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## Biological flora of central Europe: *Solidago gigantea* Aiton

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### Abstract

*Solidago gigantea* is a rhizomatous perennial herb native to northern America and introduced in Europe. It is a serious invader of disturbed mesic sites, often forming dense monospecific stands. We review the literature on taxonomy, morphology, population biology, cytology, physiology, chemistry, and ecology of this species.

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**Keywords:** *Solidago gigantea*; Ecology; Species biology; Central Europe

### Taxonomy and morphology

#### Taxonomy

*Solidago gigantea* AITON (Asteraceae) – Große Goldrute, Riesengoldrute – Giant goldenrod, late goldenrod, early goldenrod, smooth goldenrod.

Synonyms (Kartesz, 1994):

*Aster latissimifolius* (MILL.) KUNTZE var. *serotinus* KUNTZE

*Solidago glabra* DESF.

*Solidago gigantea* AITON subsp. *serotina* (KUNTZE)

MCNEILL = *S. gigantea* var.

*serotina* (KUNTZE) CRONQ. = *S. gigantea* var.

*leiophylla* FERN.

*Solidago pitcheri* NUTT.

*Solidago serotina* AITON, non RETZ.

*Solidago serotinoides* A. & D.LÖVE

*Solidago serotina* AITON var. *gigantea* (AITON) A.

GRAY

*Solidago shimmersii* (BEAUDRY) BEAUDRY

*Solidago* × *leiophallax* FRIESNER

*Solidago gigantea* AIT. belongs to the genus *Solidago* within the family of the Asteraceae. The genus comprises about 130 taxa, most of which are native to North America; *S. virgaurea* is native to Eurasia. *S. gigantea* belongs to the *canadensis* complex and to the subgenus *Triplinervae* with triple-nerved leaves. It is a variable taxon and several varieties have been distinguished (*S. gigantea* AITON var. *gigantea*, *S. gigantea* AITON var. *leiophylla* FERNALD, *S. gigantea* AITON var. *pitcheri* (NUTT.) SHINNERS, *S. gigantea* AITON var. *serotina* (KUNTZE) CRONQUIST, *S. gigantea* AITON var. *shimmersii* BEAUDRY), some of these are granted subspecies status. The taxon is also referred to as *S. gigantea* subsp. *serotina* (KUNTZE) MCNEILL.

*S. gigantea* shows variation in chromosome numbers: It occurs as three different cytotypes, all of which have also been found in Europe (Jakobs, 2004). They are listed below according to the nomenclature of Beaudry (1963, 1974); throughout the rest this article *S. gigantea* represents the whole *S. gigantea* complex:

*S. gigantea*  $2n = 2 \times = 18$  (trichomes on midveins),

*S. serotina*  $2n = 4 \times = 36$  (glabrous narrow leaves),

*S. shimmersii*  $2n = 6 \times = 54$  (glabrous wide leaves).

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Beaudry (1974) distinguished a further, tetraploid variety, *S. serotina* forma *huntingdonensis*, defined by trichomes uniformly covering the lower leaf blade. In contrast, Melville and Morton (1982) find the cytotypes to be morphologically inseparable because of overlapping variation, although there might be a tendency for stronger leaf serration and pubescence in the diploid *S. gigantea* (Morton, 1984; Jakobs et al., submitted). Therefore, all cytotypes are treated as a single species by Morton (1984), despite of being genetically separated.

HYBRIDS – In Northeast America, the hybrid *S. canadensis* L. × *S. gigantea* AIT. has been reported, which has also been identified in France (Wagenitz, 1979). In nurseries, *Solidago asteroides* SEMPLE (Syn.: *Aster ptarmicoides*) has occasionally been observed to cross with various *Solidago* species, among them *S. canadensis* and *S. missouriensis*, the hybrids were formerly known as *Solidaster* (Semple et al., 1999).

CLINAL VARIATION – *S. gigantea* shows clinal variation in both the native and the introduced range (Jakobs et al., 2004; Weber and Schmid, 1998), as demonstrated in common garden experiments in which plants of higher latitudes grew commonly larger and flowered earlier than those from further south.

## Morphology

*S. gigantea* is a tall, erect perennial herb with annual aboveground shoots and persistent belowground rhizomes. Shoots are 5–11 mm in diameter and vary from 30 to 280 cm in height. The shoots are branched only in the inflorescence, which cover on average one-third of the total shoot height, though the ratio varies widely (10–60%), depending on the population, geographic range and time of flowering. Taller plants tend to flower later in the season. Stems are glabrous between ground level and the inflorescence; they are often purplish and covered with a waxy, whitish bloom, giving a pale blue or purple cast.

*S. gigantea* has simple, alternate, and oblong to lanceolate leaves of 80–180 mm length and 10–30 mm width. Up to 90 leaves are produced per shoot during the course of the growing season; due to death of some leaves the total number of living leaves usually decreases from September onwards, although new leaves may still be produced within inflorescences. Leaves are largest in the middle of shoots and become smaller towards the apex and within the inflorescence. Leaf veins are pinnate, with three more or less conspicuous main veins; the midvein is markedly thicker than the lateral veins. Leaf edges are weakly to sharply serrate along the entire leaf, the size of teeth varying greatly among populations. Leaf blades are usually glabrous above and below, but may occasionally be pubescent on the leaf underside. Inflorescences form pyramidal panicles. The

often recurving branches contain numerous flower heads ( $1200 \pm 190$ , Schmid et al., 1988). Capitula measure 2–3 mm in diameter and the involucre is 3–4 mm in length. The bright yellow flowers are epigynous and monoecious; disk florets are perfect and fertile, ray florets are pistillate and fertile. Disk florets measure 4–8 mm in length, and the pappus 2.5–4 mm. Fruits are pubescent achenes of 1–1.8 mm length with long hairs so that they are readily dispersed in the wind.

*S. gigantea* produces long-creeping plagiotropic, mostly purple or reddish rhizomes, mostly within the upper 10–20 cm of soil. In total, 3–50 rhizomes per ramet emerge close to the base of shoots from the previous year. Higher numbers have been observed after disturbances. Rhizomes can be up to 90 cm in length and 1 cm in diameter, and are often highly branched. The density of rhizome buds may reach 22 buds/10 cm rhizome and is highest either close to the shoot base or towards the rhizome tip. Rhizomes root on the whole length; the root system shows considerable variation in size and density.

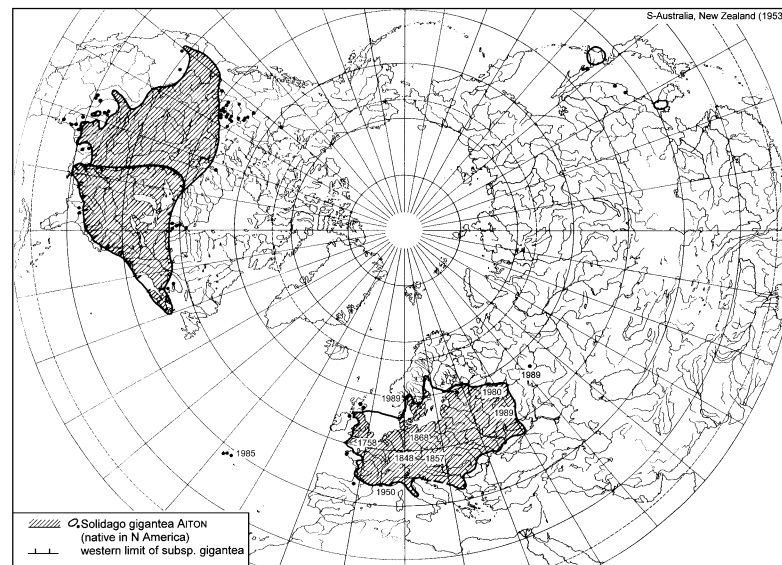
*S. gigantea* can be easily distinguished from the closely related *S. canadensis* by its longer rhizomes, brownish white pappus, glabrous stems and the denser inflorescence architecture.

## Distribution and habitat requirements

### Geographical distribution

*S. gigantea* is native to North America and introduced in Europe (Fig. 1). The native range includes large parts of continental USA and Canada, stretching from south-eastern and south-western USA to the Northwest Territory of Canada (Gleason and Cronquist, 1991; Semple et al., 1999). Restricted to summer humid temperate zones in the western USA, the zonal amplitude stretches from the meridional to the subboreal belt in the eastern part (Meusel and Jäger, 1992).

*S. gigantea* was introduced to Europe in the 18th century as an ornamental and became invasive some 100 years later. It was first introduced to the botanical garden in London in 1758 (Weber, 1998 and references therein), and soon afterwards distributed to various gardens and nurseries on the European continent. The origin of these founder populations is unknown. In the first half of the 19th century, *S. gigantea* was recorded in France (Voser-Huber, 1983) and about 50 years later in Switzerland and Germany (Keller, 1891; Wartmann and Schlatter, 1881; Wirz, 1885). The first record of spontaneous occurrences in Germany dates back to 1832, in Austria to 1857 (Wagenitz, 1979). Between 1850 and 1880, many new locations have been reported and



**Fig. 1.** Current distribution of *Solidago gigantea* in the northern hemisphere and western limit of the subsp. *gigantea* in its native range. The map was kindly provided by E.J. Jäger.

the plant began to spread throughout Central Europe (Wagenitz, 1979). Based on herbarium specimens and literature records, the expansion rate was approximately 910 km<sup>2</sup>/year (Weber, 1998). In 1950, *S. gigantea* already covered a large part of its current distribution in Europe, ranging from northern Spain to Eastern Europe and from northern Italy to southern Scandinavia (Tutin et al., 1964). In Europe, *S. gigantea* reaches from (sub-)meridional to temperate and from suboceanic to subcontinental regions, and has a latitudinal range from 42°N to 63°N (Fig. 1). Its present boundaries appear to be defined largely by climatic conditions, though further range extension in eastern direction can be expected (Meusel and Jäger, 1992; Weber, 2001). *S. gigantea* mainly occurs below 1200 m above sea level (Polatschek, 1997), but can occasionally be observed at higher altitudes.

The species occurs very widespread in Central Europe; the actual distribution map for Germany can be downloaded from <http://www.floraweb.de/MAP/scripts/esrimap.dll?name=florkart&cmd=map-flor&app=distflor&ly=gw&taxnr=5680>. The local abundance shows, however, large variation within the European range: the species forms extensive stands in Central Europe, is rather rare for example in Scandinavia, North and East Germany, and again frequent in East Poland. Besides Europe, *S. gigantea* has become naturalised in Japan (Enomoto, 2000; Tsuyuzaki, 2002), Korea and the Russian Far-East (Jäger, personal communication), Hawaii, New Zealand (Hill, personal communication), Australia (Newfield, personal communication), and on the islands of the Azores (Weber, 2003). Initially, only occupying ruderal sites such as road and railway lines and rivers, *S. gigantea* has also

established in semi-natural and natural habitats since the late 19th century (Guzikowa and Maycock, 1986; Lohmeyer and Sukopp, 1992). Increasing urbanization, road and railway construction, and the abandonment of fields may have enhanced its spread. Discarding of garden debris and planting goldenrods as feeding plant for bees may also have facilitated its invasion into new habitats (Walter, 1987). Compared to other goldenrod species introduced to Europe, the spread of *S. gigantea* has been described as fastest (Guzikowa and Maycock, 1986; Häupler and Schönfelder, 1988; Weber, 1998), and today it is considered to be a pest species in many areas (see environmental and economic impact in the section “Response to competition and management” and “Status of the species”).

## Habitats

**GENERAL HABITATS** – The species is generally described as having a broad tolerance with respect to soil moisture, light, nutrient contents, temperature, continentality or pH-range (Ellenberg et al., 2001; Voser-Huber, 1983). Although *S. gigantea* prefers rich and rather moist soils, it occurs over a wide range of soil fertility and texture conditions. It is most vigorous in ruderal and riverside habitats, but grows in drier sites such as road sites and embankments as well.

**MOISTURE** – In the native range, *S. gigantea* is considered a typical wetland species (<http://www.botany.wisc.edu/wisflora/scripts/detail.asp?SpCode=SOLGIG>) and frequently occurs in calcareous fens, sloughs or at river edges. In Europe, *S. gigantea* can be found in similar habitats but also occupies drier habitats and is

therefore characterized by a particularly broad range of tolerance for soil moisture (Landolt, 1977). In moist and wet habitats vitality is better than in drier sites, often resulting in dense monospecific stands. In drier habitats, the species frequently coexists with other species (Botta-Dukát and Dancza, 2001a) and *S. gigantea* is in such conditions less competitive. *S. gigantea* responds to drought stress with decreasing leaf area and reduction of total biomass. Mechanical restriction of the rhizomes may also restrict the dominance of *S. gigantea* in such habitats, since the sprouting is slower (Botta-Dukát and Dancza, 2001b). The species is very sensitive to flooding over longer time periods (Hartmann and Konold, 1995).

## Communities

*S. gigantea* is part of native prairie communities and open woodland in northern America (Kruse and Groninger, 2003). In the introduced range, the species often grows in nitrophilous sites where it is associated with various other perennial herbs and shrubs characteristic of these conditions (class Artemisietea, Ellenberg et al., 2001; Oberdorfer, 1992). The following communities seem to be typical: Rudbeckio-Solidagineum, Solidagineum serotinae-canadensis, Impatienti-Solidagineum, Stenactido-Solidagineum, *Urtica dioica* – *Convolvulus sepium* communities, Arction or Sisymbrium communities. *S. gigantea* frequently occurs in secondary forests dominated by *Robinia pseudoacacia* (Mucina et al., 1993) and in urban areas (Lenzin et al., 2001). It is commonly associated with *Achillea millefolium*, *Aegopodium podagraria*, *Arrhenatherum elatius*, *Artemisia vulgaris*, *Calystegia sepium*, *Cirsium arvense*, *Dactylis glomerata*, *Elymus repens*, *Galium album*, *G. aparine*, *Heracleum sphondylium*, *Symphytum officinale*, *Tanacetum vulgare* and *Urtica dioica*. The species invades semi-natural communities such as Equiseto-Alnetum, Salicion and Convolvulion (Lohmeyer and Sukopp (1992). In the western part of Europe it only rarely co-occurs with other goldenrod species, whereas such associations have frequently been reported in Eastern Europe. Once established in an area, *S. gigantea* is likely to gain dominance due to its clonal growth and high competitive ability.

## Response to abiotic factors

*S. gigantea* is a highly plastic species and responds to changes in environmental conditions by adjusting its growth pattern (Jakobs, 2004). This plasticity contributes to its stress tolerance and allows it to establish in a wide range of habitats including heavily disturbed sites.

**LIGHT** – *S. gigantea* is described as light demanding, but does occur in the shaded conditions of forest edges or even inside forests. For example, in Switzerland and

in the Czech Republic the species occurs under deciduous trees (Capek, 1971). In the native range, its vitality is strongly reduced under shady conditions, and it forms only small populations with low shoot density and small inflorescences. Similar patterns of growth in the shade have also been reported from Europe (Voser-Huber, 1983). However, our own observations in Switzerland and Germany indicate that the effect of shade seems to be less pronounced in the introduced range; indeed, we found that seed production and population density at four forest sites were higher than the average of a number of populations across Europe (Jakobs et al., 2004).

**NUTRIENTS** – *S. gigantea* mostly occurs in nitrogen-rich habitats, but is also found in relatively nutrient-poor sites such as wastelands. The species responds to increased soil nutrients with a strong increase in size, particularly in the size of inflorescences and the number of seeds produced.

**TEMPERATURE** – A more oceanic climate with moderate summer and winter temperatures favours the growth of *S. gigantea*. Positive correlations have been found between mean temperature and growth parameters such as shoot height, inflorescence height and the number of branches in the inflorescence (Voser-Huber, 1983). For germination, high spring temperatures (above 24 °C) are advantageous (Barrawasser, 2002).

**MOISTURE** – *S. gigantea* prefers moist to mesic sites but is described as having a wide tolerance for soil moisture contents. Thus the species also occurs in drier habitats, though growth and size may be reduced. Larger shoot size may be due to enhanced rhizome growth (see the section “Habitats”) or to the presence of mycorrhizae (see the section “Mycorrhiza”).

## Abundance

Owing to its clonal growth by rhizomes *S. gigantea* can form dense stands. Shoot density ranges from 29–167 shoots/m<sup>2</sup> and population (patch) size from several square meters to 50,000 m<sup>2</sup> (Jakobs et al., 2004). The local abundance depends on population, site history and environmental conditions.

## Life cycle and population biology

### Life cycle

*S. gigantea* is a rhizomatous hemicyptophyte and has a complex life cycle with rhizome and seed generations. Production of seeds, new shoots and new rhizomes occurs every year, and all aboveground shoots die back in autumn. Free carbohydrates are accumulated in the rhizome before the dormant period, particularly as free

sucrose and fructose (Szabo and Balogh, [http://www.mtk.nyne.hu/~botany/42\(1\)/Szabo.htm](http://www.mtk.nyne.hu/~botany/42(1)/Szabo.htm)).

Seedlings have never been observed within established patches of *S. gigantea*, suggesting that seeds are primarily important for long-distance dispersal and the colonization of new sites. However, seedlings may appear after a spring mowing (Hartmann et al., 1995), suggesting that successful establishment is dependent upon open conditions. In most cases, however, population increase is primarily the result of clonal growth.

The species' two modes of reproduction may increase colonization rates: light wind dispersed seed can be distributed over long distances and seedling establishment occurs even within closed vegetation (personal observation). Equally important may be the vegetative proliferation from rhizomes within established stands and in rivers currents, where small rhizome fragments easily root and sprout under favourable conditions (Ellenberg, 1982). Accordingly, Ellenberg called them “river valley-hikers”. Dispersal along river corridors can frequently be observed; for instance, goldenrod populations are currently expanding along the Tagliamento River (northern Italy; Karrenberg, personal communication).

The relative significance of sexual reproduction increases with the age of the clone, whereas clonal growth is most essential during the first years after establishment.

### Spatial distribution of plants within populations

The rhizomes grow outward from the centre of a clone. Rhizomes are rather long and branch frequently, and populations mostly consist of several or many intermingled genets. The ratio of fertile to vegetative shoots varies considerably among populations, depending on soil and light conditions. Voser-Huber (1983) found an inverse relationship between shoot density within a patch and percent flowering stems.

Established stands are species-poor in the centre and have a higher species richness towards the edges (Voser-Huber, 1983; Lukac, 1988). Lateral population expansion as a result of clonal growth was found to range from 0.3–0.8 m/year in an unmown swamp meadow in Switzerland (Gigon and Bocherens, 1985). The number of rhizomes produced per ramet in one growing season varies between 5 and 55. A high number of rhizome buds allows plants to quickly resprout after disturbances (Cornelius, 1987). The number of sprouting rhizome buds exceeds that of *S. canadensis* by a factor 10 (Voser-Huber, 1983), which may partly explain the colonization success of *S. gigantea*. Furthermore, rhizomes are on average much longer; thus the species may cover larger areas and expand population patch size over relatively short time periods (Schmid et al., 1988). Rhizome connections last several years and

longer in the absence of herbivores. Indeed, the absence of rhizome herbivory in the introduced range may be one reason for the higher number of rhizomes observed in natural populations.

Final size depends on the amount of precipitation in autumn (Jakobs, 2004). Rhizomes typically grow to a length of c. 90 cm. In favourable conditions, rhizomes are on average shorter, and thus clones are denser; the longer rhizomes, which develop under poorer conditions, may increase the chance to reach more suitable sites. In recently abandoned fields, individual clones are often easy to distinguish and frequently achieve 2–5 m diameter. Larger, older clones may contain thousands of ramets. Occasionally clones form ‘fairy circles’ around the initial centre of the genet.

### Phenology

Shoot elongation starts in spring and shoot height increases nearly linearly until the end of July. Final plant height is only reached after the formation of inflorescences and the opening of the first flowers, usually between August and September. *S. gigantea* flowers late in the season – between July and November – with a peak flowering time between mid August and the end of September. If detached, the seeds are easily dispersed by wind, but the majority of seeds remain on the stem even during winter.

Germination of seeds is highest in spring, but occurs until summer. If seedlings take a relatively long time span for germination, not all plants may come to flower in the first year of establishment (Voser-Huber, 1983).

Rhizomes may be produced within four weeks after germination. Numerous rhizome buds appear in spring and new rhizomes start to sprout in summer. The total number of rhizomes per ramet reaches 50 in the first years but is reduced in older populations, perhaps reflecting a trade-off with sexual reproduction. The first rhizome buds start to sprout in summer, but the majority do not do so before autumn or spring of the following year. Apart from vegetative reproduction, rhizomes function as storage organs. Water, nutrients and assimilates are transferred into the rhizomes after flowering (Voser-Huber, 1983).

The number of leaves per stem correlates with shoot height and the number of inflorescence branches. The lower leaves gradually die and thus the total leaf number decreases continuously during summer. The total leaf area is largest in July (Botta-Dukát and Dancza, 2001b).

### Reproduction

Reproduction occurs every year, though small shoots within established stands may remain vegetative. On the other hand, isolated shoots growing in unfavourable

conditions can flower when very small (25 cm). Under good conditions, almost all plants reproduce in their first year, and a single ramet produces up to 19,000 achenes. Long hairs improve dispersal abilities of the seeds. *S. gigantea* is self-incompatible and dependent upon insects for pollination (Voser-Huber, 1983). The inflorescences are very attractive to pollinators due to their bright yellow flowers and high amounts of pollen and nectar. Frequent visitors in Europe include members of Phalacridae, Muscidae, Syrphidae, Apidae, Formicidae, Sphecidae, and Panorpidae (Bopp, 1997; Voser-Huber, 1983).

Under resource limited conditions, sexual reproduction is reduced to the benefit of vegetative growth, raising the chances of permanent establishment in an area once occupied. Higher relative biomass allocation into rhizomes has been shown for plants exposed to high competition pressure, especially belowground competition. Within established stands, *S. gigantea* probably propagates only vegetatively, as in the case of the closely related *S. altissima* (Hartnett and Bazzaz, 1985; Meyer and Schmid, 1999). There is a trade-off between seed number and seed weight, and the number/weight ratio depends on local environmental conditions (Werner and Platt, 1976). In less favourable conditions and under frequent disturbances, more and lighter seeds are produced, guaranteeing a long distance dispersal, whereas under good conditions, fewer and larger seeds improve the chances of successful seedling establishment in surrounding sites with a closed vegetation cover (Werner and Platt, 1976).

## Germination

*S. gigantea* is described as euryoecious. Within dense stands, however, seedling germination is inhibited by diterpenoids in the closely related *S. altissima* and may equally occur in *S. gigantea* (Werner et al., 1980). *S. gigantea* seeds may germinate up to 100%, however, germination rates depend on soil conditions: on loamy soil and on peat, germination was c. 47%, whereas on filter paper, it was 99% within three weeks (Voser-Huber, 1983). In experiments conducted by Barrawasser (2002), germination started after 3–5 days, only in low temperature (14 °C) germination was retarded. The retarded germination at low temperatures may be related to slower water uptake, and subsequently reduced mobilization of resources in the seed. Length of the hypocotyl is on average 5 mm, that of the cotyledons 2–2.8 mm. A longer radicle develops under cooler conditions (10–11 mm below 27 °C, 5–6 mm above 27 °C). Length of the following leaves is also strongly temperature dependent, with an optimum of 27 °C. In darkness, the radicle remains short (max. 3.5 mm), while the hypocotyl grows up to 14 mm long.

Osmotic concentration in *S. gigantea* seedlings is highest in the hypocotyls, indicating the significance of shoot elongation for successful establishment (Barrawasser, 2002). At a later stage, when the seed's resources are limited, the osmotic concentration rises markedly in the radicle enabling nutrient uptake from the soil. Seedling establishment mostly requires open gaps, although establishment in closed meadows is occasionally observed in otherwise beneficial conditions.

## Response to competition and management

Interspecific competition – *S. gigantea* reacts plastically to interspecific competition, and the particular effect depends on the type of competitor (Fig. 2). Aboveground competition favours shoot and inflorescence height, whereas belowground competition enhances rhizome growth (Jakobs et al, in press). The morphological plasticity of the species is considered as essential factor contributing to the invasiveness of the species in Europe (Botta-Dukát and Dancza, 2001a; Jakobs et al., in press): Table 1. Indeed, *S. gigantea* often forms monospecific stands which almost no native species can invade (Balogh, 2001), making it of special concern for nature conservation. Ruderal areas usually experience a pronounced reduction in species diversity after goldenrod establishment. In species-rich dry meadows, the ecological impact may be even more severe. The average species number in meadows with goldenrods is with 12.5 species markedly lower than in adjacent areas without goldenrods with an average species number of 22.9 (Schuldes, 1988; Voser-Huber, 1983). The reduction primarily affected species such as *Lysimachia vulgaris*, *Potentilla erecta*, *Betonica officinalis*, *Filipendula ulmaria*, *Scabiosa columbaria*, *Centaurea scabiosa*, *Campanula glomerata* or *Succisa pratensis*. More abundant species appear to be less affected. In

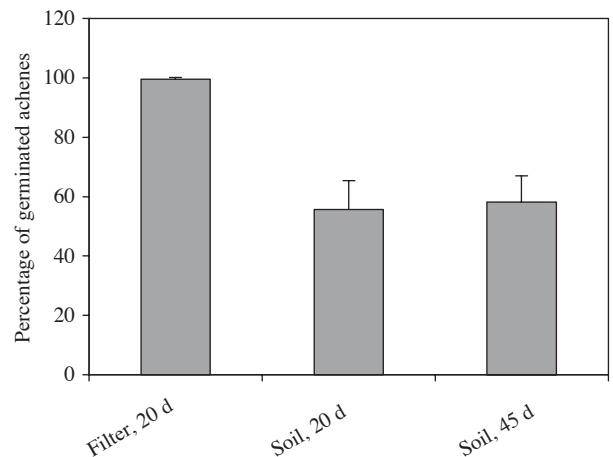


Fig. 2. Germination rates of *Solidago gigantea* on various substrates. Tests were conducted at room temperature and without pretreatment of seeds. After Voser-Huber (1983).

**Table 1.** Summary table of plant height and leaf area of European *Solidago gigantea* grown in full sunlight and 70–80% sunlight

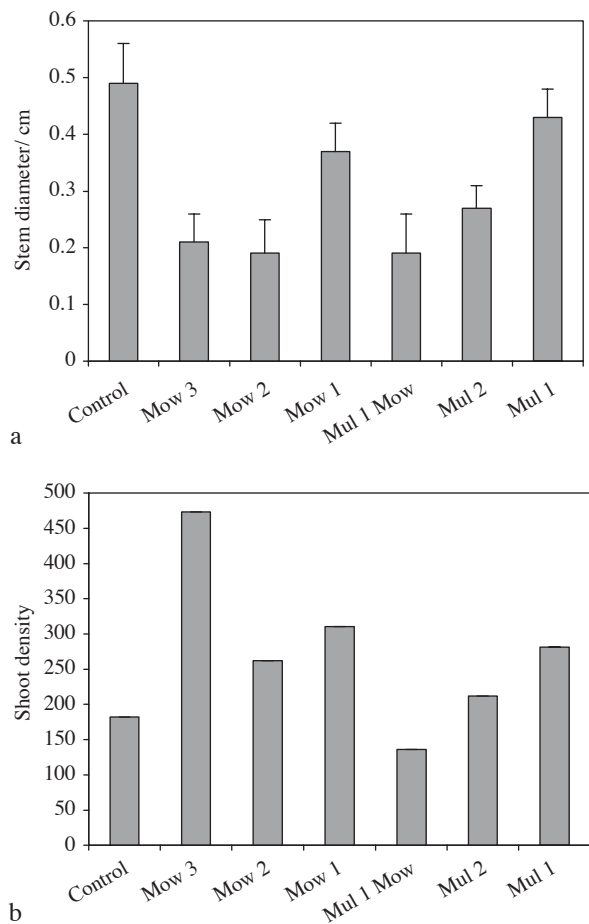
Plant trait	Sunlight	Shade	Prob > F
<i>Size</i>			
Height in May (cm)	23.4 ± 1.4	27.0 ± 3.0	n.s.
Height in July (cm)	82.0 ± 0.9	88.8 ± 1.1	*
Height in September (cm)	117.6 ± 1.6	125.1 ± 3.1	***
Leaf area (cm <sup>2</sup> )	46.3 ± 1.1	49.8 ± 0.7	**
First flower opening	43.0 ± 3.2	95.0 ± 7.1	***
Flowering time	16.3 ± 1.7	29.9 ± 3.1	***

Flower opening was measured in days after seeding (March 1, 2000), flowering time as number of days during which flowers are open. The effect of shading on shoot elongation, leaf growth and flowering time was significant, Prob > F indicates differences in an ANOVA (\* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.0001$ ).

river valleys, dense populations may suppress the rejuvenation of floodplain vegetation. Here *S. gigantea* often occurs with other invasive species such as *Impatiens glandulifera*, *Heracleum mantegazzianum*, *Reynoutria japonica*, and *Helianthus tuberosus*. Similarly, seedling establishment in forests may be impeded by dense monospecific stands (Zwölfer, 1976). Economic impacts arise mainly in perennial crops and forest nurseries, but also the quality of hay may be reduced due to high saponin contents.

**Response to management measures** – The vigour of *S. gigantea* stands can be strongly reduced by regular mowing or by a combination of mowing and rotavating the soil. Sowing native plant species has also been used to increase competition on *S. gigantea*. Hartmann et al. (1995) report results of various measures to suppress the growth of *S. gigantea* (Fig. 3). Effective measures to reduce shoot density and vitality include mowing once a year and mulching, or mowing twice a year without mulching, over a period of 3 years. Such severe disturbances, however, may also affect native species and are thus problematical in conservation sites. *S. gigantea* responds to mowing by a reduced stem diameter and by stimulating strong regrowth from rhizome buds. A single cut each year does not significantly reduce shoot density, and infrequent cutting and ploughing might even have the reverse effect by increasing population density in the following year. Mulching reduces the vitality more strongly than does mowing, perhaps because the litter inhibits the growth of goldenrods more than that of other plant species, leading to increased competition on goldenrods (Hartmann et al., 1995).

A very effective technique is flooding goldenrod stands for a period of more than ten days, particularly in swamplands or river valleys where high water levels naturally occur. Covering the soil with opaque foil for a period of 3 months also destroys goldenrods, but it kills

**Fig. 3.** Effects of management measures on (a) stem diameter and (b) shoot density as two measure of vitality of *Solidago gigantea*. After Hartmann et al. (1995).

other plant species as well. Because this management creates open space that may be recolonized by invasive species, it is only recommended in combination with the sowing of legumes and native species.

## Herbivores

In the native range, *S. gigantea* is under strong top-down control by herbivores such as gallmakers (*Eurosta solidaginis*, Diptera: Tephritidae, *Rhopalomyia* ssp., Diptera: Cecidomyidae), aphids (*Uroleucon* ssp., Hemiptera: Aphidae) and beetles (*Trirhabda*, Coleoptera: Chrysomelidae) (Abrahamson et al., 1991, 2001). In contrast, herbivory usually has little influence on populations in the introduced range. A study in Göttingen (Germany) reported various insects and also rabbits feeding on *S. gigantea*. Most of the insect species were generalists, with only the bee *Colletes daviesanus* being specialized on Asteraceae. Generalist insects included predominantly ectophagous species; endophagous taxa, nectar- and pollen collectors were less

abundant (Bopp, 1997). Jakobs et al. (2004) described the extent of herbivory in Europe as being extremely low, and the effect on the performance of *S. gigantea* as negligible.

Introduced European populations appeared more susceptible to certain herbivores and pathogens if reintroduced to the native range (Meyer et al., 2001). This could be due to a loss of defensive ability in the invasive range. If costly defence mechanisms are no longer needed in Europe, there may have been selection favouring more competitive genotypes rather than well defended ones. In contrast, in introduced areas of Japan, the species is attacked by herbivores and produces herbivore deterrents, if attacked (Moshizuki, 1990). Thus, specific habitat conditions evoke pronounced differences in the evolutionary development of the species.

Weigmann et al. (1985) report that the litter of *S. gigantea* is decomposed by Collembola and mites to an extent of 70% within a month. However, other studies have shown that the decomposition rate of litter under standard conditions is highly variable between populations (Güsewell, personal communication).

### Mycorrhiza

Arbuscular mycorrhizal (AM) fungi occur on roots of *S. gigantea*. A recent greenhouse study demonstrated an increase in biomass production in plants grown with soil inoculated with mycorrhiza, mainly affecting clonal growth (Kytoviita et al., 2003). In the field, soil moisture increases the probability of mycorrhizal colonization (Young et al., 2000).

### Physiological data

Photosynthesis rates are higher early in the season ( $19 \pm 2 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ ) than later ( $16 \pm 2 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ ) (Schmid et al., 1988). In contrast, stomatal conductance and transpiration slightly increases over time. Chlorophyll contents vary among populations and are generally higher in European populations in spring; differences even out later in the season (Jakobs, unpublished data).

### Biochemical data

*S. gigantea* contains various compounds including terpenoids, phenolic compounds, coumarines, polyacetylic substances, polysaccharides, essential oils, and diterpenebutenolides (Bader, 2004; Bornschein, 1987; Gerlach, 1965; Jurenitsch et al., 1988). The roots contain large amounts of furanoid compounds and acidic compounds (solidagoic acids) (Anthonse et al., 1973). The hydrodistilled essential oil of aerial parts of *S.*

*gigantea* contains up to 90 constituents (Kalemba et al., 2001). The saponins of *S. gigantea* have been analysed by Jurenitsch et al. (1986) and Reznicek et al. (1990, 1996).

Several goldenrod species have long been used in medicine, as indicated by the genus name *Solidago*, which derives from the Latin “solidare” – to strengthen. Saponins, flavonoids and phenolic glycosides have been identified as essential compounds for pharmaceutical use.

*S. gigantea* exhibits moderate spasmolytic and diuretic properties (Leuschner, 1995). Both may be related to the flavanoids rutosid, quercitrin and other chemically related substances. The compound 3,5 di-*O*-caffeoyl acid of several goldenrod species has anti-inflammatory properties and has no negative side-effects; it has therefore attracted some interest as a potential medication. Extracts of *S. gigantea* also show antimycotic activity, especially against *Candida pseudotropicalis* (Pepeljnjak et al., 1998).

### Status of the species

*S. gigantea* is considered to be one of the most aggressive plant invaders in Europe. Negative effects mainly concern ecology and nature conservation. In forest nurseries and reforestation areas, the species also causes economic damage (Capek, 1971). Because it causes problems in nature reserves and reforestations, it is frequently the subject of control measures, however, these are usually difficult and costly. Eradication of the species is not realistic and management must be restricted to specific areas of special ecological concern. *S. gigantea* is believed to be a suitable candidate for biological control (Capek, 1971; Zwölfer, 1976). For further information, see the section “Response to competition and management”.

*S. gigantea* has been introduced as an ornamental and is still available in garden nurseries (PPP Index).

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