1993) Management practices in tallgrass prairie: large- and small-scale experimental effects on species composition. *Journal of Applied Ecology*, **30**, 247–255.
- Ginsberg, H.S. (1983) Foraging ecology of bees in an old field. *Ecology*, **64**, 165–175.
- Gitzendanner, M.A. & Soltis, P.S. (2000) Patterns of genetic variation in rare and widespread plant congeners. *American Journal of Botany*, **87**, 783–792.
- Goldberg, D.E. (1987) Neighborhood competition in an old-field plant community. *Ecology*, **68**, 1211–1223.
- Goldberg, D.E. (1988) Response of *Solidago canadensis* clones to competition. *Oecologia*, **77**, 357–364.
- Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist*, **139**, 771–801.
- Goldberg, D.E. & Werner, P.A. (1983) The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia*, **60**, 149–155.
- Grime, J.P. (1965) Comparative experiments as a key to the ecology of flowering plants. *Ecology*, **46**, 513–515.
- Grime, J.P. (1979) *Plant strategies and vegetation processes*. John Wiley and Sons, New York.
- Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative plant ecology: a functional approach to common British species*. Unwin-Hyman, London.
- Gross, K.L., Berner, T., Marschall, E. & Tomcko, C. (1983) Patterns of resource allocation among five herbaceous perennials. *Bulletin of the Torrey Botanical Club*, **110**, 345–352.
- Gross, R.S. & Werner, P.A. (1983) Relationships among flowering phenology, insect visitors, and seed-set of individuals: experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). *Ecological Monographs*, **53**, 95–117.
- Hanson, P.J. & Dixon, R.K. (1985) Allelopathic inhibition of northern red oak by interrupted fern and goldenrod. *Proceedings of the 5th Central Hardwood Forest Conference* (eds J.O. Dawson and K.A. Majerus), pp. 269–274. Department of Forestry, University of Illinois, Urbana-Champaign.
- Harling, G. (1951) Embryological studies in the Compositae. Part 3. Astereae. *Acta Horti Bergiani*, **16**, 73–120.
- Harrington, H.D. (1954) *Manual of the plants of Colorado*. Sage Books, Denver.
- Hartnett, D.C. (1990) Size-dependent allocation to sexual and vegetative reproduction in four clonal composites. *Oecologia*, **84**, 254–259.
- Hartnett, D.C. & Abrahamson, W.G. (1979) The effects of stem gall insects on life history patterns in *Solidago canadensis*. *Ecology*, **60**, 910–917.
- Hartnett, D.C. & Bazzaz, F.A. (1983) Physiological integration among intracolonial ramets in *Solidago canadensis*. *Ecology*, **64**, 779–788.
- Hartnett, D.C. & Bazzaz, F.A. (1985a) The regulation of leaf, ramet and genet densities in experimental populations of the rhizomatous perennial *Solidago canadensis*. *Journal of Ecology*, **73**, 429–443.
- Hartnett, D.C. & Bazzaz, F.A. (1985b) The genet and ramet population dynamics of *Solidago canadensis* in an abandoned field. *Journal of Ecology*, **73**, 407–413.
- Hartnett, D.C. & Bazzaz, F.A. (1985c) The integration of neighbourhood effects by clonal genets in *Solidago canadensis*. *Journal of Ecology*, **73**, 415–427.
- Hartnett, D.C., Hickman, K.R. & Walter, L.E.F. (1996) Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management*, **49**, 413–420.
- Heath, M.C. (1992) Host species specificity of the goldenrod rust fungus and the existence of rust resistance within some goldenrod species. *Canadian Journal of Botany*, **70**, 2461–2466.
- Hegde, S.G. & Ellstrand, N.C. (1999) Life history differences between rare and common flowering plant species of California and the British Isles. *International Journal of Plant Sciences*, **160**, 1083–1091.
- Hills, J.M. & Murphy, K.J. (1996) Evidence for consistent functional groups of wetland vegetation across a broad geographical range of Europe. *Wetlands Ecology and Management*, **4**, 51–63.

- Hills, J.M., Murphy, K.J., Pulford, I.D. & Flowers, T.H. (1994) A method for classifying European riverine wetland ecosystems using functional vegetation groups. *Functional Ecology*, **8**, 242–252.
- Hirose, T. (1971) Nitrogen turnover and dry-matter production of a *Solidago altissima* population. *Japanese Journal of Ecology*, **21**, 18–32.
- Hirose, T. (1974) On the phosphorus budget of a perennial herb *Solidago altissima* population. *Botanical Magazine (Tokyo)*, **87**, 89–98.
- Hirose, T. & Werger, M.J.A. (1987) Nitrogen use efficiency in instantaneous and daily photosynthesis of leaves in the canopy of a *Solidago altissima* stand. *Physiologia Plantarum*, **70**, 215–222.
- Holderregger, R. (1997) Intrapopulational size structure of the monocarpic species *Saxifraga mutata* and its relationship to succession. *Flora*, **192**, 151–156.
- Horner, J.D. & Abrahamson, W.G. (1999) Influence of plant genotype and early-season water deficits on oviposition preference and offspring performance in *Eurosta solidaginis* (Diptera: Tephritidae). *American Midland Naturalist*, **142**, 162–172.
- Houston, F.G. & Burrell, R.C. (1948) The isolation of inulin and an unidentified C₂₀ compound from the roots of *Solidago canadensis* L. *Archives of Biochemistry*, **16**, 299–300.
- Howe, H.F. (1994) Response of early- and late-flowering plants to fire season in experimental prairies. *Ecological Applications*, **4**, 121–133.
- Hunt, C.B. (1974) *Natural regions of the United States and Canada*. W.H. Freeman, San Francisco.
- Irwin, L.L. (1985) Foods of moose, *Alces alces*, and white-tailed deer, *Odocoileus virginianus*, on a burn in boreal forest. *Canadian Field-Naturalist*, **99**, 240–245.
- Ito, I., Kobayashi, K. & Yoneyama, T. (1998) Fate of dehydro-matricaria ester added to soil and its implications for the allelopathic effect of *Solidago altissima* L. *Annals of Botany*, **82**, 625–630.
- Iwaki, H., Takada, K. & Monsi, M. (1969) Studies on the dry matter production of *Solidago altissima* community. I. The plant biomass and annual net production. *Botanical Magazine (Tokyo)*, **82**, 215–225.
- Jastrow, J.D. & Miller, R.M. (1993) Neighbor influences on root morphology and mycorrhizal fungus colonization in tallgrass prairie plants. *Ecology*, **74**, 561–569.
- Jobin, A., Schaffner, U. & Nentwig, W. (1996) The structure of the phytophagous insect fauna on the introduced weed *Solidago altissima* in Switzerland. *Entomologia Experimentalis et Applicata*, **79**, 33–42.
- Johnson, S.R. & Knapp, A.K. (1995) The influence of fire on *Spartina pectinata* wetland communities in a northeastern Kansas tallgrass prairie. *Canadian Journal of Botany*, **73**, 84–90.
- Kelley, A.P. (1922) Plant indicators of soil type. *Soil Science*, **13**, 411–423.
- Kelley, A.D. & Bruns, V.F. (1975) Dissemination of weed seed by irrigation water. *Weed Science*, **23**, 486–493.
- Kelly, C.K. & Woodward, F.I. (1996) Ecological correlates of plant range size: taxonomies and phylogenies in the study of plant commonness and rarity in Great Britain. *Philosophical Transactions of the Royal Society of London B*, **351**, 1261–1269.
- Kline, V.M. (1986) Response of sweet clover (*Melilotus alba* Desr.) and associated prairie vegetation to seven experimental burning and mowing treatments. *The prairie: past, present and future. Proceedings of the 9th North American Prairie Conference* (eds G.K. Clambey and R.H. Pemble), pp. 149–152. Tri-College University Center for Environmental Studies, North Dakota State University, Fargo.
- Kruckeberg, A.R. & Rabinowitz, D. (1985) Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics*, **16**, 447–479.
- Küchler, A.W. (1964) *Potential natural vegetation of the conterminous United States*. p. 116 + map. Special Publication no. 36. American Geographical Society, New York.
- Kunin, W.E. & Gaston, K.J. (1993) The biology of rarity: patterns, causes and consequences. *Trends in Ecology and Evolution*, **8**, 298–301.
- Larcher, W. (1995) *Physiological plant ecology: ecophysiology and stress physiology of functional groups*, 3rd edn. Springer-Verlag, New York.
- Li, H.L. (1978) Compositae. *Flora of Taiwan*, Vol. 4 (eds H.L. Li, T.S. Liu, T.C. Huang, T. Koyama and C.E. DeVol), pp. 768–965. Epoch Publishing Co, Taipei, Taiwan.
- Maddox, G.D. & Root, R.B. (1990) Structure of the encounter between goldenrod (*Solidago altissima*) and its diverse insect fauna. *Ecology*, **71**, 2115–2124.
- Maddox, G.D., Cook, R.E., Wimberger, P.H. & Gardescu, S. (1989) Clone structure in four *Solidago altissima* (Asteraceae) populations: rhizome connections within genotypes. *American Journal of Botany*, **76**, 318–326.
- Martel, J. (1998) Plant-mediated effects of soil salinity on a gall-inducing caterpillar *Epiblema scudderiana* (Lepidoptera: Tortricidae) and the influence of feeding guild. *European Journal of Entomology*, **95**, 545–557.
- Martin, C.E., Harris, F.S. & Norman, F.J. (1991) Ecophysiological responses of C3 forbs and C4 grasses to drought and rain on a tallgrass prairie in northeastern Kansas. *Botanical Gazette*, **152**, 257–262.
- Mason, H.L. (1946) The edaphic factor in narrow endemism. I. The nature of environmental influences. *Madroño*, **8**, 209–226.
- Matlack, G.R. (1987) Diaspore size, shape, and fall behavior in wind-dispersed plant species. *American Journal of Botany*, **74**, 1150–1160.
- McCue, K.A. & Holtsford, T.P. (1998) Seed bank influences on genetic diversity in the rare annual *Clarkia springvillensis* (Onagraceae). *American Journal of Botany*, **85**, 30–36.
- McEvoy, M.V. (1988) *The gall insects of goldenrods (Compositae: Solidago) with a revision of the species of Rhopalomyia (Diptera: Cecidomyiidae)*. MS Thesis, Cornell University, Ithaca, NY.
- Meagher, T.R., Antonovics, J. & Primack, R. (1978) Experimental ecological genetics in *Plantago*. III. Genetic variation and demography in relation to survival of *Plantago cordata*, a rare species. *Biological Conservation*, **14**, 243–257.
- Médail, F. & Verlaque, R. (1997) Ecological characteristics and rarity of endemic plants from southeast France and Corsica: implications for biodiversity conservation. *Biological Conservation*, **80**, 269–281.

- Medley, M. (1993) *An annotated catalog of the known or reported vascular flora of Kentucky*. PhD Thesis, University of Louisville, Louisville, KY.
- Melville, M.R. & Morton, J.K. (1982) A biosystematic study of the *Solidago canadensis* (Compositae) complex. I. The Ontario populations. *Canadian Journal of Botany*, **60**, 976–997.
- Messina, F.J. (1982) Food plant choices of two goldenrod beetles: relation to plant quality. *Oecologia*, **55**, 342–354.
- Meyer, G.A. (1998) Mechanisms promoting recovery from defoliation in goldenrod (*Solidago altissima*). *Canadian Journal of Botany*, **76**, 450–459.
- Meyer, G.A. & Root, R.B. (1993) Effects of herbivorous insects and soil fertility on reproduction of goldenrod. *Ecology*, **74**, 1117–1128.
- Meyer, A.H. & Schmid, B. (1999a) Seed dynamics and seedling establishment in the invading perennial *Solidago altissima* under different experimental treatments. *Journal of Ecology*, **87**, 28–41.
- Meyer, A.H. & Schmid, B. (1999b) Experimental demography of the old-field perennial *Solidago altissima*: the dynamics of the shoot population. *Journal of Ecology*, **87**, 17–27.
- Nakatsubo, T., Kaniyu, M., Nakagoshi, N. & Horikoshi, T. (1994) Distribution of vesicular-arbuscular mycorrhizae in plants growing in a river floodplain. *Bulletin of Japanese Society of Microbial Ecology*, **9**, 109–117.
- Nesom, G.L. (1989) The *Solidago canadensis* (Asteraceae: Astereae) complex in Texas with a new species from Texas and México. *Phytologia*, **67**, 441–450.
- Nesom, G.L. (1993) Taxonomic infrastructure of *Solidago* and *Oligoneuron* (Asteraceae: Astereae) and observations on their phylogenetic position. *Phytologia*, **75**, 1–44.
- Noble, R.E. & Murphy, P.K. (1975) Short term effects of prolonged backwater flooding on understory vegetation. *Cas-tanea*, **40**, 228–238.
- Nordstrom, L.O. (1984) Interspecific variation in the mineral element composition of seral herbs. *Journal of Biogeography*, **11**, 235–242.
- Numata, M. & Asano, S. (1969) *Biological flora of Japan*, Vol. 1 *Sympetalae-1*. Tsukiji Shokan, Tokyo.
- Parrish, J.A.D. & Bazzaz, F.A. (1979) Difference in pollination niche relationships in early and late successional plant communities. *Ecology*, **60**, 597–610.
- Pavlik, B.M., Ferguson, N. & Nelson, M. (1993) Assessing limitations on the growth of endangered plant populations. II. Seed production and seed bank dynamics of *Erysimum capitatum* ssp. *angustatum* and *Oenothera deltoides* ssp. *howellii*. *Biological Conservation*, **65**, 267–278.
- Pavlovic, N.B. (1994) Disturbance-dependent persistence of rare plants: anthropogenic impacts and restoration implications. *Restoration of endangered species: conceptual issues, planning, and implementation* (eds M.L. Bowles and C.J. Whelan), pp. 159–193. Cambridge University Press, Cambridge.
- Pilson, D. (1992a) Relative resistance of goldenrod to aphid attack: changes through the growing season. *Evolution*, **46**, 1230–1236.
- Pilson, D. (1992b) Aphid distribution and the evolution of goldenrod resistance. *Evolution*, **46**, 1358–1372.
- Platt, W.J. (1975) The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs*, **45**, 285–305.
- Platt, W.J. & Weis, I.M. (1977) Resource partitioning and competition within a guild of fugitive prairie plants. *American Naturalist*, **111**, 479–513.
- Pollard, C.J. & Amuti, K.S. (1981) Fructose oligosaccharides: possible markers of phylogenetic relationships among dicotyledonous plant families. *Biochemical Systematics and Ecology*, **9**, 69–78.
- Potvin, M.A. & Werner, P.A. (1983) Water use physiology of co-occurring goldenrods (*Solidago juncea* and *S. canadensis*): implications for natural distributions. *Oecologia*, **56**, 148–152.
- Potvin, M.A. & Werner, P.A. (1984) Seasonal patterns in water relations of two species of goldenrods (*Solidago*) grown on an experimental soil moisture gradient. *Bulletin of the Torrey Botanical Club*, **111**, 171–178.
- Prober, S.M. & Austin, M.P. (1991) Habitat peculiarity as a cause of rarity in *Eucalyptus paliformis*. *Australian Journal of Ecology*, **16**, 189–205.
- Raju, M.V.S., Coupland, R.T. & Steeves, T.A. (1966) On the occurrence of root buds on perennial plants in Saskatchewan. *Canadian Journal of Botany*, **44**, 33–37 + plate 1.
- Reader, R.J. (1993) Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology*, **81**, 169–175.
- Rebele, F. (1992) Colonization and early succession on anthropogenic soils. *Journal of Vegetation Science*, **3**, 201–208.
- Robertson, C. (1928) *Flowers and insects: lists of visitors of four hundred and fifty-three flowers*. Science Press, Carlinville, IL.
- Root, R.B. (1996) Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. *Ecology*, **77**, 1074–1087.
- Root, R.B. & Cappuccino, N. (1992) Patterns in population change and the organization of the insect community associated with goldenrod. *Ecological Monographs*, **62**, 393–420.
- Rösch, H., Van Rooyen, M.W. & Theron, G.K. (1997) Predicting competitive interactions between pioneer plant species by using plant traits. *Journal of Vegetation Science*, **8**, 489–494.
- Schaal, B.A., Leverich, W.J. & Rogstad, S.H. (1991) A comparison of methods for assessing genetic variation in plant conservation biology. *Genetics and conservation of rare plants* (eds D.A. Falk and K.E. Holsinger), pp. 123–134. Oxford University Press, New York.
- Schieving, F., Werger, M.J.A. & Hirose, T. (1992) Canopy structure, nitrogen distribution and whole canopy photosynthetic carbon gain in growing and flowering stands of tall herbs. *Vegetatio*, **102**, 173–181.
- Schmid, B. (1994) Effects of genetic diversity in experimental stands of *Solidago altissima* – evidence for the potential role of pathogens as selective agents in plant populations. *Journal of Ecology*, **82**, 165–175.
- Schmid, B. & Bazzaz, F.A. (1990) Plasticity in plant size and architecture in rhizome-derived vs. seed-derived *Solidago* and *Aster*. *Ecology*, **71**, 523–535.
- Schmid, B. & Bazzaz, F.A. (1992) Growth responses of rhizomatous plants to fertilizer application and interference. *Oikos*, **65**, 13–24.
- Schmid, B., Bazzaz, F.A. & Weiner, J. (1995) Size dependency of sexual reproduction and of clonal growth in two perennial plants. *Canadian Journal of Botany*, **73**, 1831–1837.

- Schmid, B. & Dolt, C. (1994) Effects of maternal and paternal environment and genotype on offspring phenotype in *Solidago altissima* L. *Evolution*, **48**, 1525–1549.
- Schmid, B., Miao, S.L. & Bazzaz, F.A. (1990) Effects of simulated root herbivory and fertilizer application on growth and biomass allocation in the clonal perennial *Solidago canadensis*. *Oecologia*, **84**, 9–15.
- Schmid, B., Puttick, G.M., Burgess, K.H. & Bazzaz, F.A. (1988) Correlations between genet architecture and some life history features in three species of *Solidago*. *Oecologia*, **75**, 459–464.
- Schmid, B. & Weiner, J. (1993) Plastic relationships between reproductive and vegetative mass in *Solidago altissima*. *Evolution*, **47**, 61–74.
- Schwabe, W.W. (1986) *Solidago*. *CRC handbook of flowering*, Vol. 5 (ed. A.H. Halevy), pp. 338–340. CRC Press, Boca Raton, FL.
- Schwegman, J.E. & Anderson, R.C. (1986) Effect of eleven years of fire exclusion on the vegetation of a southern Illinois barren remnant. *The prairie: past, present and future. Proceedings of the 9th North American Prairie Conference* (eds G. K. Clambey and R. H. Pemble), pp. 146–148. Tri-College University Center for Environmental Studies, North Dakota State University, Fargo.
- Scoggan, H.J. (1979) *The flora of Canada. Part 4 – Dicotyledoneae (Loasaceae to Compositae)*. National Museum of Natural Science, Publications in Botany no. 7, pp. 1117–1711. National Museums of Canada, Ottawa.
- Seaman, F., Bohlmann, F., Zdero, C. and Mabry, T.J. (1990) *Diterpenes of flowering plants: Compositae (Asteraceae)*. Springer-Verlag, New York.
- Semple, J.C. (1993) *Solidago*. *The Jepson manual: higher plants of California* (ed. J.C. Hickman), pp. 342–343. University of California Press, Berkeley.
- Semple, J.C. & Ringius, G.S. (1983) *The goldenrods of Ontario: Solidago L. and Euthamia Nutt.*, Series no. 26. University of Waterloo, Department of Biology, Waterloo, Ontario.
- Semple, J.C., Ringius, G.S., Leeder, C. & Morton, G. (1984) Chromosome numbers of goldenrods, *Euthamia* and *Solidago* (Compositae: Astereae). II. Additional counts with comments on cytogeography. *Brittonia*, **36**, 280–292.
- Semple, J.C., Zhang, J. & Xiang, C. (1993) Chromosome number determinations in fam. Compositae, tribe Astereae. V. Eastern North American taxa. *Rhodora*, **95**, 234–253.
- Sholes, O.D.V. (1981) Herbivory by species of *Trirhabda* (Coleoptera: Chrysomelidae) on *Solidago altissima* (Asteraceae): variation between years. *Proceedings of the Entomological Society of Washington*, **83**, 274–282.
- Silvertown, J. & Dodd, M. (1996) Comparing plants and connecting traits. *Philosophical Transactions of the Royal Society of London B*, **351**, 1233–1239.
- Stebbins, G.L. (1980) Rarity of plant species: a synthetic viewpoint. *Rhodora*, **82**, 77–86.
- Stoll, P., Egli, P. & Schmid, B. (1998) Plant foraging and rhizome growth patterns of *Solidago altissima* in response to mowing and fertilizer application. *Journal of Ecology*, **86**, 341–354.
- Thornthwaite, C.W. (1933) The climates of the Earth. *Geographical Review*, **23**, 433–440 + plate 5 (map).
- Tomkins, D.J. & Grant, W.F. (1974) Differential response of 14 weed species to seven herbicides in two plant communities. *Canadian Journal of Botany*, **52**, 525–533 + plate 1.
- Turner, J.A. (1928) Relation of the distribution of certain Compositae to the hydrogen-ion concentration of the soil. *Bulletin of the Torrey Botanical Club*, **55**, 199–213.
- Turner, C.L. & Knapp, A.K. (1996) Responses of a C₄ grass and three C₃ forbs to variation in nitrogen and light in tall grass prairie. *Ecology*, **77**, 1738–1749.
- Turner, C.L., Kneisler, J.R. & Knapp, A.K. (1995) Comparative gas exchange and nitrogen responses of the dominant C₄ grass *Andropogon gerardii* and five C₃ forbs to fire and topographic position in tallgrass prairie during a wet year. *International Journal of Plant Sciences*, **156**, 216–226.
- Turner, B.L. & Zhao, Z. (1992) Documented chromosome numbers 1992: 2. Miscellaneous USA and Mexican species, mostly Asteraceae. *Sida*, **15**, 147–150.
- Uriarte, M. (2000) Interactions between goldenrod (*Solidago altissima* L.) and its insect herbivore (*Trirhabda virgata*) over the course of succession. *Oecologia*, **122**, 521–528.
- US Department of Agriculture (1960) *Index of plant diseases in the United States*. Agriculture Handbook no. 165. US Department of Agriculture, Washington, DC.
- Walck, J.L. (1998) *Comparative autecology of the narrow-endemic Solidago shortii and two of its geographically-widespread congeners: an investigation into the causes of plant rarity and endemism*. PhD Thesis, University of Kentucky, Lexington.
- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1997a) A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 1. Germination phenology and effect of cold stratification on germination. *Seed Science Research*, **7**, 47–58.
- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1997b) A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 4. Role of soil moisture in regulating germination. *Seed Science Research*, **7**, 303–309.
- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1997c) A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 5. Effect of dry storage on after-ripening and survivorship. *Seed Science Research*, **7**, 311–318.
- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1997d) A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 2. Germination responses of buried seed in relation to seasonal temperature cycles. *Seed Science Research*, **7**, 209–220.
- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1997e) A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 3. Photoecology of germination. *Seed Science Research*, **7**, 293–301.
- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1998) A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 6. Seed bank. *Seed Science Research*, **8**, 65–74.

- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1999a) Relative competitive abilities and growth characteristics of a narrowly endemic and a geographically widespread *Solidago* species (Asteraceae). *American Journal of Botany*, **86**, 820–828.
- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1999b) Roles of succession, light, nutrients and disturbance on population vigor and maintenance of the rare plant *Solidago shortii* (Asteraceae). *Plant Ecology*, **145**, 133–147.
- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1999c) Ecology of the endangered species *Solidago shortii*. VII. Survivorship and flowering, and comparison with common, geographically-widespread *Solidago* species. *Journal of the Torrey Botanical Society*, **126**, 124–132.
- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1999d) Effects of competition from introduced plants on establishment, survival, growth and reproduction of the rare plant *Solidago shortii* (Asteraceae). *Biological Conservation*, **88**, 213–219.
- Walck, J.L., Baskin, J.M. & Baskin, C.C. (1999e) Ecology of the endangered species *Solidago shortii*. VI. Effects of habitat type, leaf litter and soil type on seed germination. *Journal of the Torrey Botanical Society*, **126**, 117–123.
- Weaver, J.E. (1919) *The ecological relations of roots*. Publication no. 286. Carnegie Institution of Washington, Washington, DC.
- Weaver, J.E. & Hansen, W.W. (1941) *Native midwestern pastures: their origin, composition, and degeneration*. Nebraska Conservation Bulletin no. 22. University of Nebraska, Lincoln.
- Weaver, J.E., Stoddart, L.A. & Noll, W. (1935) Response of the prairie to the great drought of 1934. *Ecology*, **16**, 612–629.
- Weber, E. (1997) Morphological variation of the introduced perennial *Solidago canadensis* L. *sensu lato* (Asteraceae) in Europe. *Botanical Journal of the Linnean Society*, **123**, 197–210.
- Weber, E. (1998) The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *Journal of Biogeography*, **25**, 147–154.
- Weber, E. (2000) Biological flora of central Europe: *Solidago altissima* L. *Flora*, **195**, 123–134.
- Weber, E. & Schmid, B. (1998) Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. *American Journal of Botany*, **85**, 1110–1121.
- Werner, P.A. & Platt, W.J. (1976) Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). *American Naturalist*, **110**, 959–971.
- Werner, P.A., Bradbury, I.K. & Gross, R.S. (1980) The biology of Canadian weeds. 45. *Solidago canadensis* L. *Canadian Journal of Plant Science*, **60**, 1393–1409.
- Witkowski, E.T.F. & Lamont, B.B. (1997) Does the rare *Banksia goodii* have inferior vegetative, reproductive or ecological attributes compared with its widespread co-occurring relative *B. gardneri*? *Journal of Biogeography*, **24**, 469–482.
- Worthley, E.G., Schott, C.D. & Hauptmann, G.A. (1967) Toxicity of some goldenrods. *Economic Botany*, **21**, 238–242.
- Yura, H. (1997) Comparative ecophysiology of *Chrysanthemum pacificum* Nakai and *Solidago altissima* L. 1. Why *S. altissima* cannot be established on the seashore. *Ecological Research*, **12**, 313–323.
- Zimmerman, U.D. & Kucera, C.L. (1977) Effects of composition changes on productivity and biomass relationships in tallgrass prairie. *American Midland Naturalist*, **97**, 465–469.
- Zwölfer, H. (1976) The goldenrod problem: possibilities for a biological weed control project in Europe. *Plant Health Newsletter*, **81**, 9–18.

BIOSKETCHES

Jeffrey Walck is an Assistant Professor at Middle Tennessee State University. His research interests include the ecology, biogeography and evolution of rare plant species. In addition, he works on the conservation management of invasive species and rare species/ecosystems, particularly rock outcrop communities.

Jerry Baskin is a Professor at the University of Kentucky. His research interests include seed germination ecology, biology of rare plants and ecology of cedar glades and barrens. He recently coedited a book (with R.C. Anderson and J.S. Fralish) entitled *Savannas, barrens, and rock outcrop plant communities of North America* (Cambridge University Press, 1999).

Carol Baskin is a Professor at the University of Kentucky. Her interests include the life cycle ecology of herbaceous plants, particularly the ecology, biogeography and evolution of seed germination. She recently published a book (with J. Baskin) entitled *Seeds: ecology, biogeography, and evolution of dormancy and germination* (Academic Press, 1998).