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Spreading of the cup plant (*Silphium perfoliatum*) in northern Bavaria (Germany) from bioenergy crops

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Abstract

Invasive species can be the cause of severe problems for biodiversity, economy and human health. The cup plant (*Silphium perfoliatum*) is native to eastern North America and is increasingly cultivated in Germany as a new bioenergy crop. Its growth characteristics and autecology do not exclude a possible invasive potential. However, there are hardly any studies on this to date. In this study, habitat requirements for spontaneous colonization and establishment of the cup plant were investigated. Therefore, a 15 m radius around eleven cup plant fields in northern Bavaria (Germany) was examined. Data on cup plant colonization, habitat type, vegetation structure, ground cover, and further site conditions using the Ellenberg indicator values were collected and analyzed by logistic regression models. Spontaneously colonized cup plants were found in a wide range of habitats. Open habitats and human settlement areas were particularly suitable, especially field margins and agricultural paths. A portion of open soil of about 25% was preferentially colonized. Cup plants occurred predominantly within the first few meters of the field margin and increasingly around cup plant fields that have existed for a longer period. Favorable for the development of stems and thus for flowering, fruiting and establishing are warmer sites with a high herb layer. Individual plants that had developed a stem persist for several years and increased their stem number over time. The number of stem-developing individuals also increased over time. Thus, there exist an enormous potential for spread in the future. However, an invasive potential could not be confirmed based on the present study, because a threat of biodiversity was not proven.

Keywords

alien, bioenergy crop, casual occurrences, dispersal distance, distribution, establishment, habitat requirements, invasive potential

Introduction

An increasing number of plant species are being introduced by humans into regions where they do not occur naturally (Seebens et al. 2017). Some of these plants can settle permanently within these new areas, often at ruderal sites but also in natural and semi-natural habitats (Kowarik and Rabitsch 2010). A few become invasive and cause severe problems for biodiversity, economy and human health (Vitousek et al. 1996; Andersen et al. 2004; Kowarik and Rabitsch 2010). Some of these species were introduced unintentionally, and others intentionally e.g. as crops. The example of the Jerusalem artichoke (*Helianthus tuberosum*) shows that large-scale cultivation of plants without previous investigation of potential invasiveness can be fatal. This species is firmly established in many European countries and is partly responsible for soil erosion and suppression of native vegetation in the floodplains of rivers (Kowarik and Rabitsch 2010). Another introduced crop that has increasingly been cultivated in Germany in recent years is the cup plant (*Silphium perfoliatum*). So far, there are hardly any studies on the possible invasiveness of this species. The cup plant was introduced to Germany in 1762 as an ornamental plant (Brennenstuhl 2010). Since 2004 it has been cultivated as a bioenergy crop (Frölich et al. 2016). Good yields, low effort after establishment and many ecological advantages compared to the predominantly cultivated biogas crop maize (*Zea mays*) are reasons for increasing cultivated cup plant fields (Frölich et al. 2016). In 2021, the cup plant was cultivated on around 10,000 ha of arable land in Germany, nearly tripling the area in one year (FNR 2022).

The cup plant is a perennial, yellow-flowering hemicryptophyte of the Asteraceae family and is native to the prairies of eastern North America (Stanford 1990; Jäger 2017). It grows 2–4 m high and can develop several hundred flower heads, each with 20–30 fruits (Stanford 1990; Dauber et al. 2016; Ende et al. 2021). The flowering period is from July on, fruits ripen from August onwards and then drop out (Jabłoński and Kołtowski 2005; Penskar and Crispin 2010; Wrobel et al. 2013; Jäger 2017). Seeds have a physiological dormancy, which can be broken by low or alternating temperatures, so that germination under Central European climate is possible (Gansberger et al. 2017). The high productivity and high reproductive potential of cup plant could lead to invasiveness, in case of spontaneous spread into sensitive habitats that are relevant for nature conservation. Following EU legislation, a species is being classified as invasive if its spread threatens biodiversity (Article 3 No. 2 EU-Regulation No. 1 143/2014). The Netherlands and Russia already classify the cup plant as potentially invasive (Matthews et al. 2015; Vinogradova et al. 2015). Detections of spontaneous occurrences of cup plants have been made in several European countries and for 15 of Germany's 16 federal states (Roskov et al. 2019; GBIF 2021). However, knowledge of dispersal distance and requirements on soil, vegetation or habitat for spontaneous colonization is low. Therefore, we investigated an area within a 15 meter radius around eleven cup plant fields in northern Bavaria (Germany) and collected data on cup plant occurrence in combination with habitat type, vegetation structure, ground cover, and other site conditions using the Ellenberg indicator values (Ellenberg and Leuschner 2010). We asked the following questions:

What are the crucial site conditions that enable a spontaneous colonization of cup plants and subsequently their establishment? How do establishing (stem-developing) individuals develop over three years? Spontaneous colonization and establishment in habitats that are relevant for nature conservation would be more problematic for biodiversity than, for example, in ruderal sites or roadsides (Nehring et al. 2015). Our study is limited to northern Bavaria over three years. Nevertheless, the results provide important insights into the habitat requirements and development of cup plant that are valid beyond this small region and are essential for assessing the possible invasiveness of cup plant.

Materials and methods

Data collection

Data were collected between 19 May and 3 Aug. 2020 in 15 m-radius around eleven cup plant fields in Upper Franconia and Upper Palatinate in Bavaria, Germany (Suppl. material 1). We recorded several parameters in invaded and uninvaded plots (Table 1). Plots had a size of 1 m × 1 m and a distance of ≥ 1 m from the field margin. Invaded plots were chosen by carefully searching the area for spontaneously colonized cup plants. Around detected individuals, we investigated a plot (= invaded plot). As control, we additionally investigated plots without cup plant (= uninvaded plots) randomly selected in the same sites using the tool "Create Random Points" in GIS (ArcGIS Version 10.2.2). The preliminary mapping of habitat types by Ende and Lauerer (2020) served as the basis for selecting uninvaded plots. They mapped habitat types up to the second subgroup according to LfU (2014). For each cup plant field, plots were selected for each presented habitat type. The number of these plots was calculated as the area of the respective habitat type around the respective field divided by 100. The minimum distance between plots (invaded and uninvaded plots alike) was 2 m. On site, we located the selected uninvaded plots using an aerial photograph (LDBV 2020) and a GPS device (eTrex Legend HCx by Garmin). We excluded plots with 100% sealed area or 100% open water area, plots in private, fenced land as well as agricultural fields. In sum, we collected data in 549 plots (224 invaded and 325 uninvaded plots).

Monitoring of establishing individuals from 2017 to 2020

In 2017, Ende and Lauerer (2020) recorded the cup plants that had developed stems and that are considered as establishing cup plants in the present study in a 20 m radius of 15 cup plant fields in northern Bavaria with a GPS device (eTrex30 by Garmin). In 2020, a 15 m radius of eleven fields was investigated. For the comparison of the numbers of establishing individuals, we extracted the data of the 15 m-radius of the eleven fields that we mapped in 2020 of the whole data of 2017. In 2017, 20 of the establishing individuals were monitored annually from 2017 to 2020 between late July and mid-October. Survival was documented, and stems were counted.

Table 1. Parameters recorded in invaded and uninvaded plots and description of the underlying methodology. Abbreviation: EIV = Ellenberg indicator value.

Parameter	Method
Habitat type	According to LfU (2014) until third subgroup
Number of spontaneously colonized cup plants	Counted, independent of developmental stage
Number of establishing cup plants	Counted, considered were plants that had developed at least one stem
Distance to the field	Distance between plot center and field margin, for invaded plots measured on site with a measuring tape, and for uninvaded plots calculated using GIS, accurate to 1 m both
Height of the herb layer	Mean maximum plant height (without cup plant), measured with a folding rule, accurate to 5 cm
Cover of herb layer (height < 1.5 m)	Visually estimated (without cup plant), accurate to 1% in the sections from 0 to 10% and from 90 to 100%, accurate to 5% in the section from 10 to 90%
Cover of shrub layer (height between 1.5 and 5 m)	Visually estimated, accurate to 1% in the sections from 0 to 10% and from 90 to 100%, accurate to 5% in the section from 10 to 90%
Cover of tree layer (height > 5 m)	
Cover of litter	
Portion of open soil	
Cover of paved ground	Visually estimated, accurate to 1% in the sections from 0 to 10% and from 90 to 100%, accurate to 5% in the section from 10 to 90%, considered were gravel, pavement, cement and tarmac
Dominant species of herb layer	Cover per species was visually estimated, accurate to 1% in the sections from 0 to 10% and from 90 to 100%, accurate to 5% in the section from 10 to 90%, considered were those species which together accounted for 75% of the total cover of herb layer
EIV light availability	Mean weighted Ellenberg indicator values, according to the cover of dominant species. Values were taken from Jäger (2017).
EIV soil nutrients	
EIV soil reaction	
EIV soil moisture	
EIV temperature	
Age of the nearest cup plant field	Survey of farmers

Data analysis

Statistical analysis and data visualization were performed with R (R Core Team 2019). We used logistic regression models (generalized linear models with binomial distributed residuals) to analyze the binary data presence and absence of cup plants respectively presence and absence of establishing (stem-developing) cup plants as dependent variables. For the analysis of cup plant establishing, we used only the plots with spontaneously colonized cup plants (invaded plots). First, we individually tested the parameters (explanatory variables) using univariate models. Depending on data structure, we occasionally exerted log or quadratic data transformation. Log transformation was natural logarithm with + 0.1 in case of zero values in data. Models were checked for influential outliers, which were defined as samples with a cook's distances > 4/(sample size) and residuals > 3. No such influential outliers occurred. Furthermore, we tested the correlations between explanatory variables. None of them had a Spearman's rho > 0.7. With all of the explanatory variables that were significant in univariate models, we built global multivariate models. We reduced the global models stepwise by using the Akaike information criterion (AIC) with the "step" function. Plots without herb layer or those where not all EIVs (Ellenberg indicator values) were available would be excluded from the global model (n = 100).

To avoid this, missing EIVs were filled using the mean value of the respective EIV calculated of all plots of the same habitat type (third subgroup) and the same site. If there were no plots of the same habitat type and site with complete EIVs, the respective plots were excluded of analysis (n = 3). We checked collinearity in global models with the variance inflation factor (function “vif” of “car” package by Fox and Weisberg (2019)). Values > 10 were achieved in the global model of cup plant colonization for the parameter habitat type in the subgroup levels. Therefore, we inserted the main groups of habitat types in the global model. Results of subgroups were analyzed descriptively. We calculated *p*-values of the parameters in multivariate models with the Wald-test of “Anova” function of “car” package (Fox and Weisberg 2019). Significant differences between the habitat types in the final model of cup plant colonization were analyzed using the Tukey’s post-hoc test (“glht” function of “multcomp” package by Hothorn et al. (2008)). For analyzing the stem number of establishing individuals over time, a linear regression model was aimed for. Because the assumptions, i.e. normality and homoscedasticity of residuals, visually checked, were not satisfied, we executed a correlation analysis.

Significance level was always $p < 0.05$. We used the function “ddply” of “plyr” package (Wickham 2011) for descriptive statistics and the function “visreg” of “visreg” package (Breheny and Burchett 2017) for visualization of logistic regression results. For evaluation of model results, distributions of all explanatory variables are shown in Suppl. material 2.

Results

Spontaneous occurrences of cup plant

Spontaneously colonized cup plants were found within 15 m radius of each of the eleven surveyed fields. 224 of the 549 plots (41%) had spontaneous occurrences with 1 to 60 individuals per plot and 2 in median. The probability of spontaneous occurrence of cup plants was significantly affected by habitat type specified as main group (Table 2). Open habitats and human settlement areas showed a significantly higher probability of cup plant occurrence than woody habitats (shrubs, trees and forests) or inland waters, including riparian areas (Fig. 1A). Looking at the sub-groups of habitat types, most occurrences of cup plants were in fringes, ruderal areas and perennial herb communities with low or moderate species richness (habitat types K11 and K12, Table 3), which were mainly grass dominated field margins. 63 to 77% of these plots were invaded. The other subgroup of open habitats was grassland, which was less invaded than fringes, ruderal areas and perennial herb communities. Cup plant occurrences were found in intensively used grasslands in use (G11, 20% invaded plots) or lain fallow (G12, 14% invaded plots). Extensively used grasslands (G21) and lawns (G4) had no occurrences of cup plants at all. However, cup plants were also found frequently on unpaved and paved cycle paths, footpaths and agricultural paths (V32, V33). Both habitat types belong to the main

Table 2. Results of the final logistic regression model of spontaneous cup plant colonization depending on environmental variables. (Logistic regression, $p < .001$, $n = 546$). Significant parameters are shown in bold. Abbreviation: EIV = Ellenberg indicator value.

Parameter		Estimate	SE	*p*-value
Habitat type main group compared to IW (Inland waters, including riparian areas)	**OH (Open habitats)**	**15.32**	**580.2**	**.002**
	HS (Human settlement areas)	**15.19**	**580.2**	
	WH (Woody habitats)	**13.73**	**580.2**	
log (Distance to the field)		**- 1.668**	**0.151**	**< .001**
EIV soil nutrients		1.482	0.927	.110
(EIV soil nutrients)^2		- 0.129	0.082	.116
EIV temperature		0.521	0.315	.099
Age of nearest cup plant field		**0.329**	**0.076**	**< .001**
log (Height of herb layer + 0.1)		0.321	0.167	.054
Portion of open soil		**0.069**	**0.028**	**.013**
(Portion of open soil)^2		**- 0.001**	**< 0.001**	**.005**
Cover of herb layer		- 0.012	0.007	.067

group of human settlement areas and had 49 to 60% invaded plots. Other traffic areas such as paved roads (V12) and green spaces along traffic routes (V51) were not colonized by cup plant. From the main group of woody habitats (shrubs, trees and forests), most habitat types were invaded, however partly in few plots (2 to 23%). Cup plants occurred in tree rows and tree groups (B31, 23% invaded plots), deciduous and coniferous plantations (L71, N71, N72, 2 to 13% invaded plots), pine forests (N11, 20% invaded plots) and woodland mantles (W12, 14% invaded plots), however not in scrubs and hedges (B11) or copses (B21). There were also no occurrences of cup plants in riparian areas of naturally arisen running waters (F14) and ditches (F21).

Apart from habitat type, the spontaneous occurrence of cup plants was also significantly negatively dependent on distance to the field (Table 2). Within the first 3 m distance to the field, the probability of cup plant occurrence decreased nearly by half (Fig. 1B). In mean, spontaneously colonized cup plants had a distance of 2.1 m to the field. The maximum distance was 14 m. Besides, the probability of cup plant occurrence increased significantly with the age of the nearest cup plant field, which ranged from 2 to 11 years (Table 2, Fig. 1C). There was an increase in probability of cup plant occurrence of around 6% per year. The portion of open soil also significantly affected the probability of cup plant occurrence. The cup plant preferred an open soil portion of about 25% (Fig. 1D). More or less open soil resulted in lower probability of cup plant occurrence. More than 50% open soil was mainly found on unpaved, heavily compacted paths, occasionally also under dense scrubs or hedges. EIVs for soil nutrients and temperature as well as height of the herb layer added information to the model, but they were no significant parameters. Ellenberg indicator values (EIV) for soil reaction, light availability and soil moisture, covers of litter, shrub and tree layer, and cover of paved ground had no influence on the probability of cup plant occurrence.

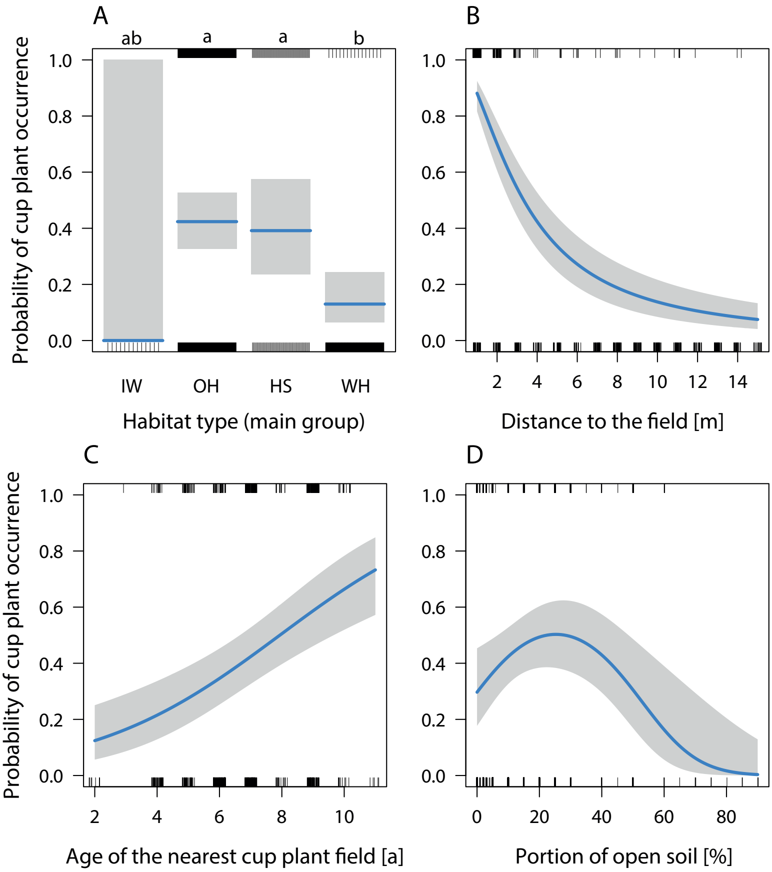

Figure 1. Probability of cup plant occurrence depending on the significant parameters of the final model (Table 2) **A** habitat type (main groups). Abbreviations: IW = Inland waters, including riparian areas, OH = Open habitats, HS = Human settlement areas, WH = Woody habitats (shrubs, trees and forests) **B** distance to the field **C** age of the nearest cup plant field **D** portion of open soil. Parameters were fitted by the final model (Logistic regression, Table 2) with all other parameters held constant on median. The fitted probabilities of cup plant occurrence (blue line) and the 95%-confidence interval (grey band) are given. In addition, invaded plots (dashes in the top) and uninvaded plots (dashes in the bottom) are shown with a slight offset in case of multiple plots of one value. (n = 546).

Establishing of cup plants

Establishing cup plants, by which we mean those that had developed a stem, were also found within 15 m radius of each of the eleven surveyed fields. In 132 of the 224 plots (59%) where cup plant occurred spontaneously, between 1 and 13 individuals were establishing. The median was 1. One of the essential parameters for establishing was EIV temperature (Table 4). The higher the value, i.e. the warmer the site, the higher the probability of establishing (Fig. 2A). It must be mentioned that the values only cover a small range from 5 to 8, while the entire range is from 1 to 9. Distance to the

Table 3. Mapped habitat types and their spontaneous colonization by the cup plant. Grouping, naming and abbreviations preceding the habitat types are based on LfU (2014). (*n* = 549).

Main group	Subgroup			Number of plots (invaded/ uninvaded)	Portion of plots invaded/ with establishing (stem-developing) cup plants [%]
	First	Second	Third		
Inland waters including their riparian areas	F: Running waters	F1: Naturally arisen	F14: Moderately modified	3 (0/3)	0/0
		F2: Anthropogenic generated	F21: Ditches	10 (0/10)	0/0
Open habitats	G: Grasslands	G1: Intensively used	G11: In use	54 (11/43)	20/20
			G12: Lain fallow	7 (1/6)	14/14
		G2: Extensively used	G21: On moist to moderate dry sites	17 (0/17)	0/0
		G4: Trampled grass and park lawns		4 (0/4)	0/0
	K: Fringes, ruderal areas and perennial herb communities	K1: Of planar to high montane zone	K11: Species-poor	59 (37/22)	63/37
			K12: Moderate species-rich	138 (106/32)	77/42
Human settlement areas	V: Traffic area	V1: Roads	V12: Paved	2 (0/2)	0/0
		V3: Cycle paths, footpaths, agricultural paths	V32: Paved	57 (34/23)	60/42
			V33: Unpaved	41 (20/21)	49/20
		V5: Green spaces along traffic routes	V51: Of young to medium age	5 (0/5)	0/0
Woody habitats (shrubs, trees and forests)	B: Copses, thickets, scrubs, hedges and cultivated woody plants	B1: Scrubs and hedges	B11: Of predominantly native, site-appropriate species	16 (0/16)	0/0
		B2: Copses	B21: Of predominantly native, site-appropriate species	1 (0/1)	0/0
		B3: Tree rows and tree groups	B31: Of predominantly native, site-appropriate species	26 (6/20)	23/19
	L: Deciduous (mixed) woodlands and forest plantations	L7: Deciduous (mixed) plantations, not site-appropriate	L71: Of predominantly native species	8 (1/7)	13/0
	N: Coniferous (mixed) woodlands and forest plantations	N1: Pine forests	N11: On nutrient-poor, base-deficient sites	5 (1/4)	20/0
		N7: Coniferous plantations	N71: Structure-poor age-cohorts	34 (4/30)	12/3
			N72: Structure-rich	48 (1/47)	2/2
	W: Woodland mantles, pioneer stages of woodland, special forms of woodland use	W1: Woodland mantles	W12: On moist to moderate dry sites	14 (2/12)	14/7

Table 4. Results of the final logistic regression model of cup plant establishing depending on environmental variables. (Logistic regression, $p < .001$, $n = 223$). Included in the analysis were only the plots with spontaneous cup plant occurrence. Significant parameters are shown in bold. Abbreviation: EIV = Ellenberg Indicator Value.

Parameter	Estimate	SE	*p*-value
EIV temperature	**1.067**	**0.356**	**.003**
EIV soil moisture	- 0.430	0.270	.111
Distance to the field	**0.207**	**0.087**	**.017**
Height of the herb layer	**0.020**	**0.007**	**.003**

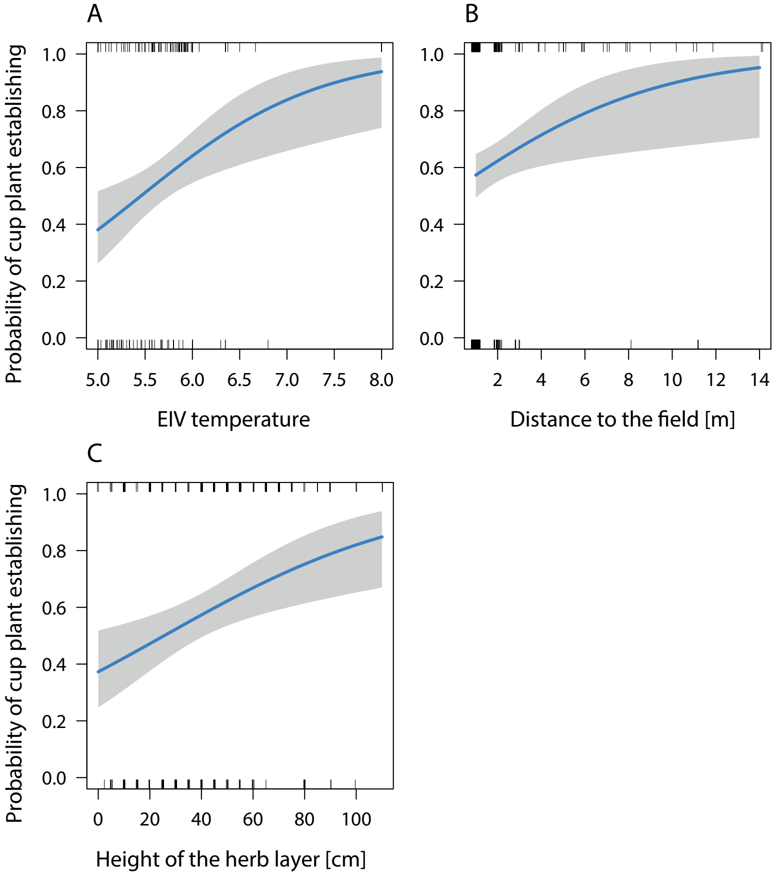

Figure 2. Probability of cup plant establishing depending on the significant parameters of the final model (Table 4) **A** EIV temperature. Abbreviation: EIV = Ellenberg indicator value **B** distance to the field **C** height of the herb layer. Parameters were fitted by the final model (Logistic regression, Table 4) with all other parameters held constant on median. The fitted probabilities of cup plant establishing (blue line) and the 95%-confidence interval (grey band) are given. In addition, plots with (dashes in the top) and without (dashes in the bottom) establishing cup plants are shown with a slight offset in case of multiple plots of one value. (n = 223).

field was a significantly affecting parameter once again. However, the probability of establishing increased with increasing distance to the field (Table 4, Fig. 2B). Thus, it is the opposite way than regarding cup plant occurrence in general where the relationship between distance to the field and probability of cup plant occurrence was significantly negative. Establishing cup plants had a mean distance of 2.5 m to the field. Height of the herb layer also showed a significantly positive relationship with the probability of cup plant establishing (Table 4, Fig. 2C). At a very low vegetation height of a few centimeters, cup plants were establishing in about 40% of the invaded plots. At a vegetation height of 1 m, establishing cup plants were found in 80% of the plots. EIV soil moisture was also a parameter of the final model, but it was not significant. All other

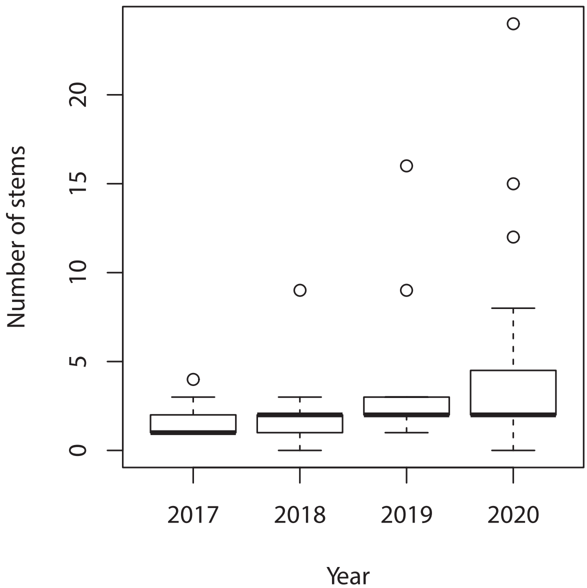

Figure 3. Number of stems of the establishing individuals monitored over the years. (n = 20, except in 2018 n = 19).

parameters (EIVs for soil reaction, light availability and soil nutrients, covers of litter, herb, shrub and tree layer, covers of paved ground and of open soil, age of the nearest cup plant field, and habitat type) did not affect the probability of cup plant establishing. Cup plants were establishing in all of the habitat types with cup plant occurrences except deciduous plantations and pine forests (habitat types L71 and N11, Table 3).

Development of establishing cup plants over time

In 2017, 46 establishing (stem-developing) cup plants were mapped within the 15 m radius of the eleven surveyed fields, whereas in 2020 there were 295 establishing individuals. On average, this corresponds to almost a doubling per year. The 20 establishing individuals of 2017 that were monitored over the years were proven every year until 2020, with one exception: One individual plant was missing in 2018; however, it was found alive in the following years. The number of stems of these 20 individuals increased significantly over the years (Fig. 3, Spearman's rho = .38, $p < .001$).

Discussion

The present study is the first one which comprehensively investigates habitat requirements of the cup plant for spontaneous colonization and establishment in Germany. Results showed that cup plants were able to invade a wide range of habitats and were found around all of the eleven investigated fields in northern Bavaria.

One of the most crucial parameters for spontaneous cup plant occurrence was the distance to the cup plant field. On average, cup plants were spread at distances of only 2.1 m, and there was a strongly negative relationship between cup plant occurrence and distance to the field (Fig. 1B). Fruits as well as root parts if they contain buds can serve as diaspores (Stanford 1990; Czarapata 2005). Dispersal of root parts would presuppose a cutting or damage of roots which could happen e.g. when ploughing. Because all of the investigated fields were not ploughed since cup plant is cultivated there, we assume that all of the detected spontaneously settled cup plants are developed from seeds. The vectors for the dispersal of cup plant fruits have not been well investigated so far. According to Jäger (2017), fruits are dispersed by shaking of fruiting stems which fits in with the low dispersal distances in the present study. However, single individuals were still found up to 14 m distant to the field, which nearly corresponds to the limit of investigated radius of 15 m. This dispersal distance cannot be achieved by shaking. Hence, there must be another dispersal vector. The fruits of cup plant are equipped with two tiny wings that could enable them to fly (Kowalski and Wierciński 2004) and thus be carried over longer distances. Nevertheless, wind dispersal seems not to play a major role, because most of the cup plants were detected in the immediate vicinity of the fields. Ende and Lauerer (2020) documented a spread of cup plants of up to 700 m along a street and presumed agricultural machines as vector. In fact, losing of crop and thus of fruits from the trailer is quite possible and must be kept in mind regarding the prevention of cup plant spread. A dispersal of the fruits and of root parts via water would also be conceivable and was suspected by Ende et al. (2021) and Vladimirov (2021). Altogether, we suspect a certain dispersal potential of cup plant – even over longer distances.

The probability of spontaneous cup plant occurrence increased almost linearly with increasing field age (Fig. 1C). This is not surprising, because the spontaneously colonized cup plants are perennial and can persist over many years (Stanford 1990). Every year, plants can be added and accumulate to an increasing number with increasing field age. Cup plant fields are usually used for 10 to 15 years, sometimes even longer (Dauber et al. 2016; Frölich et al. 2016; Hartmann and Lunenberg 2016; Bernas et al. 2021). The fields investigated in our study were between 2 and 11 years old. A further increase in spontaneous colonization can be expected in the coming years. Together with the continuously increasing area that is cultivated with the cup plant (FNR 2022), this results in an enormous spreading potential for the future emanating from the fields throughout Germany.

Another important parameter for the spontaneous colonization of cup plants seems to be the portion of open soil. In our study, cup plants occurred preferentially on about 25% open soil (Fig. 1D). It is a matter of speculation why just this value is optimal for colonization. A lower portion of open soil goes along with a higher cover of vegetation, of paved ground, or of litter. However, none of these parameters was significantly decisive for cup plant occurrence. Notwithstanding this, these three factors could still impede germination and/or seedling development. It is known that cup plant seedlings develop slowly and are therefore very sensitive to competing vegetation in the first year (Köhler and Biertümpfel 2016). In the present study, a high portion of open soil was mainly found on unpaved paths and occasionally under dense scrubs or hedges. Colonization is more difficult on paths due to strong soil compaction and under woody formations due to lower light availability. Stanford (1990) confirms that cup plants need full sun for optimal growth.

All other parameters (besides habitat type), i.e. Ellenberg indicator values (EIV) for soil reaction, light availability and soil moisture, cover of litter, of shrub and of tree layer, as well as the cover of paved ground, did not influence the probability of cup plant occurrence.

In the first year of growth, cup plants develop only a rosette of leaves. From the second year on it can develop stems, flowers, and respectively fruits (Wrobel et al. 2013). These stem-developing individuals were considered as establishing in the present study. Such establishing individuals were also found around each of the eleven surveyed fields. More than half of the plots that were colonized by cup plants also had establishing individuals (59%). A flower development could not be assessed because the cup plant blooms between July and October in Central Europe (Jabłoński and Kołtowski 2005; Wrobel et al. 2013; Jäger 2017) and data were collected between May and early August. However, most of these individuals had only one stem, were not very tall and less vigorous than the cultivated cup plants on the field. We therefore assume that most of these plants could only develop a few flowerheads at most.

In the study area the following habitat types were represented: open habitats, human settlement areas, woody habitats, and inland waters including their riparian areas. However, cup plant did not invade these habitat types equally (Fig. 1A). The habitat type had a significant impact on the probability of cup plant occurrence. Cup plants preferred open habitats such as field margins and human settlement areas especially paths, but also occurred spontaneously in intensively used grasslands. All these habitat types are cut regularly, so that successful fruit development and further spread are unlikely. This is reflected in the significantly positive relationship between the probability of cup plant establishing and the height of the herb layer in the present study (Fig. 2C). Due to the nutrient-rich and species-poor characteristic of the mentioned habitat types their value for biodiversity is quite low. Hence, an invasion of cup plant is initially unproblematic here. Open habitats without management were hardly represented in our study. However, cup plant occurrences in ruderal and fallow areas are frequently detected in Germany (Buhr and Kummer 2009; Brennenstuhl 2010; Nezadal et al. 2011; Schönfelder 2012; Klug 2015; Parolly and Rohwer 2016; Jäger 2017; Kämpfe 2017). There a successful fruit development and further spread is conceivable.

In the present study, the cup plant also invaded woody habitats, although the probability of its occurrence was only about one third as high as in open habitats. The herb layer of woody habitats is usually not managed, which is why reproduction and further spread of cup plant is potentially possible. However, an extensive spread in forests or plantations is not expected, because cup plant needs full sun for optimal growth (Stanford 1990). Additionally, the probability of establishing grew with increasing EIV temperature in the present study (Fig. 2A). The cup plant therefore prefers warmer sites for stem development than it needs for rosette stage. Stanford (1990) confirms that cup plants develop best at around 20 °C. In fact, only three of the cup plants that invaded forests and plantations, have developed stems. In tree rows and tree groups stem development succeeded more often because the required light, warmth and absent management is available there. Less management could also be the reason for the positive relationship between the probability of cup plant establishing and distance to the field (Fig. 2B). In contrast to the general occurrence of cup plant, its establishing increased with the distance to the field. Usually, the habitats in the immediate field vicinity are intensively mowed and managed, which prevents stem development. Habitats farther away from the fields may be more heterogeneously structured, which is why stem development may succeed more often. In literature, there is little evidence of spontaneous detections of cup plants in woody habitats. Only Reuther and Tillich (1996) detected it in a scrub fringe in Germany. In its native range in eastern North America, it colonizes amongst others in woods, thickets and roadside ditches (Penskar and Crispin 2010). However, cup plants preferentially colonize there near rivers: in open prairie clearings in moist sandy bottomlands, in lakesides, and in ravines (Stanford 1990; Penskar and Crispin 2010; Gansberger et al. 2015). In Germany, too, the cup plant was frequently found in the riparian areas of standing and running water (Oberdorfer 1994; Brandes 2003; Wölfel 2013; Parolly and Rohwer 2016; Jäger 2017; Schönfelder 2017). In the present study, inland waters including their riparian area were not invaded. However, this habitat type was hardly represented in our study. Furthermore, not even a significant relationship between EIV soil moisture and cup plant occurrence or establishing could be proven in the present study. This was possibly because all the investigated sites had an average EIV soil moisture. But the preference of cup plants for moist sites was also confirmed by experimental studies in Germany by Ende et al. (2021), where it showed higher biomass and reproductive potential under moist soil conditions. Therefore, special attention must be paid to moist habitats because they are often valuable for nature conservation and could be colonized by the cup plant (Ende et al. 2021). In our study, other valuable ecosystems were also hardly represented. Only two sites fall into this category: A pine forest on a nutrient-poor, base-deficient site where one single spontaneously colonized cup plant in rosette stage occurred and a species-rich, extensively used grassland where no cup plant occurred. According to literature, no spontaneously colonized cup plants have been detected in valuable ecosystems in Germany so far. However, future colonization cannot be excluded.

Once a spontaneously colonized cup plant has developed stems, the question arises whether and how they develop over time. Our results showed that all of the monitored establishing cup plants survived and new ones were added over the observational period of three years. The number of establishing individuals increased six-fold within these three years. The number of stems per plant increased over this time. Boe et al. (2019) also observed that the cup plant develops more stems with increasing age. All these individuals might develop flowers and eventually reproduce. Therefore, the reproductive potential increases over time both per plant and per population. The factor time is therefore of great importance for assessing the invasive potential of the cup plant.

Conclusion

The present study demonstrated an enormous spreading potential of the cup plant. Regarding the future, spontaneous occurrences are likely to expand as the number of cup plant fields increases. The cup plant is able to colonize and establish in a wide range of habitats, especially in less managed open habitats with disturbances. An invasive behavior has not yet been detected. However, there are still some unanswered questions regarding its possible invasiveness. Further studies, especially on dispersal vectors and competitive strength, as well as further documentation of spontaneous occurrences, are necessary to assess the risk of the continuing spread of cup plants and its impact on the native flora and fauna. Until further knowledge is available, we recommend cautious handling of the cup plant. Fields should be located at a safe distance to valuable ecosystems and watercourses to avoid possible dispersal of diaspores via water and an invasion of these ecosystems. Agricultural machines should be cleaned thoroughly after use and covered before leaving the field to prevent dispersal of fruits over long distances.

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Supplementary material 1

Characteristics of cup plant fields around which data were collected

Authors: L. Marie Ende, Marianne Lauerer

Data type: table (PDF file)

Link: https://doi.org/10.3897/neobiota.79.94283.suppl1

Supplementary material 2

Distribution of parameters in all plots independent whether invaded or uninvaded

Authors: L. Marie Ende, Marianne Lauerer

Data type: figure (PDF file)

Link: https://doi.org/10.3897/neobiota.79.94283.suppl2

Supplementary material 3

Dataset invaded and uninvaded plots

Authors: L. Marie Ende, Marianne Lauerer

Data type: table (csv document)

Link: https://doi.org/10.3897/neobiota.79.94283.suppl3

Supplementary material 4

Dataset establishing cup plants

Authors: L. Marie Ende, Marianne Lauerer

Data type: table (csv document)

Link: https://doi.org/10.3897/neobiota.79.94283.suppl4