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Research Article

Competitiveness of the Exotic *Silphium perfoliatum* against the Native *Urtica dioica*: A Field Experiment

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Silphium perfoliatum (cup plant) is native to North America and is increasingly used as a bioenergy crop in Germany. Spontaneous occurrences of this species have already been detected in several European countries. To assess the possible risk to biodiversity by spreading of *S. perfoliatum*, we investigated the competitiveness of this species against the native and highly competitive *Urtica dioica* over four years in a field experiment in Bayreuth (Germany). *S. perfoliatum* grew well among *U. dioica*, although its biomass was strongly reduced by surrounding *U. dioica*. Projection area, plant height, and reproductive potential were less or similarly reduced by surrounding *U. dioica* as by the intraspecific competition. Moreover, *S. perfoliatum* significantly suppressed the growth of the competitive *U. dioica*. A settlement and establishment of *S. perfoliatum* in the native flora of Central Europe and a suppression of uncompetitive plant species are therefore conceivable.

1. Introduction

Invasive species are one of the major factors promoting global species extinction and the loss of biodiversity [1]. In the European Union, 39 invasive plant species are known and tried to be controlled [2]. It would probably be more successful to identify and manage risky species before they become invasive. Many of today's invasive plant species in Europe were introduced intentionally as ornamental plants or crops [3, 4]. However, an investigation of the potential invasiveness of exotic plant species is hardly executed before they are cultivated on a large scale [5].

One such intentionally introduced species for which there are hardly any studies on the possible invasive potential is *Silphium perfoliatum* L. (cup plant). Native to eastern North America, it was introduced to Europe in the 18th century as an ornamental plant [6]. It has been used as an alternative bioenergy crop in Germany since 2004 [7]. The predominant bioenergy crop at present is *Zea mays* L. (maize) [7, 8]. Its cultivation goes along with major ecological damage due to high application of machines, fertilizers, and pesticides [7, 8]. *S. perfoliatum* is an appropriate alternative with many ecological advantages over *Z. mays* [7–10]. In Germany, more than 10,000 ha are cultivated with *S. perfoliatum* so far [11]. This perennial, yellow-flowering, and tall herb is of the Asteraceae family. It develops shoots from the second year on and persists for many years [6]. As a bioenergy crop, *S. perfoliatum* can be used for more than 15 years [12]. It is easy to cultivate, highly productive, competitive, and strongly reproductive [6, 7]. These traits make it attractive as a crop but also potentially dangerous if it spreads from its fields. The latter is already documented in northern Bavaria (Germany) [13]. Furthermore, spontaneous occurrences are noted in Germany and in several other European countries, e.g., Belgium, Austria, and Poland [14, 15]. In the Netherlands and Russia, *S. perfoliatum* is already classified as "potentially invasive" [16, 17].

According to EU legislation, a species is being classified as invasive if its spread threatens biodiversity (Article 3, No.

2 EU-Regulation No. 1143/2014). To pursue the question of an invasive potential and especially the possible threat to biodiversity posed by *S. perfoliatum* in Central Europe, we investigated the competitiveness of this species for the first time over four years in a field experiment in the Ecological Botanical Gardens of the University of Bayreuth in Germany. The central questions were as follows:

(i) Initial phase (first to second year of growth):

(1) Is *S. perfoliatum* able to settle among native plants?

(ii) Establishment phase (second to fourth year of growth):

(1) Is *S. perfoliatum* able to establish among native plants?
(2) Is *S. perfoliatum* able to suppress native plants?
(3) Is *S. perfoliatum* able to reproduce among native plants?

As the confronted native plant species, we chose *Urtica dioica* L. (common nettle). It is widely spread in Central Europe and belongs to the Urticaceae family [18–20]. Like *S. perfoliatum*, *U. dioica* is a perennial herbaceous plant that grows tall and is very competitive [19–21]. It occurs in nutrient-rich habitats and develops dominance stocks that are one of the most common fringe communities in Central Europe [20]. So far, *S. perfoliatum* settles predominantly in the immediate surroundings of its agricultural fields, which are mostly nutrient-rich fringes [13]. Therefore, *S. perfoliatum* can potentially coexist with *U. dioica*.

Assessing the competitiveness of the exotic *S. perfoliatum* against the competitive native *U. dioica* provides valuable insights that are relevant for evaluating a possible threat to biodiversity by *S. perfoliatum* and its invasive potential.

2. Materials and Methods

2.1. Experimental Setup. The experiment was carried out from May 2019 to August 2022 as a field experiment at the Ecological Botanical Gardens of the University of Bayreuth (Germany). Mean air temperatures over the growing seasons from April to August each year were between 13.7 and 15.8°C (Table 1). Precipitation sum during this period varied between 195 and 342 mm among the years.

On 11 March 2019, triple the number of seeds we needed plants for the experiment of *S. perfoliatum* (Metzler & Brodmann Saaten GmbH, Ostrach, Germany) and *U. dioica* (Jelitto Perennial Seeds, Schwarmstedt, Germany) were sown in the greenhouse (Figure 1). Two and a half weeks after sowing, 1.5 times the required number of seedlings that we needed for the experiment were pricked out and continued to be cultivated in the greenhouse. On 16 May 2019, the saplings were planted in the field. This date is set as the start of the experiment. Only plants that appeared to be vital were pricked out and planted. Plants that were infested with pests and those that grew particularly large or small were not selected for the cultivation and the experiment. After planting in the field, the plants were watered only for the first two weeks. The experimental setup included three treatments for each of the two species (*S. perfoliatum* and *U. dioica*): Control treatment without competition, surrounded by eight plants of *S. perfoliatum* and surrounded by eight plants of *U. dioica* (Figure 2). Each treatment was repeated 9 times ($n = 9$). They were planted in three blocks of two rows each (Figure 3). In each block, the treatments in which the surrounding species were the same were placed next to each other. Two adjacent plots shared three surrounding plants (Figure 3). The order of the treatments and the order of the central species were randomly chosen, resulting in $n = 3$ per block. One individual of *S. perfoliatum* surrounded by *U. dioica* was much less vigorous from the first year on and died in the fourth year. This individual was excluded from the analysis in all years, resulting in $n = 8$ for this treatment.

Table 1: Precipitation sum and mean air temperature (based on 24 h mean values at a height of 2 m) over the growing seasons (April to August). Data were measured in the Ecological Botanical Gardens by the Micrometeorology group of the University of Bayreuth.

Year	Growing season	Precipitation sum (mm)	Mean temperature (°C)
2019	1	226	15.7
2020	2	318	14.8
2021	3	342	13.7
2022	4	195	15.8

2.2. Data Collection. At the end of each growing season, we surveyed growth parameters of the central plants (Table 2, Figure 1). As plant height, we measured the maximum height by calculating the mean of the five highest shoots. Projection area was calculated as an ellipse with $A = \pi ab/4$, where a is the measured maximum diameter of the projection area and b the perpendicular diameter to it [22]. The number of living shoots taller than 15 cm was counted for each plant of *S. perfoliatum*. Aboveground biomass was harvested, dead biomass was removed, and the fresh weight of living biomass was measured with a scale (PM 4600 Delta Range, Mettler-Toledo GmbH, Greifensee, Switzerland, same scale for all further weight measurements). A representative subsample of at least one-third of the plant was taken and its fresh weight was measured. This subsample was dried in an oven at 90°C until the weight was constant. Dry weight was measured and extrapolated to the total living aboveground biomass per plant. The number of capitula of *S. perfoliatum* was counted in the subsample from the stage of full flowering on (=fully expanded ray florets or later stages) and extrapolated to the total capitula per plant. In the second year, we harvested three ripe capitula per plant of *S. perfoliatum*, counted the number of fruits per capitulum, and calculated the mean of the three capitula.

2.3. Data Analysis. Statistical analysis and data visualization were performed with R version 4.2.2 [23]. We used linear models (LMs) and checked the following assumptions using

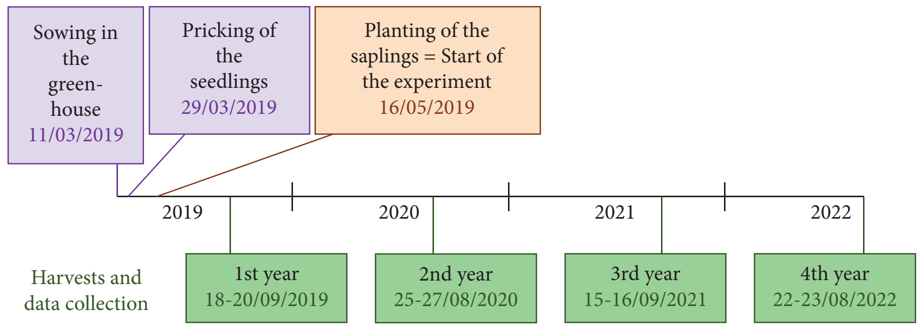

FIGURE 1: Timeline of the experiment. Dates are given as day/month/year.

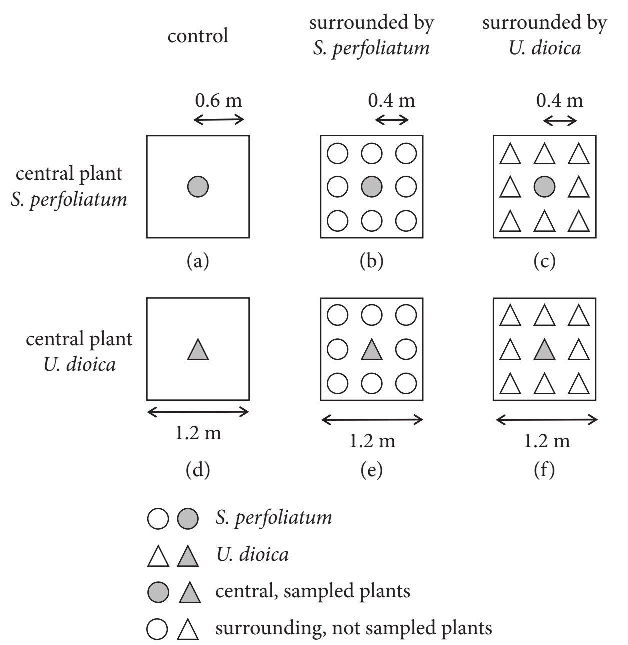

FIGURE 2: Treatments of *S. perfoliatum* and *U. dioica*. Both species were planted as control without competition (a, d), surrounded by eight plants of *S. perfoliatum* (b, e) and surrounded by eight plants of *U. dioica* (c, f). Distances between surrounding plants and to the respective central plant were 0.4 m. Distances of control plants to plot edges were 0.6 m. $n = 9$ per treatment.

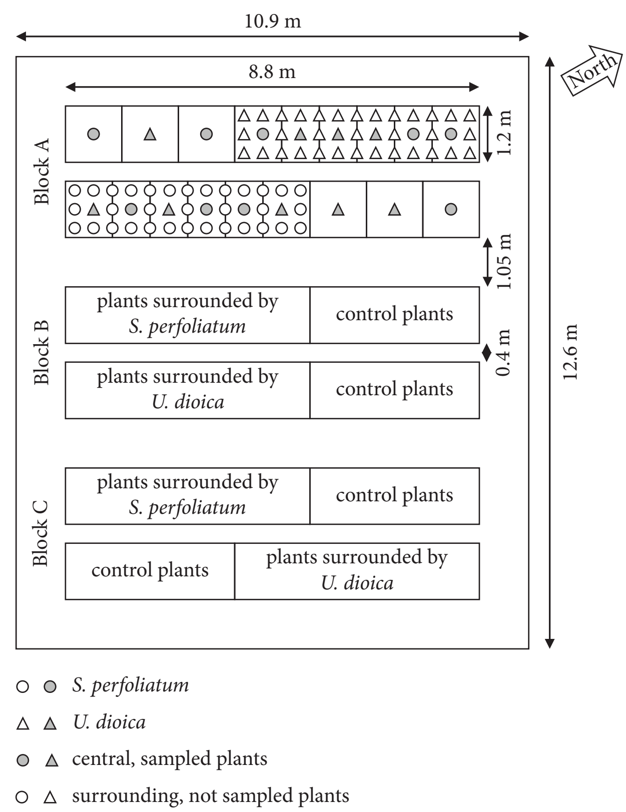

FIGURE 3: Experimental setup in the field at the Ecological Botanical Gardens of the University of Bayreuth (Germany). In each block, competition treatments per surrounding species were placed next to each other, with two adjacent plots sharing three surrounding plants. The order of treatments and the order of central species were randomly chosen.

the diagnostic plots: normal distribution of residuals and homoscedasticity of the residuals [24, 25]. In case of non-normal distribution or heteroscedasticity of residuals, we transformed the parameters or used generalized linear models (GLMs). Log-transformation was executed with the natural logarithm. We checked the influence of block (Figure 3) with a LM, respectively, a GLM. Because it was not significant in each case, we eliminated the block for final models. We extracted the p values of the parameters in models with the "Anova" function with the F-test statistics of "car" package [26]. Significant differences between the treatments were identified with the Tukey's post hoc test on the models ("glht" function of "multcomp" package [27]). For differences within one year, it was applied to separate univariate models. The level of significance was always 0.05.

As a measure of competition, we used the relative neighbor effect (RNE) [28], which is calculated as follows (1):

$$\mathrm{RNE} = \frac{\mathrm{parameter}_{\mathrm{control}} - \mathrm{parameter}_{\mathrm{competition}}}{x}. \quad (1)$$

In equation (1), x is the parameter with the higher value: $\mathrm{parameter}_{\mathrm{control}}$ or $\mathrm{parameter}_{\mathrm{competition}}$. This index ranges from −1 to 1. Negative values indicate facilitation and positive values indicate suppression by surrounding plants. Positive values correspond to the relative reduction of the parameter by competition in comparison to the control treatment.

TABLE 2: Parameters surveyed on the central plants in the four years of growth.

Year of growth	Harvest date	Plant height	Projection area	Aboveground biomass	Number of shoots	Number of capitula	Number of fruits
1	18 to 20/9/2019	—	—	*x*	—	—	—
2	25 to 27/8/2020	*x*	*x*	*x*	*x*	*x*	*x*
3	15 to 16/9/2021	*x*	*x*	—	*x*	*x*	—
4	22 to 23/8/2022	*X*	*x*	—	*x*	*x*	—
Investigated species		*S. perfoliatum* and *U. dioica*			*S. perfoliatum*		

x = parameter was surveyed in the particular year and — = parameter was not surveyed in the particular year.

3. Results

3.1. Growth of Silphium perfoliatum in the Initial Phase. The growth of *S. perfoliatum* in the initial phase (first and second year of growth) was strongly affected by the treatment and the age of the plants (Table 3). In the control treatment (without competition), plants had the highest living aboveground biomass in both years: 409 ± 84 g (mean ± standard deviation) in the first and 2141 ± 665 g in the second year of growth (Figure 4). Biomass was significantly reduced by intraspecific competition by 74% in the first and 86% in the second year (Figure 4, Table 4). However, competition by the surrounding *U. dioica* generated a significantly higher reduction by about 90%. The strong increase in biomass from the first to the second year of growth is due to the growth strategy of *S. perfoliatum*. In the first year, it usually develops only a rosette of leaves and in the second year upright flowering shoots. In the present study, however, seven of the 26 plants developed one shoot already in the first year (one in the control treatment and three in each competition treatment). In the second year, each plant developed shoots.

3.2. Growth of Silphium perfoliatum in the Establishment Phase. Plant height of *S. perfoliatum* in the establishment phase (from the second year on) was the most affected by precipitation sum during the growing seasons from April to August (Table 5). Control plants were in the fourth and driest year 1.9 ± 0.2 m high (mean ± standard deviation) and in the third and wettest year 2.8 ± 0.2 m high (Figure 5(a)). Treatment had also a significant effect on plant height (Table 5), although the competitive effects were low (Table 6). Intraspecific competition led only in the fourth year to a significant reduction of plant height (21% compared to control plants). Surrounding *U. dioica* reduced plant height significantly in each year by 11 to 16%. This competitive effect was only in the second year significantly higher than by intraspecific competition. Calculated over the whole establishment phase, the suppression of plant height by surrounding plants was not significant (Table 6). Additionally, plant height was slightly but significantly positively affected by the year of growth (Table 5). Nevertheless, there was no increasing plant height with increasing plant age measured due to the stronger effect by precipitation sum.

Projection area of *S. perfoliatum* in the establishment phase was also the most affected by precipitation sum (Table 5). Projection area of the control plants ranged from 1.2 ± 0.5 m^2 in the fourth, driest year to 5.0 ± 2.5 m^2 in the third, wettest year (Figure 5(c)). Treatment had also a significant effect on projection area (Table 5). Intraspecific competition reduced projection area by 58 to 89% compared to the control plants (Table 6). The reduction by interspecific competition by *U. dioica* was similar and ranged from 52 to 83%. Throughout the establishment phase, suppression of projection area by competition was significant, but independent of the surrounding plant species (Table 6). However, there was a significant interaction between treatment and precipitation (Table 5). The suppressive effect of surrounding species on projection area increased with decreasing precipitation with both surrounding plant species, shown by higher RNE's in years with higher precipitation (Table 6).

Number of shoots per plant of *S. perfoliatum* in the establishment phase was most affected by the treatment (Table 5). Control plants developed between 22 ± 4 (second year) and 38 ± 10 (fourth year) living shoots per plant (Figure 6(a)). Surrounding by *S. perfoliatum* and *U. dioica*

Table 3: Effects on biomass of *S. perfoliatum*.

Parameter	Df	Estimate	F value	p
Treatment	2		**182.91**	**<0.001**
Year of growth	1	**1.62**	**178.05**	**<0.001**
Treatment × year of growth	2		**3.47**	**0.040**

LM calculated with living aboveground dry biomass (log-transformed) as the dependent variable. Independent variables were the treatment (control without competition, surrounded by *S. perfoliatum*, and surrounded by *U. dioica*), year of growth (1 to 2), and their interaction. Estimates are given for significant numerical parameters. They give the slope of the fitted regression line. Significant effects are highlitghed in bold type. LM: $p < 0.001$, Adjusted $R^2 = 0.91$, and $n = 52$.

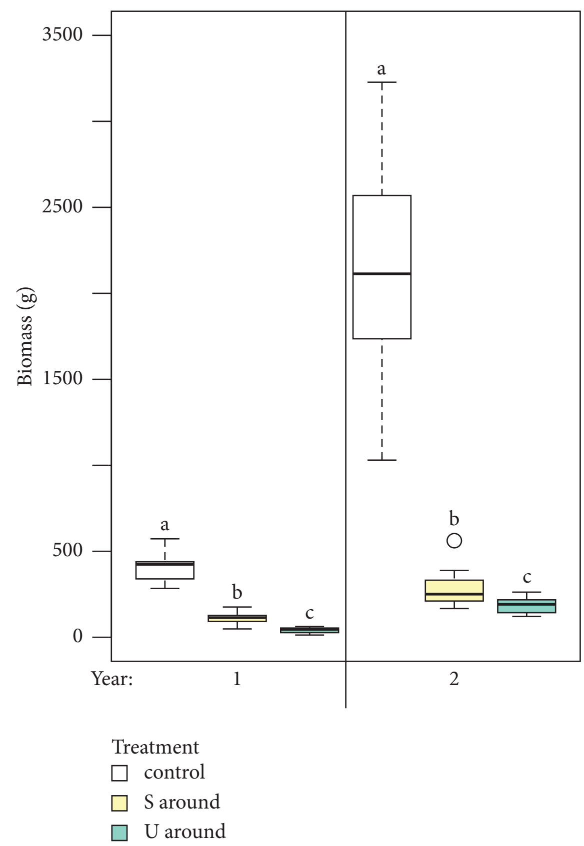

Figure 4: Living aboveground dry biomass per plant of *S. perfoliatum* depending on treatment: control without surrounding plants (white box), surrounded by *S. perfoliatum* (S around, yellow box), and surrounded by *U. dioica* (U around, green box). $n = 9$ (except U around $n = 8$). Different letters indicate significant differences in the respective year (Tukey's post hoc test on LMs with log-transformed living aboveground dry biomass).

Table 4: Relative neighbor effect (RNE) based on the living aboveground dry biomass.

Central species	Year of growth	n	Surrounding species	Biomass
S. perfoliatum	1	9	*S. perfoliatum*	**0.74**
		8	*U. dioica*	**0.90***
	2	9	*S. perfoliatum*	**0.86**
		8	*U. dioica*	**0.91***
	1-2	18	*S. perfoliatum*	**0.84**
		16	*U. dioica*	**0.91***

RNE is calculated as equation (1). The higher the RNE is, the higher is the competitive effect. Bold type indicates that the parameter in the given treatment is significantly lower than the control; * indicates that the parameter in the given treatment is significantly lower than in the treatment with the other surrounding species (Tukey's post hoc test on LM with log-transformed living aboveground dry biomass).

Table 5: Effects on the growth of *S. perfoliatum* and *U. dioica* and on reproductive parameters of *S. perfoliatum*.

Parameter	Df	Estimate	F value	p	Estimate	F value	p
Plant height		*S. perfoliatum* LM: $p < 0.001$, adjusted $R^2 = 0.81$, and $n = 78$			*U. dioica* LM: $p < 0.001$, adjusted $R^2 = 0.59$, and $n = 81$		
Treatment	2		**15.08**	**<0.001**		**3.37**	**0.040**
Precipitation	1	**0.01**	**167.13**	**<0.001**	**0.01**	**37.97**	**<0.001**
Year of growth	1	**0.20**	**7.97**	**0.006**		0.02	0.900
Treatment × precipitation	2		1.53	0.223		**12.09**	**<0.001**
Treatment × year of growth	2		0.57	0.566		**8.80**	**<0.001**
Projection area		*S. perfoliatum* LM, log-transformation: $p < 0.001$ and adjusted $R^2 = 0.79$ and $n = 78$			*U. dioica* LM, log-transformation: $p < 0.001$ and adjusted $R^2 = 0.81$ and $n = 81$		
Parameter	Df	Estimate	F value	p	Estimate	F value	p
Treatment	2		**59.85**	**<0.001**		**92.11**	**<0.001**
Precipitation	1	**0.01**	**124.65**	**<0.001**	**0.01**	**90.62**	**<0.001**
Year of growth	1	**0.25**	**18.82**	**<0.001**	**0.67**	**10.25**	**0.002**
Treatment × precipitation	2		**5.33**	**0.007**		2.19	0.119
Treatment × year of growth	2		1.57	0.214		**9.59**	**<0.001**
S. perfoliatum		Number of shoots per plant GLM, Poisson-distribution: $p < 0.001$ and $n = 78$			Number of capitula per plant GLM, Poisson-distribution: $p < 0.001$ and $n = 78$		
Parameter	Df	Estimate	F value	p	Estimate	F value	p
Treatment	2		**285.82**	**<0.001**		**258.14**	**<0.001**
Precipitation	1	**0.003**	**13.32**	**<0.001**	**0.017**	**191.08**	**<0.001**
Growing season	1	**0.469**	**30.07**	**<0.001**	**0.293**	**10.26**	**0.002**
Treatment × precipitation	2		0.03	0.971		0.92	0.403
Treatment × year of growth	2		2.02	0.140		1.16	0.320

LM resp. GLM calculated with the resp. parameter as dependent variable. Independent variables were treatment (control without competition, surrounded by *S. perfoliatum*, and surrounded by *U. dioica*), precipitation (sum of April to August of the respective year), year of growth (2 to 4), and their interactions. Estimates are given for significant numeric parameters. They give the slope of the fitted regression line. Significant effects are highlighted in bold.

led to a strong but not significantly different reduction of shoot number by 77% (by *S. perfoliatum*), resp. 86% (by *U. dioica*) in comparison to the control in mean over the years (Table 6). The year of growth also had a significantly positive effect on shoot number. With increasing age, the number of shoots increased (Table 5, Figure 6(a)). The effect of precipitation on shoot number was also significant, but much lower than of the year of growth (Table 5).

3.3. Growth of Urtica dioica in the Establishment Phase. Plant height of *U. dioica* in the establishment phase was, as of *S. perfoliatum*, the most affected by precipitation sum during the growing seasons from April to August (Table 5). Control plants were the smallest in the fourth and driest year with 1.5 ± 0.1 m (mean ± standard deviation) and the tallest with 2.4 ± 0.3 m in the third and wettest year of growth (Figure 5(b)). Treatment and its interactions with

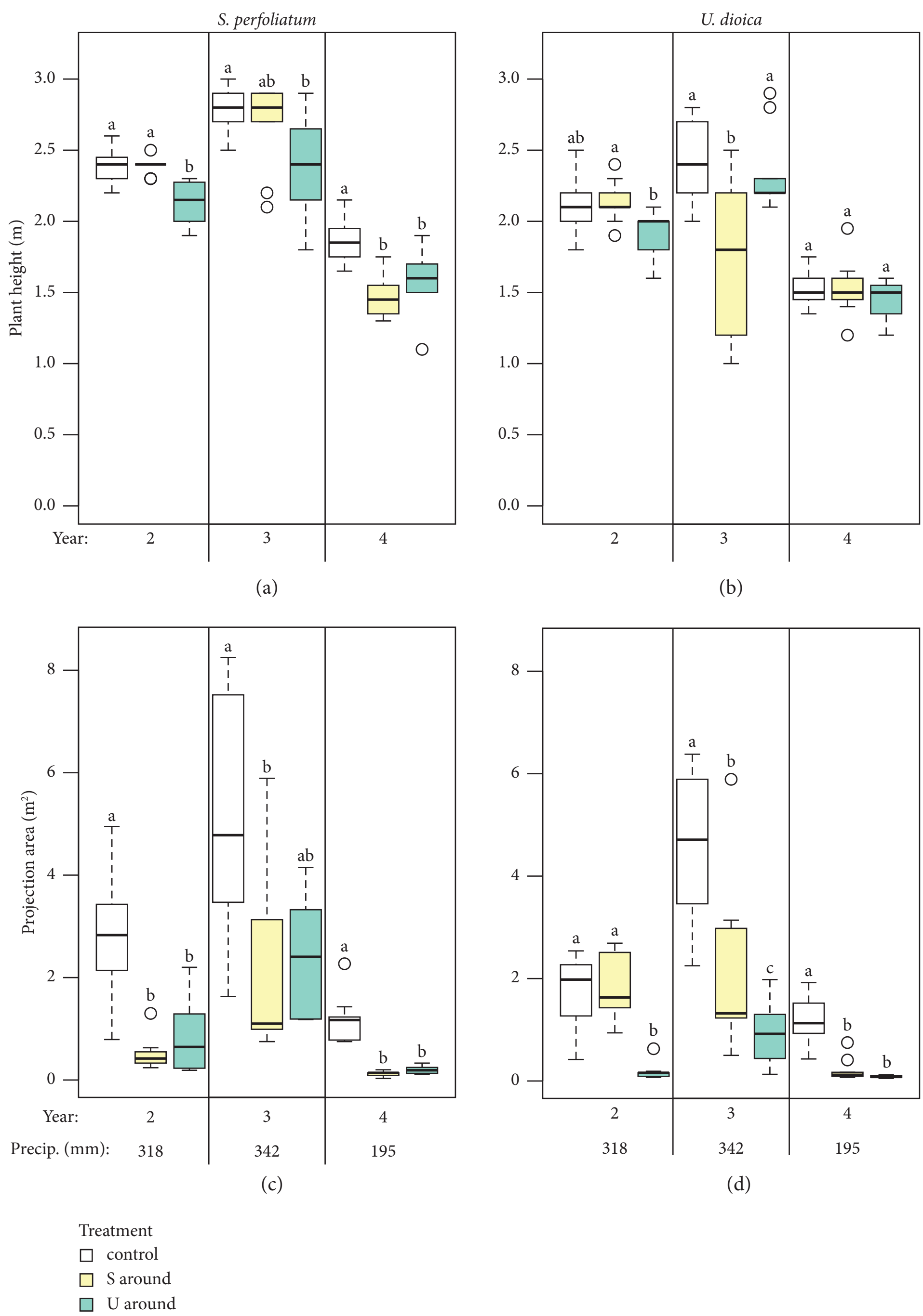

Figure 5: Plant projection area (a, b), plant height (c, d) of *S. perfoliatum* (a, c), and *U. dioica* (b, d) depending on the treatment: control without surrounding plants (white box), surrounded by *S. perfoliatum* (S around, yellow box), and surrounded by *U. dioica* (U around, green box). Precipitation is given as the sum of April to August of the respective year. $n = 9$ (except *S. perfoliatum* with U around $n = 8$). Different letters indicate significant differences in the respective year (Tukey's post hoc test on LMs with nontransformed plant height or log-transformed projection area).

precipitation and year of growth had also significant effects on plant height (Table 5). Intraspecific competition did not significantly reduce plant height in any year (Table 6). In contrast, the plant height of *U. dioica* was significantly reduced by 26% by surrounding *S. perfoliatum* in the third and precipitation-richest year of growth. In the other and drier years, surrounding *S. perfoliatum* did not suppress the plant height of *U. dioica*.

Projection area of *U. dioica* was similarly affected by treatment as by precipitation (Table 5). Projection area of the control plants ranged from $1.2 \pm 0.5\,m^2$ in the fourth to $4.5 \pm 1.6\,m^2$ in the third year of growth and increased with increasing precipitation sum (Figure 5(d)). Intraspecific competition significantly reduced the projection area by 81 to 93% compared to control plants in each year. Suppression of projection area by surrounding *S. perfoliatum* was lower

Table 6: Relative neighbor effect (RNE) based on growth and reproductive parameters.

Central species	Year of growth	n	Surrounding species	Plant height	Projection area	Number of shoots per plant	Number of capitula per plant
S. perfoliatum	2	9	*S. perfoliatum*	0.01	**0.82**	**0.68**	**0.92***
		8	*U. dioica*	**0.11***	**0.71**	**0.81***	**0.89**
	3	9	*S. perfoliatum*	0.04	**0.58**	**0.77**	**0.94***
		8	*U. dioica*	**0.14**	0.52	**0.86***	**0.89**
	4	9	*S. perfoliatum*	**0.21**	**0.89**	**0.83**	**1.00***
		8	*U. dioica*	**0.16**	**0.83**	**0.88**	**0.82**
	2–4	27	*S. perfoliatum*	0.07	**0.70**	**0.77**	**0.94***
		24	*U. dioica*	0.14	**0.62**	**0.86**	**0.88**
U. dioica	2	9	*S. perfoliatum*	−0.02	−0.06	No data	
		9	*U. dioica*	0.09*	**0.89***		
	3	9	*S. perfoliatum*	**0.26***	**0.53**		
		9	*U. dioica*	0.03	**0.81***		
	4	9	*S. perfoliatum*	0.00	**0.82**		
		9	*U. dioica*	0.05	**0.93**		
	2–4	27	*S. perfoliatum*	**0.10***	0.43		
		27	*U. dioica*	0.06	**0.85***		

RNE is calculated as equation (1). The higher the RNE is, the higher is the competitive effect. Bold type indicates that the parameter in the given treatment is significantly lower than the control. * indicates that the parameter in the given treatment is significantly lower than in the treatment with the other surrounding species. Tukey's post hoc tests on LMs with nontransformed plant height or log-transformed projection area and on GLMs with Poisson-distribution with the number of shoots or number of capitula per plant.

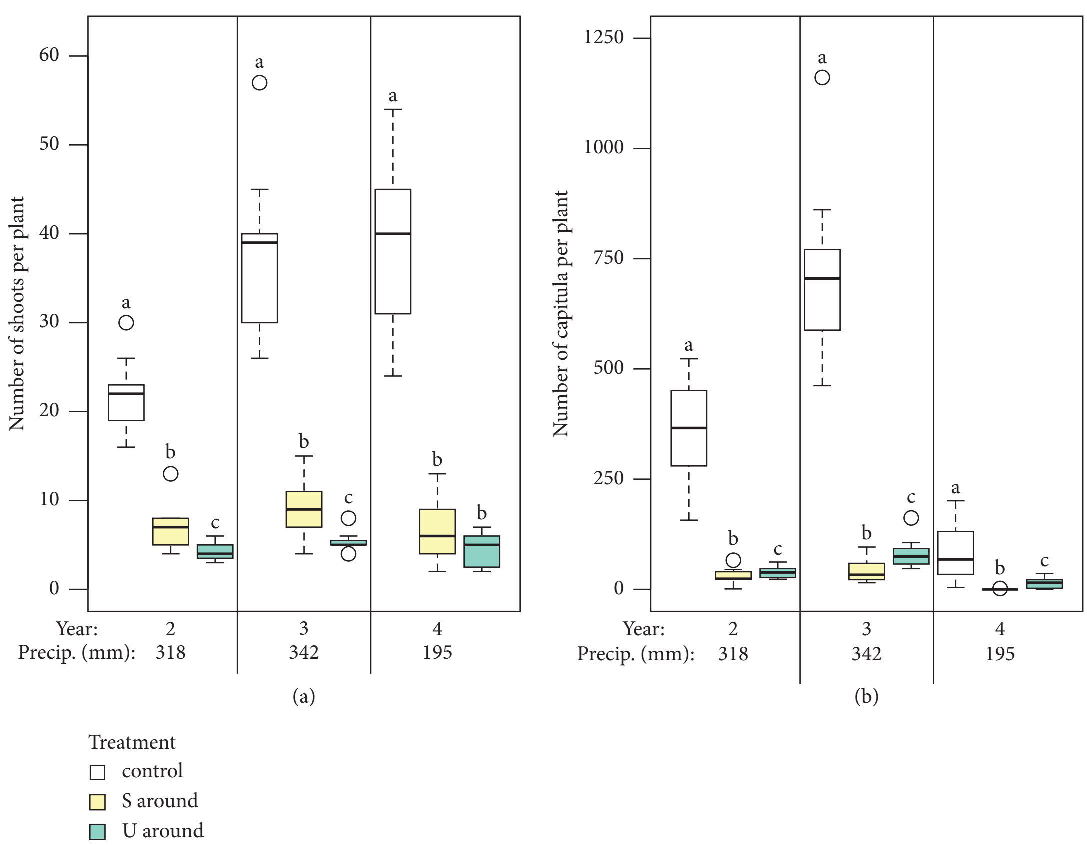

Figure 6: Number of living shoots (a) and number of capitula (b) per plant of *S. perfoliatum* depending on the treatment: control without surrounding species (white box), surrounded by *S. perfoliatum* (S around, yellow box), and surrounded by U. dioica *U. dioica* (U around, green box). Precipitation is given as the sum of April to August of the respective year. Capitula were counted from the stage of full flowering on (=fully expanded ray florets or later stages). $n = 9$ (except *S. perfoliatum* U around $n = 8$). Different letters indicate significant differences in the respective year (Tukey's post hoc test on GLMs with Poisson-distribution).

but increased with time, which is reflected in a significant interaction of treatment and year of growth. In the second year, there was no significant difference of projection area between the control plants and the plants surrounded by *S. perfoliatum*, whereas in the fourth year the reduction of the projection area of *U. dioica* by surrounding *S. perfoliatum* was similar to intraspecific competition and amounted to 82% compared the control plants.

3.4. Reproductive Potential of Silphium perfoliatum. Number of capitula per plant of *S. perfoliatum* was strongly affected by precipitation sum during the growing seasons from April to August and by the treatment (Table 5). In the fourth and driest year, control plants developed the fewest capitula with 82 ± 74 per plant (mean $\pm$ standard deviation) and in the third and wettest year the most with 718 ± 207 capitula per plant (Figure 6(b)). Control plants had the most capitula in each year. Suppression by surrounding *S. perfoliatum* was very high and amounted to 92 to 100% reduction of the number of capitula compared to the control (Table 6). Suppression by surrounding, *U. dioica* was significantly lower and between 82 and 89%. The year of growth had also a significantly but lower positive effect on the number of capitula.

The number of fruits per capitulum was 30.8 ± 5.4 in the second year of growth and was independent of the treatment (LM, $p = 0.362$, Adjusted $R^2 = 0.00$, and $n = 26$).

4. Discussion

4.1. Settlement of Silphium perfoliatum among Native Plants. The competitiveness of the exotic *S. perfoliatum* against the native *U. dioica* was investigated over four years in a field experiment. We considered the first two years as initial phase where settlement takes place.

In the initial phase, growth of *S. perfoliatum*, measured as living aboveground biomass was strongly reduced by competition; both with intraspecific competition and with interspecific competition by *U. dioica*. However, *U. dioica* had a stronger suppressive effect on *S. perfoliatum* (90-91% biomass reduction compared to the control plants) than *S. perfoliatum* to itself (intraspecific competition with 74–86% reduction of biomass). Nevertheless, all suppressed plants survived the two years. All were vital and vigorous except for one individual. This one *S. perfoliatum* growing surrounded by *U. dioica* was less vigorous from the first year on. In the fourth year, this individual died. We strongly suppose that the reason was root damage and not competition, because this plant was weak from the beginning on.

Usually, *S. perfoliatum* develops only a leave rosette in the first year of growth and no shoots [6, 29, 30]. In the present study, a few individuals already developed one shoot in the first year, mainly under competition. This was also observed in the field experiment by Ende et al. [31]. We assume that in both studies, reasons were the early sowing and the precultivation under optimal conditions in the greenhouse before planting them out in the experimental sites in spring. Under more natural conditions, the plants would germinate and grow later in spring, so their growing season is shorter and the development of shoots in the first year of growth is not to be expected.

In the present study, *S. perfoliatum* was thus well able to grow among the highly competitive *U. dioica*. However, settlement requires successful germination and seedling development. This was not investigated in the present study, because *S. perfoliatum* was planted as saplings among plants of the same age of *U. dioica*. It is known that seedlings of *S. perfoliatum* develop slowly and are therefore not very competitive in the first weeks [32]. It was also observed that spontaneous colonization of *S. perfoliatum* took preferentially place in vegetation with about 25% open soil [13]. Additionally, this species requires full sun for optimal growth [6]. All these point to difficulties for *S. perfoliatum* settling among dense and established native vegetation. However, there are apparently many suitable habitats for *S. perfoliatum*, especially in the areas around agricultural fields, because a study in northern Bavaria (Germany) recorded numerous spontaneous occurrences at such sites [13]. Moreover, the growth of *S. perfoliatum* has been demonstrated to be higher in moist soil conditions than in dry [31]. This makes successful settlement in moist habitats more likely [31].

We, therefore, assume that settlement of *S. perfoliatum* is possible among native plants, especially among weakly competitive plant species and in vegetation covers with disturbances and moist soil conditions.

4.2. Establishment of Silphium perfoliatum among Native Plants. As establishment phase of *S. perfoliatum,* we define the time from the second year of growth on, when this species usually starts to develop shoots and flowers [6, 29, 30].

The plant height is an important parameter for competing plants, because it is decisive for the access of sunlight and thus for the rate of photosynthesis [33]. The plant height of *S. perfoliatum* was hardly affected by surrounding plants from the second to the fourth year of growth in the present study. Much more affecting than competition for plant height was the precipitation sum during the growing seasons from April to August. This is in line with other studies where *S. perfoliatum* grew higher with higher precipitation or higher soil moisture [31, 34–36].

In contrast, the projection area of *S. perfoliatum* was strongly reduced by competition, similarly with *S. perfoliatum* and *U. dioica* as surrounding plants. Precipitation sum during the growing seasons had also a positive effect on the projection area of *S. perfoliatum*. Furthermore, the RNE—which is a measure for the reduction of projection area of *S. perfoliatum* by surrounding plants compared to the control plants—decreased with increasing precipitation. *S. perfoliatum* is therefore more competitive and more resilient with higher precipitation regarding the projection area.

The number of shoots of *S. perfoliatum* was mainly reduced by competition by about 80% irrespective of the surrounding plant species. Interestingly, in contrast to the other two growth parameters, the number of shoots per plant was hardly affected by precipitation. More decisive was the age of the plants. With increasing plant age, shoot number increased even under competition and even with decreasing precipitation. This is in line with the results of another experiment where the number of shoots of *S. perfoliatum* was also not affected by soil moisture [31]. Bury et al. [34] and Boe et al. [37] confirmed the correlation between shoot number and plant age. The fact that *S. perfoliatum* develops less shoots under denser populations is confirmed in several studies [34, 37, 38].

Although, the growth of *S. perfoliatum* was reduced by competition, *U. dioica* did not suppress *S. perfoliatum* more than *S. perfoliatum* itself. According to Weber [20], *U. dioica* is able to develop dominance stocks, where other plant species have hardly a chance to grow. However, in the present study, *S. perfoliatum* grown among *U. dioica* was still vital and productive. *S. perfoliatum* is therefore apparently able to establish among native plants once it has settled there, especially with high precipitation and on moist soils. Among less competitive plant species than *U. dioica*, an establishment of *S. perfoliatum* is even more likely.

4.3. Suppression of Native Plants by Silphium perfoliatum. With the present study, we not only intended to investigate the potential of *S. perfoliatum* to settle and establish among native vegetation but also aimed to address the important question whether *S. perfoliatum* could suppress native plants. For this purpose, we considered the years two to four of the field experiment.

The plant height of *U. dioica* was primarily affected by the precipitation sum during the growing seasons from April to August. Competition by surrounding plants hardly reduced the plant height of *U. dioica*, no matter whether it was intraspecific competition or interspecific competition by *S. perfoliatum*. Only in the one year with high precipitation, *S. perfoliatum* significantly reduced the plant height of *U. dioica* by 26% compared to the control plants. This shows once again that *S. perfoliatum* benefits from soil moisture and can thus exert competitive pressure on neighboring plants. In a pot experiment in Germany, the plant height of *U. dioica* was reduced significantly but similarly by intraspecific competition as by competition by the exotic *Impatiens glandulifera* Royle [39]. These different results of an intraspecific competitive effect are probably due to the different experimental setups (pot vs. field) and the associated different conditions in terms of space and water.

The projection area of *U. dioica* was reduced by about 80% in each year due to intraspecific competition. When *S. perfoliatum* was the surrounding species of *U. dioica*, the competitive effect increased with plant age. In the second year, there was no significant effect, whereas in the fourth year, the surrounding *S. perfoliatum* reduced the projection area of *U. dioica* by 82% compared to the control plants. This was a similar effect as by intraspecific competition in this year. It remains unclear whether this trend continues over further years. However, *S. perfoliatum* can persist for several decades [6], which could lead to a very high suppressive effect.

It is known that *U. dioica* is very competitive [20, 21]. Because *S. perfoliatum* was able to restrict its growth, we assume that other less competitive native plant species would be more suppressed by *S. perfoliatum*. This effect could become stronger with increasing plant age of *S. perfoliatum*, as well as in years with high precipitation and in habitats with high soil moisture.

4.4. Reproductive Potential of Silphium perfoliatum among Native Plants. Rhizome fragments of *S. perfoliatum* can serve as diaspores, and thus it enables a vegetative reproduction if the rhizomes become split [6, 40]. In the present study, the potential of generative reproduction of *S. perfoliatum* under different competition treatments was investigated. It is known that the flowers of *S. perfoliatum* are visited by insects and fertile seeds are developed–also in Central Europe [9, 10, 30, 41].

In the present study, *S. perfoliatum* developed about 30 fruits per capitulum. This was independent of the competition treatment. However, the number of capitula per plant of *S. perfoliatum* was significantly and strongly reduced by competition. With intraspecific competition, the number of capitula of *S. perfoliatum* was reduced by 92 to 100% compared to the control plants. *U. dioica* as surrounding species caused a reduction of 82 to 89% that was significantly lower than by *S. perfoliatum* to itself. Besides, the number of capitula significantly increased with the precipitation sum during the growing seasons from April to August. This is in line with other studies where the number of capitula increased with increasing soil moisture [31, 42]. The number of capitula was also significantly positively affected by the age of the plant. With sufficient precipitation, the reproductive potential therefore could increase over the years.

Thus, the generative reproductive potential of *S. perfoliatum* is severely restricted under competition and more so under dry soil conditions than under moist ones. Nevertheless, even if *S. perfoliatum* produces only a few capitula, it can reproduce generatively due to the large number of fruits per capitulum.

5. Conclusions

The present study is the first to investigate the competitiveness of the introduced *S. perfoliatum* against native plant species in Central Europe. We used *U. dioica* as a native model species because it is vigorous, competitive, and prefers nutrient-rich habitats similar to *S. perfoliatum* [13, 19–21].

The growth of *S. perfoliatum* was strongly reduced by competition, except the parameter plant height. However, it still grew and developed well especially in years with high precipitation. We assume that *S. perfoliatum* can settle and establish in the native flora of Central Europe. Furthermore, *S. perfoliatum* has a high competitive effect, especially with increasing plant age and with high precipitation because it was able to reduce the growth of the highly competitive *U. dioica*. A suppression of less competitive plant species is therefore conceivable. *S. perfoliatum* thus has both a high competitive effect and a high competitive response. It is known that low-competitive species are often valuable for nature conservation. A suppression of these species by

S. perfoliatum could lead to a threat to biodiversity, so that *S. perfoliatum* could be classified as "invasive" (Article 3, No. 2 EU-Regulation No. 1143/2014).

Data Availability

The data are available in Table S1 in the Supplementary Materials.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this study.

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Supplementary Materials

Table S1: dataset on which the calculations and figures of the present study are based. (*Supplementary Materials*)

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