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STOMATAL STRUCTURE IN *SOLIDAGO* L. SPECIES AS THE INDEX OF THEIR ADAPTATION OPPORTUNITIES

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The study of the adaptability of alien plant species is very important. According to this characteristic there is possible to forecast their further spreading in the secondary distribution range. This is especially relevant for the species having already "escaped" from cultivation and started actively invading the natural communities. Well known that the structure of the leaf blade reflects the adaptability of the species. The purpose of this study is to compare the stomatal structure of cultivated *Solidago* L. species to assess their adaptive capacity. Alien specimens from the collection of Padova botanical garden (Italy): *S. altissima* L., *S. caesia* L., *S. canadensis* L., *S. graminifolia*(L.) Salisb., *S. juncea* Aiton, *S. latifolia* L., *S. lepida* DC., *S. rugosa* Mill., *S. sempervirens* L., *S. serotinoides* Á. Löve & D. Löve (= *S. gigantea* var. leiophylla Fernald), *S. uliginos*a Nutt. were the objects of the study. The stomata were characterized by 21 quantitative characteristics. Various strategies were being implemented to increase the total transpiration area of plants: increasing the size of stomata; increasing the number of stomata; increasing the area of the leaf blade; increasing the number of leaves on the shoot; increasing the number of the shoots. In terms of the relative transpiration area index (I_{ot}, %), the species are divided into three groups with a high (25–50), medium (15–25) and low (<15) I_{ot}. Our article is considered as a basis for monitoring the dissemination of alien species. The high value of I_{ot} indicates the greater adaptiveness of alien species and can be used to predict the further expansion of their secondary distribution range and increase the chances of transforming into an invasive taxon.

Keywords: *Solidago*, leaves, stoma, invasion plants

Introduction

North American *Solidago* L. species have been cultivated in European botanical gardens since the end of the 17th century (Kowarik, 2003). The most complete collection of this genus is represented in the oldest botanical garden of Europe – in Padua (Italy). The garden was established in 1545 by the decision of the Venetian Senate with the aim of growing "medicinal herbs" for the Faculty of Medicine of the University of Padua. In 1997, like the "prototype of all botanic gardens", it was listed by UNESCO as a World Heritage Site (Buffa et al., 1999).

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Solidago altissima L., *S. caesia* L., *S. canadensis* L., *S. graminifolia* (L.) Salisb., *S. juncea* Aiton, *S. latifolia* L., *S. lepida* DC., *S. rugosa* Mill., *S. sempervirens* L., *S. serotinoides* Á. Löve & D. Löve (= *S. gigantea* var. leiophylla Fernald) and *S. uliginos*a Nutt. grow in the historic part of the garden. All these species naturally grow on the territory of North America and have established into Europe through an intentional introduction. Three of them (*S. altissima*, *S. canadensis*, and *S. gigantea*) are naturalized in Europe (Tutin et al., 1976) and invaded the natural phytocenoses, i.e. belong to the group of invasive species (Lambdon et al., 2008; Vinogradova et al., 2010). In recent years *S. graminifolia* has been an active expansion of the secondary distribution range. It is marked as invasive in Poland and Belarus. The aboriginal *S. virgaurea* L. is included in the collection, too.

The quantitative characteristics of stomata are highly dependent on environmental conditions; therefore, it is not always possible to carry out a comparative analysis of different taxa on these parameters. Here, in the Botanical Garden of Padua, the plants grow side by side, on the same agricultural background, in partial shade. This allows comparing the characteristics of the stomatal apparatus of various species. It is known that the adaptive capacity of plants can be assessed by the morpho-anatomical feathers of the leaves (Marin et al., 1988; Kiseleva, 2009; Egorova et al., 2016; Vinogradova et al., 2018). For example, a small number of stomata and their small size provide the permanent opening of stomata and excessive transpiration, which may indicate low adaptability of plants to light and humidity conditions. The correlation between some micromorphological structures and the degree of plant's adaptation to various ecological conditions is proved for many species: *Crataegus* spp. (Foroughbakhch et al., 2000; Ganeva et al., 2009), *Calystegia soldanella* (L.) Roem. & Schult., *Euphorbia paralias* L. and *Otanthus maritimus* L. (Ciccarelli et al., 2009), *Amelanchier ovalis* Medic (Ganeva and Uzunova, 2010b), *Prunus armeniaca* L. (Laajimi et al., 2011), *Pinus roxburghii* Sarg. (Tiwari et al., 2013), *Mespilus germanica* L. (Koçyiğit et al., 2015), *Cornus* spp. (Klymenko and Klymenko, 2017), *Typha domingensis* Pers. (Akhta et al., 2017), *Cydonia oblonga* Mill., *Pseudocydonia sinensis* (Thouin) C.K. Schneid. and *Chaenomeles japonica* (Thunb.) Lindl. ex Spach (Vinogradova et al., 2018).

The evaluation of adaptive capacity is very relevant for alien species. It gives a possibility to predict the further expansion of their secondary distribution range. For genus *Solidago*, this is doubly relevant since already several species of this genus "escape" from cultivation and began to be actively invaded the natural cenoses. There are data on the leave's structure only for alien *S. canadensis*, *S. gigantea* (= *S. serotinoides*) and *S. graminifolia* as well as aborigen *S. virgaurea* (Szymura and Wolsky, 2011; Vinogradova, 2012). Data for other *Solidago* spp. concerned only macromorphology of these species (Weber, 2000). Our work is the first study of leaf anatomy for the most part of *Solidago* spp., which is cultivated in Europe.

The purpose of this work is a comparative analysis of the stomatal characteristics of cultivated *Solidago* species to assess the adaptive capabilities of these alien species.

Material and methods

Plant material

Samples of the following alien *Solidago* species from the collection of the botanical garden in Padua are the objects of the study: *S. altissima*, *S. caesia*, *S. canadensis*, *S. graminifolia*, *S. juncea*, *S. latifolia*, *S. lepida*, *S. rugosa*, *S. sempervirens*, *S. serotinoides*, and *S. uliginos*a. During the visit to the garden at the beginning of June 2017, we collected leaves per each species. For the analysis, 3 shoots of each species were selected, and from each shoot 3 leaves were selected from the basal part of the stem (total 9 leaves per each species).

Ultrastructure of leaves

To study the features of the stomatal apparatus, the method of obtaining lacquer replicas was used. Unfortunately, it was not possible to obtain clear prints of the epidermis in *S. latifolia* due to a thin wax coating covering the leaves, and this species is not included in our study. The following micro-morphological features were analyzed: the number of guard cell of the stoma, the length of the polar axis of the stoma (l), the length of the equatorial diameter (d), the shape of the stomata (by the ratio l/d), the area of the one stoma (s ellipse= $\pi(l/2)\ (d/2)$), the number of stomata in the field of the microscope view (n), the total transpiratory area (= $s \times n$). The relative transpiration area (relative transpiration index, I_{ot}) was calculated as the ratio of the total average transpiration area to the total area of the underside of the leaf blade, according to the formula:

$$I_{ot} = \frac{\sum n\pi LD}{\sum S} 100\%$$

These seven signs were studied for both the upper and lower sides of the leaf blade, and then their ratio was determined. Thus, the stomatal apparatus of 10 species are characterized by 21 quantitative traits.

Morphology of the stomatal apparatus was examined with the Keyence VHX-1000E digital microscope. The number of stomata in the field of the microscope view with an increase of × 1,500 was determined in 10 replicates. The total number of stomata for each species to determine their size is 50–100.

Analysis of data

Basic statistical analyses were performed using PAST 3.15. Data were submitted ANOVA and differences between means compared through the Tukey-Kramer test (α = 0.05). All data are presented as M ±m, where *M* – arithmetic average, *m* – arithmetic average deviation.

Results and discussions

The size of the leaf blades in the studied species decreases in the following order: *S. sempervirens* → *S. juncea* → *S. altissima* → *S. serotinoides* → *S. canadensis* → *S. rugosa* → *S. lepida* → *S. caesia* → *S. uliginos*a → *S. graminifolia*. In three species (*S. altissima*, *S. canadensis*, and *S. rugosa*) the leaves are amphystomatic, i.e. the stomata are located only on the lower (abaxial) side of the leaf; in other species, the leaves are hypostomatic, and the stomata are located on both the lower and the upper (adaxial) side of the leaf blade (Figure 1A, B).

Figure 1A Plant habitus and microphotographs of stomata on the abaxial and adaxial side of the leaf blade 1 – *Solidago altissima* L.; 2 – *Solidago caesia* L.; 3 – *Solidago canadensis* L.; 4 – *Solidago graminifolia* (L.) Salisb.; 5 – *Solidago juncea* Aiton; 6 – *Solidago lepida* DC.

Figure 1B Plant habitus and microphotographs of stomata on the abaxial and adaxial side of the leaf blade 7 – *Solidago rugosa* Mill.; 8 – *Solidago sempervirens* L.; 9 – *Solidago serotinoides* Á. Löve & D. Löve; 10 – *Solidago uliginosa* Nutt.

The samples were significantly divided into 2 groups (Figure 2, Table 1), according to the size of stomata from the abaxial side of the leaf blade. The first group, characterized by large stomata (36–40 × 28–30 µm), includes *S. sempervirens*, *S. altissima*, and *S. juncea*.

All other species are included in the second group (19–28 × 16–22 µm), with the exception of *S. serotinoides*. *S. serotinoides* are distinguished by the highest variability of this feature (27–41 × 20–34 µm) and in Figure 2 is not even displayed since it occupies an intermediate position between the two groups and overlaps all other samples.

In most samples, the shape of the stomata is rounded: the ratio of the average length of the polar axis to the average length of the equatorial diameter is 1.2–1.4. Only in *S. serotinoides* on the adaxial side of the leaf blade, stomata are elongated, and this ratio is 1.7.

Table 1 Quantitative characteristic of stomata in *Solidago* L. species

Species	Polar axis (*l*) (µm)			Equatorial diameter (*d*) (µm)			*l*/*d*		
	min	max	$\bar{x}$ ±S*x*	min	max	$\bar{x}$ ±S*x*	min	max	$\bar{x}$ ±S*x*
				Abaxial side of the leaf blade					
S. sempervirens	36	44	39.7 ±0.8	25	36	30.3 ±0.8	1.0	1.5	1.3 ±0.0
S. altissima	26	51	36.4 ±0.8	23	31	27.7 ±0.4	1.1	1.9	1.3 ±0.0
S. juncea	29	37	32.6 ±0.4	24	32	28.2 ±0.4	1.0	1.3	1.2 ±0.0
S. uliginosa	23	36	27.7 ±0.7	17	25	21.6 ±0.4	1.1	1.6	1.3 ±0.0
S. caesia	18	30	26.3 ±0.7	14	23	20.0 ±0.7	1.1	1.6	1.3 ±0.0
S. canadensis	21	32	26.3 ±0.6	15	28	20.2 ±0.4	0.9	2.1	1.3 ±0.0
S. lepida	17	28	23.9 ±0.5	11	21	18.0 ±0.4	1.0	1.9	1.3 ±0.0
S. graminifolia	17	25	22.6 ±0.4	13	23	19.0 ±0.4	1.0	1.8	1.2 ±0.0
S. rugosa	14	28	19.4 ±1.2	11	21	15.9 ±0.8	0.9	1.5	1.2 ±0.0
S. serotinoides	27	41	32.8 ±0.9	20	34	24.5 ±0.8	1.0	2.0	1.4 ±0.1
				Adaxial side of the leaf blade					
S. sempervirens	33	42	37.1 ±0.6	27	35	30.3 ±0.4	1.1	1.4	1.2 ±0.0
S. altissima					stomata are absent				
S. juncea	28	43	33.5 ±0.9	18	30	25.5 ±0.8	1.1	1.8	1.3 ±0.1
*S. uliginos**a***	21	32	24.9 ±1.0	19	23	21.3 ±0.4	1.0	1.5	1.2 ±0.1
S. caesia	23	25	24.3 ±0.7	14	20	17.3 ±1.8	1.3	1.6	1.4 ±0.1
S. canadensis					only one stoma				
S. lepida	18	27	23.2 ±0.5	15	23	17.4 ±0.5	1.1	1.7	1.3 ±0.0
S. graminifolia	18	27	23.1 ±0.3	13	23	19.0 ±0.4	1.0	1.8	1.2 ±0.0
S. rugosa					stomata are absent				
S. serotinoides	26	31	29.0 ±1.5	15	18	17.0 ±1.0	1.4	2.0	1.7 ±0.2

Note: min, max – minimal and maximal measured values; $\bar{x}$ – arithmetic mean; S*x* – standard error of the mean

The most species (5 of 7) have hypostomatic leaves, i.e., the number of stomata is greater on the abaxial side of the leaf than on the adaxial side, and stomata are larger (Figure 2). In *S. graminifolia*, the size of the stomata on the adaxial and the abaxial side of the leaf blade is not significantly different, and the number of stomata on the underside of the leaf (average 5.6) is lower than on the adaxial side (average 6.8 in the field of the microscope view). In *S. sempervirens*, the stomata on the abaxial side of the leaf are larger than on the adaxial one (as for the most species), but their number on the abaxial side (as in *S. graminifolia*) is lower than on the adaxial side (2.4 contrary 3.0). These parameters are shown in Figure 3, 4.

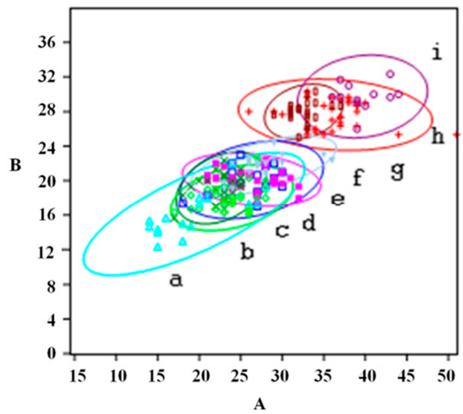

Figure 2 The stomatal size of *Solidago* species on the underside of the leaf blade
a – *Solidago rugosa* Mill.; b – *Solidago graminifolia* (L.) Salisb.; c – *Solidago lepida* DC.; d – *Solidago canadensis* L.; e – *Solidago caesia* L.; f – *Solidago uliginosa* Nutt.; g – *Solidago juncea* Aiton; h – *Solidago altissima* L.; i – *Solidago sempervirens* L.

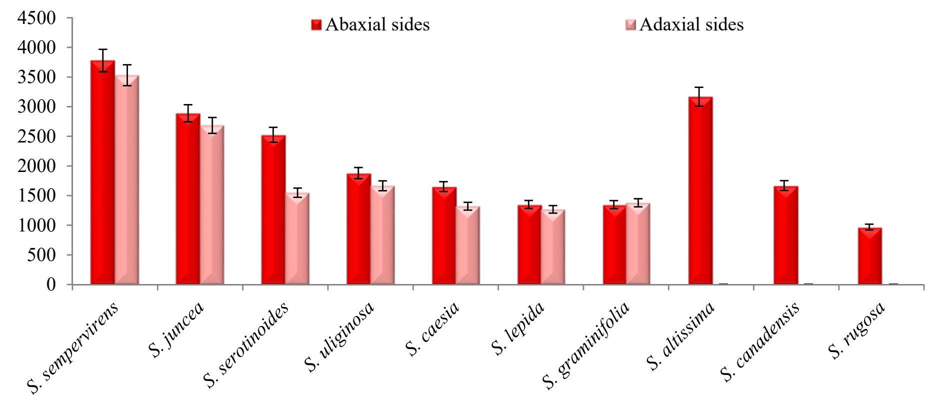

Figure 3 The average area of the one stoma on the leaf blades of *Solidago* spp. (μm^2) (each value represents the mean of three independent experiments (±SD)

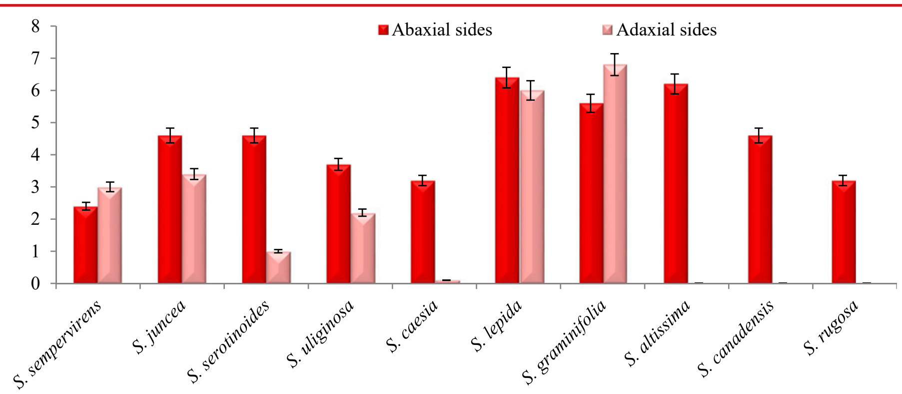

Figure 4 The average number of stomata in the field of the microscope on the leaf blades of *Solidago* spp. (each value represents the mean of three independent experiments (±SD)

When comparing these two figures, it is clearly seen that the average area of one stoma negatively correlates with the average number of stomata, therefore the variability of the average transpiration area is relatively low (Figure 5). In order to make a correct comparison of species over the area of transpiration, the relative transpiration index (I_{ot}) have been calculated: the ratio of the total average transpiration area to the total area of the abaxial side of the leaf blade.

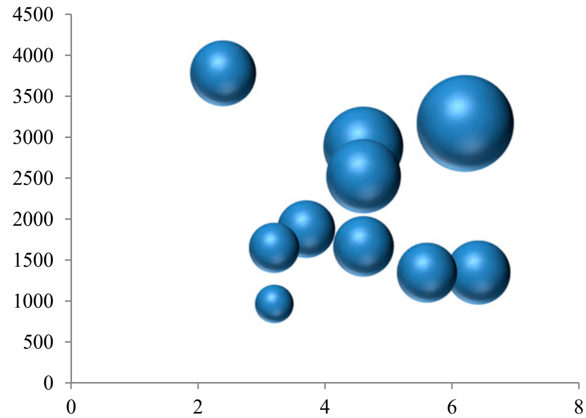

Figure 5 The average total transpiration area in the field of view of the microscope on the underside of the leaf blade of *Solidago* spp. (μm^2)

According to this index I_{ot}, the studied species line up in the following order (%): *S. altissima* (50), *S. juncea* (34), *S. serotinoides* (29), *S. sempervirens* (23), *S. lepida* (22), *S. canadensis* (19), *S. graminifolia* (19), *S. uliginos*a (18), *S. caesia* (13) and *S. rugosa* (8).

Our data on the stomatal characteristics in various *Solidago* species are correlated quite well with the invasive activity of these taxa. In this respect, the relative transpiration area index is especially indicative. *S. altissima* and *S. serotinoides*, which are widespread in the secondary distribution range, have at the same time the largest relative transpiration area (from 25 to 50%). *S. juncea*, which also has a high value of this indicator, is already beginning to be invaded the natural cenoses of Russia. This species was collected by A.A. Notov in the Tver region (Herbarium collections MW, MHA). *S. sempervirens*, *S. lepida* and *S. uliginos*a have an index from 15 to 25%. They are similar on this parameter with the invasive *S. canadensis* and *S. graminifolia*, they are able to adapt well to the conditions of the Old World. They are less decorative and their presentation in the culture is not enough. This prevents (for now!) to the wide distribution of these species. *S. caesia* and *S. rugosa* are poorly adapted to the conditions of the new homeland (I_{ot} <15 %), the latter also had short shoots with few leaves in the beds in the Padua Botanical Garden.

Thus, we can take into consideration the stomatal structure (in addition to other features) for the prediction of the possible expansion of some alien species in their secondary distribution range. If an alien species has I_{ot} >25%, it is more likely to transform into an invasive taxon. Such species require stronger control measures of their dissemination.

Conclusions

In *Solidago* species cultivated in the Botanical Garden of Padua, the size of stomata is generally negatively correlated with the average number of stomata. Various strategies are being implemented to increase the total transpiration area of the plants. At the cellular level, this is an increase in stoma size (*S. sempervirens*, *S. altissima*, *S. juncea*) and an increase in the number of stomata (*S. altissima*) up to the formation of hypostomatic leaves, i.e. the location of numerous stomata on both sides of the leaf blade (*S. lepida*, *S. graminifolia*). At the organism level, the strategy of alien species is either to increase the area of the leaf blade, which is especially characteristic of rosette leaves (*S. sempervirens*, *S. juncea*, *S. uliginos*a), or to increase the number of leaves on the shoot (*S. lepida*) or to increase the number of shoots (*S. serotinoides*, *S. graminifolia*). According to the index of the relative area of transpiration, species are divided into a group with a high (25–50%) relative area of transpiration (*S. altissima*, *S. serotinoides*, *S. juncea*), an average (15–25%) area (*S. sempervirens*, *S. lepida*, *S. uliginos*, *S. canadensis*, and *S. graminifolia*) and a low (less than 15%) relative area of transpiration (*S. caesia* and *S. rugosa*).

The high value of the index of the relative area of transpiration indicates greater adaptability of alien species and can (among other features) be used to predict the further expansion of their secondary distribution range and increase the chances to transform into an invasive taxon.

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