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RELATIVE COMPETITIVE ABILITIES AND GROWTH CHARACTERISTICS OF A NARROWLY ENDEMIC AND A GEOGRAPHICALLY WIDESPREAD SOLIDAGO SPECIES (ASTERACEAE)¹

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Relative competitive ability and growth characteristics of the narrow endemic *Solidago shortii* were compared to those of the geographically widespread *S. altissima*. Competition and growth studies were conducted over the entire growing season in an ambient-temperature greenhouse, using a 3:1 (v/v) native limestone soil/river sand mixture. Results from a de Wit replacement series experiment (relative yield, relative yield total, plant height, aggressivity values) with *S. shortii*, *S. altissima*, and *Festuca arundinacea* (common competitor) suggested the following competitive hierarchy: *S. altissima = F. arundinacea > S. shortii*. Using classical growth analysis, we found that the competitive hierarchy was related closely to components of plant size (dry mass, height, leaf area, leaf area duration) and not to relative growth rate or any of its components (net assimilation rate, leaf area ratio, leaf weight ratio, specific leaf area). *Solidago shortii* allocated proportionately more dry mass to roots (but not to rhizomes) and had significantly greater root/shoot and (root + rhizome)/shoot ratios than did *S. altissima*. Thus, while the morphological traits of *S. shortii* enable it to tolerate drier habitats than *S. altissima*, in moist sites *S. shortii* easily would be overtopped and shaded out by *S. altissima*. Low competitive ability may be one of several factors contributing to the narrow endemism of *S. shortii*.

Key words: Asteraceae; competition; endemism; growth analysis; rare plant species; Solidago altissima; Solidago shortii.

Competitive interactions occur at relatively high frequencies in natural communities (Connell, 1983; Schoener, 1983; Goldberg and Barton, 1992). Distribution patterns, relative abundances, and diversity of species, and thus community structure, are influenced strongly by competition (Keddy, 1990; Goldberg and Barton, 1992). As such, competitive ability could be expected, as suggested first by Griggs (1940), to play an important role in habitat requirements and/or geographic ranges of narrowly endemic (rare) plant species (sensu Kruckeberg and Rabinowitz, 1985). Indeed, Baskin and Baskin (1988) concluded that interspecific competition for light was the single most important proximal cause of plant endemism in nonforested rock outcrop vegetation types in unglaciated eastern United States and that special edaphic requirements or lack of genetic variation per se were unimportant. Thus, narrow endemics occur in habitats in which competition is of minor importance, as also suggested by other researchers (Gankin and Major, 1964; Médail and Verlaque, 1997).

Understanding the causes of narrow endemism is accomplished best by comparing closely related species to "control" for dissimilar life history characteristics and evolutionary histories (Karron, 1987). Several studies have investigated competitive abilities of narrow endemics, but in the majority of them the competitive ability of an endemic was tested against that of a noncongener: annual or perennial grass (Cotter and Platt, 1959; Rollins, 1963; Breeden, 1968; Caudle, 1968; Ware, 1991) or of a mixture of garden/crop or weed species (Kruckeberg, 1954; Wiggs and Platt, 1962; Miller, 1977). In only a relatively few cases (Gottlieb and Bennett, 1983; Snyder, Baskin, and Baskin, 1994; also see Hart, 1980; Prober, 1992) has the competitive ability of a narrow endemic been tested against that of a geographically widespread, closely related congener. The Oregon endemic Stephanomeria malheurensis and its geographically widespread parental taxon S. exigua subsp. coronaria, which co-occur on a sagebrush-covered hillside of volcanic tuff, had equal competitive abilities (Gottlieb and Bennett, 1983). The middle Tennessee limestone cedar glade endemic Echinacea tennesseensis was a slightly better competitor than its closest extant relative E. angustifolia var. angustifolia, a geographically widespread North American prairie species (Snyder, Baskin, and Baskin, 1994).

Although most rock outcrop endemics grow only in shallow soils of the rock outcrop, several of them may invade disturbed (early successional) habitats with deep soil, such as roadsides, pastures, and fields, adjacent to outcrops (Cotter and Platt, 1959; Murdy, 1966; Baskin and Baskin, 1986). A case in point is the narrow endemic Solidago shortii T. & G. (Asteraceae). Plants of this species mostly grow in shallow (droughty), rocky limestone habitats, but they also have invaded relatively deep (moist) soil in old-field-like habitats at a few sites, near rock outcrops, that are maintained in an early-successional stage by anthropogenic disturbance (primarily mowing). Although the geographically widespread, weedy species S. altissima L. (S. canadensis L. var. scabra T. & G.) co-occurs with S. shortii in the old-fieldlike habitats, it is absent from, or occurs only sparingly with S. shortii, in the xeric, rocky sites (Buchele, Baskin, and Baskin, 1989, 1992; J.L. Walck, J.M. Baskin, and

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C.C. Baskin, personal observations). Therefore, we hypothesized that *S. shortii* is a poorer competitor relative to *S. altissima*, and thus *S. shortii* is restricted to rocky sites due to its relatively low competitive ability.

Solidago shortii is a federally endangered species with its present distribution limited to a 12.2 km² area in Fleming, Nicholas, and Robertson Counties, Kentucky, centered around Blue Licks Battlefield State Park in Robertson County. It occurs primarily in rocky (limestone) habitats: glade-like areas, pastures, powerline right of ways, roadside ledges, and redcedar and/or hardwood thickets/woodlands. Solidago shortii grows best in full sun, and thus its vigor declines as succession progresses to the thicket and woodland stages. The species was extirpated from the type locality on Rock Island at the Falls of the Ohio River near Louisville, Jefferson County, Kentucky, apparently over 100 yr ago (Buchele, Baskin, and Baskin, 1989). The type locality was a rocky (limestone) habitat maintained in a very early stage of primary succession by seasonal flooding (letter to Drs. J. Torrey and A. Gray from Dr. C. Short, 28 May 1842; Gray Herbarium Archives, Harvard University, Cambridge, Massachusetts).

Solidago altissima is native from Nova Scotia to northeastern Ontario and Montana south to Florida, eastern Texas, New Mexico, and Arizona, and from Nuevo León and Tamaulipas to Oaxaco, Mexico (Croat, 1972; Scoggan, 1979; Melville and Morton, 1982; Nesom, 1989). It is naturalized in Australia (Auld and Medd, 1987), Europe (Weber, 1997), Japan (Numata and Asano, 1969), Taiwan (Li, 1978), 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 nonmanaged roadsides (Werner, Bradbury, and Gross, 1980).

Solidago shortii and S. altissima are C_3 herbaceous polycarpic hemicryptophytes with vegetative reproduction by rhizomes and sexual reproduction by achenes (Werner, Bradbury, and Gross, 1980; Buchele, 1988; Buchele, Baskin, and Baskin, 1991). Both species are in the same subsection of Solidago (Nesom, 1993).

One objective of this study was to test the hypothesis that *S. shortii* is a poorer competitor than *S. altissima*. Using a de Wit (1960) replacement series (substitutive) design, *S. shortii* and *S. altissima* were grown in competition with each other, and in addition each species was grown in competition with a common competitor, *Festuca arundinacea* Schreb., a nonnative grass that occurs with both *Solidago* species in the Blue Licks area (Buchele, Baskin, and Baskin, 1992).

Although replacement series experiments determine the relative severities of inter- and intraspecific competition (Goldberg and Scheiner, 1993; Hamilton, 1994), they do not provide information on the underlying cause(s) of differences in competitive abilities of species (Keddy and Shipley, 1989). Therefore, a second objective of this study was to conduct a classical growth analysis in an attempt to identify morphological and/or physiological traits of the two *Solidago* species that may influence competitive ability. Although plant species often respond differently when grown together than when grown separately, a classical growth analysis on isolated individuals offers useful ecological information for understanding competitive interactions (Patterson, 1982; Radosevich, Holt, and Ghersa, 1997).

To our knowledge, this is the first study to compare the relative competitive abilities and/or growth characteristics of a narrow endemic of rocky habitats with a geographically widespread, co-occurring congener.

MATERIALS AND METHODS

General—Competition studies were conducted in the 1992 and 1994 growing seasons, and a growth study was conducted in the 1992 growing season, in an ambient-temperature greenhouse (no heating or airconditioning, windows open all year), located in Lexington, Kentucky. Temperatures in the greenhouse are about equal to those out of doors (Baskin and Baskin, 1985). Photosynthetic photon flux density (400–700 nm) at plant level in the greenhouse ranged from ~6 mol·m⁻²·d⁻¹ on cloudy days to 25 mol·m⁻²·d⁻¹ on clear days between March and October (Snyder, Baskin, and Baskin, 1994) (full sun = ~50 mol·m⁻²·d⁻¹ at summer solstice).

Soil used was a 3:1 (v/v) mixture of Ordovician-age Lexington Limestone-derived topsoil and river sand. *Solidago shortii, S. altissima,* and *F. arundinacea* grow on soil derived from the Lexington Limestone Formation in the Blue Licks area, as well as on soil derived from Ordovician-age Clays Ferry and Kope Formations (Buchele, 1988; Buchele, Baskin, and Baskin, 1989). Soil was kept at or near field capacity during the competition and growth studies. Plastic pots 14.5 cm (diameter) \times 15 cm (depth) and 14.5 cm \times 12 cm were used in the competition and growth studies, respectively. Pots in both studies were placed randomly on greenhouse benches.

Freshly matured achenes of both *S. shortii* (mean mass per achene = 0.370 mg) and *S. altissima* (0.070 mg) were collected on 10 November 1991 and 31 October 1993 in Fleming or Robertson Counties, Kentucky. The 1991 and 1993 achenes were sown on soil in 33 cm (width) \times 49 cm (length) \times 9 cm (depth) metal flats on 21 December 1991 and 12 December 1993, respectively, in the greenhouse. Caryopses of *F. arundinacea* (cv. KY-31) were obtained from Kentucky Garden Supply, Lexington, and sown on soil in metal flats on 4 May 1992 and on 26 March 1994. Soil was watered to field capacity each day, except if frozen in winter.

Seedlings of a species were about the same size when transplanted from the metal flats to pots filled with soil in both competition and growth studies. Leaf area for *S. shortii, S. altissima,* and *F. arundinacea* was about equal at the time when they were transplanted: *Solidago* species were \sim 4 mm tall with 4–5 leaves, and *F. arundinacea* 5 cm tall with 2–3 leaves. Plants that died after transplanting were replaced with ones of comparable size for the first 2 wk of each study, after which no plants needed to be replaced. Banrot[®] and Di-syston[®] were applied once to all plants in both studies to control damping-off fungi and aphids, respectively.

Competition studies—In the de Wit (1960) replacement series design, overall density is held constant, and proportions of each of two species grown together are varied from 0 to 100%. Further, experiments must be conducted at sufficiently high densities, and for time periods long enough, to be within the range of constant final yield (Connolly, 1986). Within this range, qualitative interpretations of replacement series indices would not change (Cousens and O'Neill, 1993).

To determine constant final yield of each species, monocultures of 1, 2, 4, 8, 12, and 16 plant(s) per pot were planted. Six replications were used per density. At a density of one, the seedling was placed at the center of the pot (Fig. 1A). At 2–16 seedlings per pot, seedlings were planted equally spaced from neighboring plants in a single ring, each seedling \sim 4 cm from the center of the pot. Seedlings of both *Solidago* species were transplanted on 1–4 May 1992 and those of *F. arundinacea* on 16 May 1992. Plants were harvested on 17–20 October 1992,





Fig. 1. Diagrams of the arrangement of plants in monoculture (A) or replacement series (B) (\bigcirc = species *i*, \bullet = species *j*)

 \sim 24 and 22 wk after transplanting *Solidago* species and *F. arundinacea*, respectively.

The density used in the replacement series was 12 plants per pot. This number was within the constant final yield, reached at 8–16 plants per pot for each species ($P \ge 0.2354$). Five proportions of two species (*i*, *j*) were used in the replacement series: 0*i*:12*j*, 3*i*:9*j*, 6*i*:6*j*, 9*i*:3*j*, and 12*i*:0*j*. The three species were grown in three mixture combinations: *S.* shortii \times *S.* altissima, *S.* shortii \times *F.* arundinacea, and *S.* altissima \times *F.* arundinacea. The planting design was similar to that in the monoculture planting density of 12 (Fig. 1B). Replications of six and ten pots per proportion were used in 1992 and 1994, respectively. Seedlings of all three species were transplanted on 22–26 May 1992 and on 24–28 April 1994. Plants were harvested on 1–5 November 1992 and on 20– 23 October 1994, ~23 and 26 wk after transplanting, respectively.

On the day plants were harvested, roots + rhizomes (washed free of soil) and shoots (including inflorescences) were dried separately at 80°C for 24 h and weighed. Height of the main shoot of each *Solidago* genet was recorded before they were dried in 1994.

Relative yield (RY) and relative yield total (RYT) were calculated for each species (Table 1). In replacement diagrams, actual RY of each species was plotted against the appropriate planting proportion. Expected RY for a species occurs when plants of this species grow equally well in mixture and in monoculture. Comparisons of actual RY of each species with their expected RY (diagonal dashed line in replacement diagrams) indicate (1) competition if the actual RY curve of one species is concave and that of the second convex, (2) niche differentiation if actual RY curves of both species are concave. If actual RY curves are linear (i.e., do not differ from expected), the ability of one species to interfere with the other is equivalent. Values of RYT of 1.0 imply that there is competition, >1.0 imply niche differentiation, and <1.0imply mutual antagonism (Harper, 1977).

Gain or loss of biomass due to interspecific competition was determined by calculating aggressivity (A) for each species (Table 1). An aggressive species will have a higher aggressivity index than a subordinate species (McGilchrist and Trenbath, 1971; Snyder, Baskin, and Baskin, 1994).

Actual RYs were compared to their expected values [0.25 (or 0.75)] for species *i* (or *j*) at 3*i*:9*j* proportion, 0.50 for species *i* and *j* at 6*i*:6*j*, and 0.75 (or 0.25) for species *i* (or *j*) at 9*i*:3*j*] and actual RYTs to their expected value (1.0) at each proportion by *t* tests. Mean aggressivity values among the species and mean height of genets for each Solidago species among proportions were compared by a one-way analysis of

TABLE 1. Formulae used in a replacement series experiment (Harper, 1977; Snyder, Baskin, and Baskin, 1994) and in a classical growth analysis (Hunt, 1978; Causton and Venus, 1981; Patterson, 1993).

Parameter		Formula	
Replacement series experiment ^a			
Relative yield of species i (RY _i)	=	$rac{Y_{ij}}{Y_{ii}}$	
Relative yield of species j (RY _j)	=	$rac{Y_{ji}}{Y_{jj}}$	
Relative yield total (RYT)	=	$\mathbf{R}\mathbf{Y}_i + \mathbf{R}\mathbf{Y}_j$	
Aggressivity of species $i(A_i)$	=	$rac{\mathbf{R}\mathbf{Y}_i}{p} - rac{\mathbf{R}\mathbf{Y}_j}{q}$	
Aggressivity of species $j(A_j)$	=	$\frac{\mathbf{R}\mathbf{Y}_j}{q} - \frac{\mathbf{R}\mathbf{Y}_i}{p}$	
Classical growth analysis ^b			
Relative growth rate (RGR) ^c	=	$\frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$	
Net assimilation rate (NAR) ^{c,d}	=	$\frac{W_2 - W_1}{A_2 - A_1} \times \frac{\log_e A_2 - \log_e A_1}{t_2 - t_1}$	
Leaf area ratio (LAR)	=	$\frac{A}{W}$	
Leaf weight ratio (LWR)	=	$rac{W_{ ext{leaf}}}{W}$	
Specific leaf area (SLA)	=	$rac{A}{W_{ ext{leaf}}}$	
Dry matter production (DMP) ^c	=	$W_2 - W_1$	
Leaf area duration (LAD) ^c	=	$\frac{(A_2 - A_1) \times (t_2 - t_1)}{\log_e A_2 - \log_e A_1}$	

^a Abbreviations: Y_{ij} (or Y_{ji}) = total yield (root + rhizome + shoot) of species *i* (or *j*) when grown with species *j* (or *i*); Y_{ii} (or Y_{jj}) = mean total yield of species *i* (or *j*) in monoculture; *p* and *q* = proportions of species *i* and *j*, respectively, in mixture (p + q = 1).

^b Abbreviations: $W = \text{total dry mass} (\Sigma \text{ of all plant parts, except otherwise indicated}) of individual plants; <math>t = \text{time of harvest}; A = \text{total leaf area of individual plants.}$

^c Calculations were made for paired plants on the basis of ranking by total dry mass in each of two sequential harvests (cf. Hunt, 1978; Causton and Venus, 1981).

^d Formula for calculating NAR was for the case in which W vs. A relationship is linear (cf. Radford, 1967).

variance (ANOVA). Protected least significant difference tests (PLSDs, P = 0.05) were used as the multiple comparison procedure; *t* tests compared mean genet height of *S. shortii* and *S. altissima* when these two species were grown together at the same proportion. A two-way ANOVA was used to test for differences in actual RYs between the 1992 and 1994 growing seasons (SAS, 1985).

Growth study—Seedlings of *S. shortii* and *S. altissima* were transplanted individually into pots on 28 April 1992. Thirteen harvests were conducted over a 23-wk growth period (28 April–6 October 1992). A harvest consisted of 12 randomly selected individuals of each *Solidago* species. Harvest 1 (i.e., 0 wk after transplanting) was obtained directly from the metal flats, and harvests 2–13 (1–23 wk after transplanting) from pots: harvests 2–6 at 1-wk-, 7–11 at 2-wk-, and 12 and 13 at 4-wk intervals. At each harvest, prints of fresh leaves were made using Diazo-type paper for ammonia developing, and leaf area (one side only) was determined by mass/area relationships. Plant material was separated



Fig. 2. Replacement series diagrams illustrating mean (\pm 1 SE, SE shown if ≥ 0.05) relative yield and relative yield total as a function of species proportions. The diagonal dashed lines are the expected relative yields when plants of a species grow equally well in mixture and in monoculture. *F.a.* = *Festuca arundinacea, S.a.* = *Solidago altissima, S.s.* = *S. shortii*

into roots, rhizomes, stems, leaves (including cotyledons), and inflorescences, dried for 24 h at 80°C, and weighed.

To study growth in height, six seedlings each of *S. shortii* and *S. altissima* were transplanted individually into pots on 28 April 1992. Height of the main shoot of the same plant was measured (1) on the day of transplanting, (2) at weekly intervals for the first 4 wk after transplanting, and (3) at 2-3 wk intervals for the remainder of the growth period.

Total dry mass (W) and total leaf area (A) of individual plants were needed from each harvest to calculate growth parameters (Table 1). Parameters determined were relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), leaf weight ratio (LWR), specific leaf area (SLA), dry matter production (DMP), and leaf area duration (LAD). RGR measures the average efficiency of each unit of dry matter in the rate of production of new dry matter. Differences in RGR may result from NAR, a physiological component that approximates net photosynthesis, and/or LAR, a morphological component that measures leafiness of the plant. NAR and LAR are related to RGR by RGR = NAR × LAR. Differences in LAR may result from LWR, i.e., investment in leaf biomass, and/or SLA, which indicates thin leaves of relatively large area (high SLA) or thick leaves of small area (low SLA). LWR and SLA are related to LAR by LAR = LWR \times SLA (Hunt, 1978; Causton and Venus, 1981; Lambers and Dijkstra, 1987). DMP measures the amount of dry mass produced during a particular time interval, and differences in DMP may be explained by NAR and/or LAD. LAD is the photosynthetic potential of a plant, i.e., a measurement of the whole opportunity for assimilation a plant possesses during a growth period. NAR and LAD are related to DMP by $DMP = NAR \times LAD$ (Watson, 1952; Květ et al., 1971; Patterson, 1993).

Differences in root, rhizome, and shoot dry masses, height, leaf area, number of leaves, and root/shoot and (root + rhizome)/shoot ratios between the two species were determined. Resource allocation patterns were calculated for each species as the percentage of total dry mass in each plant part.

The formula for calculating NAR varies depending on whether the relationship between W (dependent variable) and A (independent variable) is linear, quadratic, or exponential (Radford, 1967). A regression and all-possible-regressions selection procedure determined that the most appropriate NAR formula to use in the study was for the case in which the relationship W vs. A was linear. That is, the linear relationship had the lowest Cp value (11.8) and highest R^2 value (0.78), and all independent variables were significant (P = 0.0001) (SAS, 1985).

An ANOVA was used to test the effects and interaction of species and harvest date for each growth parameter: univariate repeated-measures ANOVA for height growth and two-way ANOVA for all other growth parameters. Data were plotted and *t* tests performed at each harvest to detect consistent differences between the two species during the growth period (SAS, 1985). Significant harvest effect and/or species \times harvest would be expected due to growth of plants and ontogenetic drift of parameters (cf. Kvët et al., 1971; Hunt, 1978; Radosevich, Holt, and Ghersa, 1997). Variances of some data were heteroscedastic, but ANOVA results are robust when sample sizes are equal (Neter, Wasserman, and Kutner, 1990). Allocation data were arc-sine transformed before they were analyzed; they were back transformed for presentation. Greenhouse-Geisser corrected probabilities are reported for the repeated-measures ANOVA (SAS, 1985).

RESULTS

Competition studies—Values of actual RYs did not differ significantly between the 1992 and 1994 growing seasons (year effect, $P \ge 0.0537$; year × proportion, $P \ge 0.3360$); thus, values were pooled over years in all analyses. Actual RYs of *S. shortii* were significantly less than expected at each proportion when grown with *S. altissima* or with *F. arundinacea* (P = 0.0001), whereas those of *S. altissima* and *F. arundinacea* were significantly greater than expected ($P \le 0.0075$) (Fig. 2). On the other hand, actual RYs of *S. altissima* and *F. arundinacea*, when grown together, were not significantly different from expected values at each proportion ($P \ge 0.2157$). RYT was not significantly different from 1.0 at all proportions in these three mixture combinations ($P \ge 0.1258$).

Mean aggressivity differed significantly among the three species (P = 0.0001) (Table 2). Aggressivity of *S. shortii* was significantly less than that of *S. altissima* and of *F. arundinacea*, but aggressivities of the latter two species were not significantly different.

Height of *S. altissima* genets increased significantly with increase in number of *S. shortii* genets per pot, whereas that of *S. shortii* genets decreased significantly with increase in number of *S. altissima* genets per pot (*P*

TABLE 2. Aggressivities (mean \pm 1 SE) of *Solidago shortii* (*S.s.*), *S. altissima* (*S.a.*), and *Festuca arundinacea* (*F.a.*) when grown with each other. Values in the competitor columns or in the overall mean column with different letters are significantly different (PLSD, P = 0.05).

	Competitor			
Species	S.s.	<i>S.a.</i>	F.a.	mean
S.s.		$-1.40 \pm 0.10a$	$-1.30 \pm 0.14a$	-1.35a
<i>S.a.</i>	$1.40~\pm~0.10b$		$0.06 \pm 0.10c$	0.73b
<i>F.a.</i>	$1.30~\pm~0.14b$	$-0.06 \pm 0.10c$		0.62b

= 0.0001) (Fig. 3). In addition, height of *S. shortii* genets was significantly less than that of *S. altissima* genets when these two species were grown together (P = 0.0001). Solidago shortii genets were significantly shorter in mixture with *F. arundinacea* than in monoculture (P = 0.0001), but height of *S. shortii* did not vary significantly when grown at different proportions with *F. arundinacea* (Fig. 4A). Solidago altissima genets were of equal height when grown at different proportions with *F. arundinacea* and in monoculture (P = 0.3799) (Fig. 4B).

Growth study—RGR, NAR, LAR, LWR, and SLA varied significantly between *S. shortii* and *S. altissima* over the growth period (harvest effect, P = 0.0001; species × harvest, $P \le 0.0301$), but no consistent differences for these growth parameters were found between the two species (species effect, $P \ge 0.0893$) (Fig. 5). On the other hand, consistent differences between *S. shortii* and *S. altissima* were found for DMP and LAD (species effect, P = 0.0001; harvest effect, P = 0.0001, species × harvest, P = 0.0001; harvest effect, P = 0.0001, species × harvest, P = 0.0001) (Fig. 6). Solidago altissima had higher DMP than *S. shortii* during weeks 2–19 of the growth period, significantly greater for *S. altissima* than for *S. shortii* during weeks 3–23 of the growth period ($P \le 0.0240$).



Fig. 3. Height (mean ± 1 SE, SE shown if ≥ 4) of *Solidago shortii* (*S.s.*) and *S. altissima* (*S.a.*) genets in the replacement series. Values with different uppercase letters within species or with different lower-case letters within mixtures are significantly different (PLSD or *t* test, $P \leq 0.05$).



Fig. 4. Height (mean ± 1 SE, SE shown if ≥ 4) of *Solidago shortii* (*S.s.*) (A) or *S. altissima* (*S.a.*) (B) genets in replacement series with *Festuca arundinacea* (*F.a.*). Values with different letters within species of *Solidago* are significantly different (PLSD, P = 0.05).



Fig. 5. Mean (\pm 1 SE) relative growth rate (A), net assimilation rate (B), leaf area ratio (C), leaf weight ratio (D), and specific leaf area (E) of *Solidago shortii* and *S. altissima* during a 23-wk growth period in an ambient-temperature greenhouse. Means of each parameter with an asterisk are significantly different within a harvest (*t* test, $P \le 0.05$); those without an asterisk are not. SE shown only if greater than size of data points.

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Fig. 6. Mean $(\pm 1 \text{ SE})$ dry matter production (A) and leaf area duration (B) of *Solidago shortii* and *S. altissima* during a 23-wk growth period in an ambient-temperature greenhouse. Means of each parameter with an asterisk are significantly different within a harvest (*t* test, $P \leq 0.05$); those without an asterisk are not. SE shown only if greater than size of data points.

Root, rhizome, and shoot dry masses, height, and leaf area differed significantly between the two Solidago species ($P \le 0.0221$) and among harvests (P = 0.0001) (Fig. 7). Although root dry mass was similar between the two species over the growth period (species \times harvest, P =0.6700), rhizome and shoot dry masses, height, and leaf area were not ($P \le 0.0061$). Root dry mass of S. altissima was significantly greater than that of S. shortii only during weeks 2–7 of the growth period ($P \le 0.0319$). On the other hand, S. altissima had significantly greater rhizome dry mass, shoot dry mass, height, and leaf area than S. shortii during weeks 19 and 23, 2-23, 8-23, and 2-23, respectively, of the growth period ($P \le 0.0427$). Number of leaves did not differ significantly between S. shortii and S. altissima (P = 0.2537) and were similar between them over the growth period (species \times harvest, P = 0.9635; however, they did differ significantly among harvests (P = 0.0001).

Significant differences occurred between S. shortii and S. altissima in the percentage of dry mass allocated to roots, rhizomes, and stems $(P \le 0.0228)$, but not to leaves and inflorescences ($P \ge 0.3171$) (Fig. 8). Harvest had a significant effect on root, rhizome, stem, leaf, and inflorescence allocation (P = 0.0001). Percentage allocation to roots, rhizomes, stems, and leaves varied between the two species over the growth period (species imesharvest, $P \leq 0.0007$; inflorescence, P = 0.8208). Both species allocated proportionately similar amounts of dry mass to roots during weeks 0-7 of the growth period $(\sim 34\%; P \ge 0.1135)$, but S. shortii allocated more than S. altissima during weeks 9–23 (45.2 vs. 34.6%; $P \leq$ 0.0213). Although S. shortii allocated proportionately more dry mass to stems than S. altissima during weeks 0-5 of the growth period (7.6 vs. 4.9%; $P \le 0.0076$), S.



Fig. 7. Mean (± 1 SE) root (A), rhizome (B), and shoot (C) dry masses, height (D), and leaf area (E) of *Solidago shortii* and *S. altissima* during a 23-wk growth period in an ambient-temperature greenhouse. The arrow in panel (B) indicates the harvest in which rhizomes were first observed. Means of each parameter with an asterisk are significantly different within a harvest (t test, $P \leq 0.05$); those without an asterisk are not. SE shown only if greater than size of data points.

altissima allocated more than S. shortii during weeks 7–23 (16.8 vs. 11.4%; $P \le 0.0457$). Percentage allocation of dry mass to leaves was similar during the growth period for both species (~51%; $P \ge 0.1191$). Solidago shortii and S. altissima allocated proportionately similar amounts of dry mass to sexual reproduction (~5%; P = 0.2434), but S. altissima allocated significantly more than S. shortii to vegetative reproduction (3.2 vs. 0.3%; P = 0.0003).

The root/shoot ratio differed significantly between the two species (P = 0.0316), but the (root + rhizome)/shoot ratio did not (P = 0.3846), and both harvest and species × harvest were significant for root/shoot and (root + rhizome)/shoot ratios (P = 0.0001). Solidago shortii and S. altissima had similar root/shoot (~0.58) and (root + rhizome)/shoot (~0.58) ratios during weeks 0–7 of the growth period ($P \ge 0.0994$). However, S. shortii had significantly greater root/shoot (0.89) and (root + rhizome)/ shoot (0.88) ratios than S. altissima (0.58 and 0.63) during weeks 9–23 ($P \le 0.0211$).

DISCUSSION

Values of RYT were not different from 1.0 in any of the three mixture combinations, i.e., the three species



Fig. 8. Dry mass allocation of *Solidago shortii* (A) and of *S. altissima* (B) plants during a 23-wk growth period in an ambient-temperature greenhouse. Percentage allocation to rhizomes for *S. shortii* was 0-0.7 during the growth period. Infl. = inflorescences, rhiz. = rhizomes.

competed for the same resources when grown together (Fig. 2). However, whereas plants of S. altissima and F. arundinacea grew equally well in mixture and monocultures, this clearly was not the case when S. shortii was grown with either of these species. The concave RY curve of S. shortii indicates the effect of interspecific competition on plants of this species when grown with S. altissima or with F. arundinacea was greater than that of intraspecific competition. On the other hand, the convex curves of S. altissima and F. arundinacea indicate the effect of interspecific competition on plants of either of these two species when grown with S. shortii was less than that of intraspecific competition (cf. Harper, 1977). Thus, the competitive hierarchy suggested by the de Wit diagrams is: S. altissima = F. arundinacea > S. shortii. Height of genets (Figs. 3, 4) and aggressivity values (Table 2) support this hierarchy.

The superiority of *S. altissima* when grown with *S. shortii* is consistent with its large size (Figs. 6, 7), and not with RGR, NAR, LAR, LWR, or SLA (Fig. 5). Indeed, when *S. shortii* and *S. altissima* were grown together, *S. altissima* was significantly taller than *S. shortii* (Fig. 3). Among the many determinants of competitive ability, plant size has been found to be an important trait in other studies (Keddy and Shipley, 1989; Hills and Murphy, 1996; Rösch, Van Rooyen, and Theron, 1997). Keddy (1989) reasoned that since large plants can intercept more light and consequently allocate more resources for uptake of soil nutrients than small ones, large plants would have better competitive success than small plants.

NAR and leaf area, i.e., the "efficiency" and "capacity," respectively, of photosynthesis, are major determinants of yield in plants, and therefore of competitive ability. In particular, LAD has been suggested to be of relevance to studies of potential competitiveness (Watson, 1952; Patterson, 1982). Leaf area and LAD of *S. altissima* were significantly greater than those of *S. shortii* (Figs. 6, 7), but NAR and RGR did not differ significantly between the two species (Fig. 5). Other investigators also have found a poor correlation between yield and NAR (e.g., Patterson, 1993) or between yield and RGR (e.g., Roush and Radosevich, 1985).

Lack of difference in NAR between *S. shortii* and *S. altissima* is not too surprising since maximum net photosynthetic rates are similar among *Solidago* species: *S. altissima* and *S. juncea* (Potvin and Werner, 1983), *S. canadensis* and *S. missouriensis* (Turner, Kneisler, and Knapp, 1995), and *S. altissima*, *S. canadensis*, and *S. gigantea* (Schmid et al., 1988). Mean NAR for *S. shortii* and *S. altissima* over the entire growth period (0.529 and 0.535 mg·cm⁻²·d⁻¹, respectively) was within the range of values reported for other herbaceous dicotyledons (0.5–1.0 mg·cm⁻²·d⁻¹; Larcher, 1995).

Mean RGR for 130 herbaceous annuals and perennials and tree seedlings in the local flora of Sheffield, England, ranged from 0.031 to 0.314 $g \cdot g^{-1} \cdot d^{-1}$ (mean = 0.152) (Grime and Hunt, 1975). In the present study, mean RGR of *S. shortii* and *S. altissima* seedlings (0–5 wk after transplanting) was 0.120 and 0.124 $g \cdot g^{-1} \cdot d^{-1}$, respectively (Fig. 5). Meyer (1993) reported a mean RGR of 0.117 $g \cdot g^{-1} \cdot d^{-1}$ for plants of *S. altissima* without insects and 0.097–0.118 $g \cdot g^{-1} \cdot d^{-1}$ for those with aphids, beetles, or spittlebugs. Thus, mean seedling RGR of both *Solidago* species was near the middle of the range of mean RGRs of the 130 species studied by Grime and Hunt (1975).

Percentage allocation of dry mass to plant parts (except stems) and root/shoot and (root + rhizome)/shoot ratios were similar for S. shortii and S. altissima during April-June (Fig. 8). In contrast, S. shortii allocated proportionately more dry mass to roots and less to stems and rhizomes than S. altissima during July-October. Further, S. shortii had higher root/shoot and (root + rhizome)/shoot ratios than S. altissima during July-October. For plants of S. altissima collected from the field, ~ 5 , 13, 44, 27, and 11% of dry mass were allocated to roots, rhizomes, stems, leaves, and inflorescences, respectively (Gross et al., 1983; Abrahamson and McCrea, 1986). In contrast, for rhizome-derived plants of S. altissima grown in a greenhouse ~ 8 , 37, 28, 22, and 5% of dry mass were allocated to roots, rhizomes, stems, leaves, and inflorescences, respectively (Abrahamson, Anderson, and Mc-Crea, 1988) and for seed-derived plants \sim 37, 8, 19, 30, and 6%, respectively (present study). Schmid, Bazzaz, and Weiner (1995) reported that for seed-derived plants of S. canadensis grown in an experimental garden, a comparatively large proportion of the dry mass was allocated to roots and leaves, whereas for rhizome-derived plants a particularly large proportion was allocated to new rhizomes. With respect to allocation to stems and inflorescences, there was little difference between seedand rhizome-derived plants of S. canadensis. Thus, although allocation to various plant parts differs among experimental conditions, S. altissima allocates more dry mass to above- than to belowground plant parts.

Competitive abilities, physiological and morphological traits, and distribution along soil moisture gradients of the *S. shortii/S. altissima* species pair are similar to those reported for the *S. juncea/S. altissima* species pair. Using

reciprocal transplants in an experimental field study, Werner (unpublished data, cited in Potvin and Werner, 1983) found that *S. juncea*, a dry-site species, survived at the dry end of a soil moisture gradient with and without surrounding vegetation. At the wet end of the gradient, *S. juncea* grew large only in the absence of vegetation, and it grew poorly in its presence. In contrast, *S. altissima*, a wet-site species, grew best at the wet end of the gradient with and without neighboring plants and poorly at the dry end.

Morphological differences between *S. juncea* and *S. altissima* were more important in determining species distribution along the soil moisture gradient than was physiology. Assimilation rate, stomatal conductance, water-use efficiency, leaf water potential, and stomatal response to low water potential were similar for the two species. However, *S. juncea* survived better than *S. altissima* on dry sites due to (1) greater belowground allocation of biomass, (2) smaller leaf area, and (3) earlier completion of growth and flowering in the growing season (Potvin and Werner, 1983, 1984).

Solidago altissima is a better competitor than S. shortii due to its relatively larger size and, thus, greater light interception and photosynthate production. However, since plants of S. shortii have a smaller leaf area, higher percentage allocation to roots, and higher root/shoot ratio than S. altissima, S. shortii is more drought adapted than S. altissima. Indeed, we have observed that S. altissima wilts more easily than S. shortii in the field and in pots in the greenhouse. Buchele, Baskin, and Baskin (1989) never observed S. shortii wilting in the field, even though soil moisture content frequently dropped below the permanent wilting percentage in the upper layer of soil. On the other hand, the small-sized growth form of S. shortii would be more easily overtopped and thus shaded out by neighboring plants on moist sites than would S. altissima. Thus, S. shortii survives within the geographic range of S. altissima since it apparently is the most drought tolerant of the two species. As such, S. shortii grows in rocky habitats where S. altissima does not become established. Low competitive ability appears to be one of the factors preventing S. shortii from maintaining its presence in mesic habitats in the Blue Licks area, and it may be one of several factors contributing to the narrow endemism of the species.

LITERATURE CITED

- ABRAHAMSON, W. G., S. S. ANDERSON, AND K. D. MCCREA. 1988. Effects of manipulation of plant carbon nutrient balance on tall goldenrod resistance to a gallmaking herbivore. *Oecologia* 77: 302– 306.
 - —, AND K. D. MCCREA. 1986. Nutrient and biomass allocation in *Solidago altissima*: effects of two stem gallmakers, fertilization, and ramet isolation. *Oecologia* 68: 174–180.
- AULD, B. A., AND R. W. MEDD. 1987. Weeds: an illustrated botanical guide to the weeds of Australia. Inkata Press, Melbourne.
- BASKIN, J. M., AND C. C. BASKIN. 1985. Does seed dormancy play a role in the germination ecology of *Rumex crispus? Weed Science* 33: 340–343.
- ———, AND ———. 1986. Distribution and geographical/evolutionary relationships of cedar glade endemics in southeastern United States. Association of Southeastern Biologists Bulletin 33: 138–154.
 - -----, AND -------. 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.

- BREEDEN, J. E. 1968. Ecological tolerances in the seed and seedling stages of two species of *Petalostemon* (Leguminosae). Ph.D. dissertation, Vanderbilt University, Nashville, TN.
- BUCHELE, D. E. 1988. A community ecology and life history study of Solidago shortii T. & G. (Asteraceae), a federally endangered species endemic to Kentucky. M.S. thesis, University of Kentucky, Lexington, KY.
- —, J. M. BASKIN, AND C. C. BASKIN. 1989. Ecology of the endangered species *Solidago shortii*. I. Geography, populations, and physical habitat. *Bulletin of the Torrey Botanical Club* 116: 344– 355.
- , _____, AND _____. 1991. Ecology of the endangered species Solidago shortii. II. Ecological life cycle. Bulletin of the Torrey Botanical Club 118: 281–287.
- _____, ____, AND _____. 1992. Ecology of the endangered species Solidago shortii. V. Plant associates. Bulletin of the Torrey Botanical Club 119: 208–213.
- CAUDLE, C. F. 1968. Studies on the life history and hydro-economy of Astragalus tennesseensis (Leguminosae). Ph.D. dissertation, Vanderbilt University, Nashville, TN.
- CAUSTON, D. R., AND J. C. VENUS. 1981. The biometry of plant growth. Edward Arnold, London.
- CONNELL, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122: 661–696.
- CONNOLLY, J. 1986. On difficulties with replacement-series methodology in mixture experiments. *Journal of Applied Ecology* 23: 125– 137.
- COTTER, D. J., AND R. B. PLATT. 1959. Studies on the ecological life history of *Portulaca smallii*. *Ecology* 40: 651–668.
- COUSENS, R., AND M. O'NEILL. 1993. Density dependence of replacement series experiments. Oikos 66: 347–352.
- CROAT, T. 1972. Solidago canadensis complex of the Great Plains. Brittonia 24: 317–326.
- DE WIT, C. T. 1960. On competition. Verslagen van Landbouwkundige Onderzoekingen 66: 1–82.
- GANKIN, R., AND J. MAJOR. 1964. Arctostaphylos myrtifolia, its biology and relationship to the problem of endemism. Ecology 45: 792– 808.
- GOLDBERG, D. E., AND A. M. BARTON. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* 139: 771–801.
- ——, AND S. M. SCHEINER. 1993. ANOVA and ANCOVA: field competition experiments. *In* S. M. Scheiner and J. Gurevitch [eds.], Design and analysis of ecological experiments, 69–93. Chapman and Hall, New York, NY.
- GOTTLIEB, L. D., AND J. P. BENNETT. 1983. Interference between individuals in pure and mixed cultures of *Stephanomeria malheurensis* and its progenitor. *American Journal of Botany* 70: 276–284.
- GRIGGS, R. F. 1940. The ecology of rare plants. *Bulletin of the Torrey Botanical Club* 67: 575–594.
- GRIME, J. P., AND R. HUNT. 1975. Relative growth-rate: its range and adaptive significance in a local flora. *Journal of Ecology* 63: 393–422.
- GROSS, K. L., T. BERNER, E. MARSCHALL, AND C. TOMCKO. 1983. Patterns of resource allocation among five herbaceous perennials. *Bulletin of the Torrey Botanical Club* 110: 345–352.
- HAMILTON, N. R. S. 1994. Replacement and additive designs for plant competition studies. *Journal of Applied Ecology* 31: 599–603.
- HARPER, J. L. 1977. Population biology of plants. Academic Press, London.
- HART, R. 1980. The coexistence of weeds and restricted native plants on serpentine barrens in southeastern Pennsylvania. *Ecology* 61: 688–701.
- HILLS, J. M., AND K. J. MURPHY. 1996. Evidence for consistent functional groups of wetland vegetation across a broad geographical range of Europe. Wetlands Ecology and Management 4: 51–63.
- HUNT, R. 1978. Plant growth analysis. The Institute of Biology's Studies in Biology Number 96. Edward Arnold, London.
- KARRON, J. D. 1987. A comparison of levels of genetic polymorphism

and self-compatibility in geographically restricted and widespread plant congeners. *Evolutionary Ecology* 1: 47–58.

KEDDY, P. A. 1989. Competition. Chapman and Hall, London.

— . 1990. Competitive hierarchies and centrifugal organization in plant communities. *In* J. B. Grace and D. Tilman [eds.], Perspectives on plant competition, 265–290. Academic Press, San Diego, CA.

——, AND B. SHIPLEY. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54: 234–241.

- KRUCKEBERG, A. R. 1954. The ecology of serpentine soils. III. Plant species in relation to serpentine soils. *Ecology* 35: 267–274.
- , AND D. RABINOWITZ. 1985. Biological aspects of endemism in higher plants. Annual Review of Ecology and Systematics 16: 447– 479.
- KVĚT, J., J. P. ONDOK, J. NEČAS, AND P. G. JARVIS 1971. Methods of growth analysis. *In Z.* Šesták, J. Čatský, and P. G. Jarvis [eds.], Plant photosynthetic production: manual of methods, 343–391. Dr. W. Junk, The Hague.
- LAMBERS, H., AND P. DIJKSTRA. 1987. A physiological analysis of genotypic variation in relative growth rate: can growth rate confer ecological advantage? *In* J. van Andel, J. P. Bakker, and R. W. Snaydon [eds.], Disturbance in grasslands: causes, effects and processes, 237–252. Dr. W. Junk, Dordrecht.
- LARCHER, W. 1995. Physiological plant ecology: ecophysiology and stress physiology of functional groups, 3rd ed. Springer-Verlag, New York, NY.
- LI, H. L. 1978. Compositae. In H. L. Li, T. S. Liu, T. C. Huang, T. Koyama, and C. E. DeVol [eds.], Flora of Taiwan, vol. 4, 768–965. Epoch Publishing Company, Taipei, Taiwan.
- MCGILCHRIST, C. A., AND B. R. TRENBATH. 1971. A revised analysis of plant competition experiments. *Biometrics* 27: 659–671.
- MÉDAIL, F, AND R. VERLAQUE. 1997. Ecological characteristics and rarity of endemic plants from southeast France and Corsica: implications for biodiversity conservation. *Biological Conservation* 80: 269–281.
- MELVILLE, M. R., AND J. K. MORTON. 1982. A biosystematic study of the *Solidago canadensis* (Compositae) complex. I. The Ontario populations. *Canadian Journal of Botany* 60: 976–997.
- MEYER, G. A. 1993. A comparison of the impacts of leaf- and sapfeeding insects on growth and allocation of goldenrod. *Ecology* 74: 1101–1116.
- MILLER, G. L. 1977. An ecological study of the serpentine barrens in Lancaster County, Pennsylvania. *Proceedings of the Pennsylvania* Academy of Science 51: 169–176.
- MURDY, W. H. 1966. The systematics of *Phacelia maculata* and *P. dubia* var. *georgiana*, both endemic to granite outcrop communities. *American Journal of Botany* 53: 1028–1036.
- NESOM, G. L. 1989. The *Solidago canadensis* (Asteraceae: Asteraea) complex in Texas with a new species from Texas and México. *Phytologia* 67: 441–450.

— 1993. Taxonomic infrastructure of *Solidago* and *Oligoneuron* (Asteraceae: Astereae) and observations on their phylogenetic position. *Phytologia* 75: 1–44.

- NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. Applied linear statistical models: regression, analysis of variance, and experimental designs. R. D. Irwin, Homewood, IL.
- NUMATA, M., AND S. ASANO. 1969. Biological flora of Japan, vol. 1. Sympetalae—1. Tsukiji Shokan, Tokyo.
- PATTERSON, D. T. 1982. Effects of light and temperature on weed/crop growth and competition. *In* J. L. Hatfield and I. J. Thomason [eds.], Biometeorology in integrated pest management, 407–420. Academic Press, New York, NY.
 - -----. 1993. Effects of temperature and photoperiod on growth and

development of sicklepod (*Cassia obtusifolia*). Weed Science 41: 574–582.

- POTVIN, M. A., AND P. A. WERNER. 1983. Water use physiologies of co-occurring goldenrods (*Solidago juncea* and *S. canadensis*): implications for natural distributions. *Oecologia* 56: 148–152.
- _____, AND _____. 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. 1992. Environmental influences on the distribution of the rare *Eucalyptus paliformis* and the common *E. fraxinoides*. *Australian Journal of Ecology* 17: 51–65.
- RADFORD, P. J. 1967. Growth analysis formulae—their use and abuse. Crop Science 7: 171–175.
- RADOSEVICH, S., J. HOLT, AND C. GHERSA. 1997. Weed ecology: implications for management, 2d ed. John Wiley and Sons, New York, NY.
- Rollins, R. C. 1963. The evolution and systematics of *Leavenworthia* (Cruciferae). *Contributions from the Gray Herbarium of Harvard* University 192: 3–98.
- Rösch, H., M. W. VAN ROOYEN, AND G. K. THERON. 1997. Predicting competitive interactions between pioneer plant species by using plant traits. *Journal of Vegetation Science* 8: 489–494.
- ROUSH, M. L., AND S. R. RADOSEVICH. 1985. Relationships between growth and competitiveness of four annual weeds. *Journal of Applied Ecology* 22: 895–905.
- SAS. 1985. SAS user's guide: statistics. SAS Institute, Cary, NC.
- SCHMID, B., F. A. BAZZAZ, AND J. WEINER. 1995. Size dependency of sexual reproduction and of clonal growth in two perennial plants. *Canadian Journal of Botany* 73: 1831–1837.
- ——, G. M. PUTTICK, K. H. BURGESS, AND F. A. BAZZAZ. 1988. Correlations between genet architecture and some life history features in three species of *Solidago*. *Oecologia* 75: 459–464.
- SCHOENER, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122: 240–285.
- SCOGGAN, H. J. 1979. The flora of Canada. Part 4—Dicotyledoneae (Loasaceae to Compositae). National Museum of Natural Sciences, Publications in Botany Number 7(4): 1117–1711. National Museums of Canada, Ottawa.
- SEMPLE, J. C. 1993. Solidago. In J. C. Hickman [ed.], The Jepson manual: higher plants of California, 342–343. University of California Press, Berkeley, CA.
- SNYDER, K. M., J. M. BASKIN, AND C. C. BASKIN. 1994. Comparative ecology of the narrow endemic *Echinacea tennesseensis* and two geographically widespread congeners: relative competitive ability and growth characteristics. *International Journal of Plant Sciences* 155: 57–65.
- TURNER, C. L., J. R. KNEISLER, AND A. K. KNAPP. 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.
- WARE, S. 1991. Influence of interspecific competition, light and moisture levels on growth of rock outcrop *Talinum* (Portulacaceae). *Bulletin of the Torrey Botanical Club* 118: 1–5.
- WATSON, D. J. 1952. The physiological basis of variation in yield. Advances in Agronomy 4: 101–145.
- 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.
- WERNER, P. A., I. K. BRADBURY, AND R. S. GROSS. 1980. The biology of Canadian weeds. 45. Solidago canadensis L. Canadian Journal of Plant Science 60: 1393–1409.
- WIGGS, D. N., AND R. B. PLATT. 1962. Ecology of Diamorpha cymosa. Ecology 43: 654–670.