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RESEARCH ARTICLE

Dispersal and persistence of cup plant seeds (*Silphium perfoliatum*): do they contribute to potential invasiveness?

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Abstract

Background and aims – The cup plant (*Silphium perfoliatum*) is being grown in Germany as a promising new bioenergy crop with an increasing area under cultivation in the last years. Its alien status, its high productivity, and high reproductive potential could carry the risk of this species becoming invasive. The present study investigates the dispersal and persistence of cup plant seeds, to contribute to the assessment of its invasive potential.

Material and methods – For this purpose, four experimental studies were conducted in Germany, Central Europe: wind dispersal distance was measured in a field experiment for wind speeds up to 7 $m.s^{-1}$. The seeds were offered to rodents in different habitats near to a cup plant field. We observed seed persistence and germination over 4 weeks storing in water and over 4 years storing in different soil depths.

Key results – Cup plant seeds are dispersed by wind only over a few meters. In the forest, rodents removed 100% of the offered seeds, in open habitats none. Independent of the duration of storage in water, germination rate of the cup plant seeds was constantly high. Most of the seeds already germinated in water in the first two weeks. Stored on the soil surface and at 10 cm soil depth, the seeds germinated already in the first two years. Stored at 30 cm depth, one third of the seeds retained their germination ability over four years.

Conclusion – Wind serves as short-distance dispersal vector for cup plant seeds. Rodents remove the seeds, but it is unknown whether they disperse them or just eat them. Water could disperse the seeds, which retain their germination ability, over long distances. The cup plant could therefore spread and possibly become invasive in Central Europe, and therefore measures are suggested to prevent its dispersal and spontaneous settlement.

Keywords

anemochory, bioenergy crop, dispersal, hydrochory, invasive potential, *Silphium perfoliatum*, soil seed bank, water, wind, zoochory

INTRODUCTION

Biogas plants are one source for regenerative energy (FNR 2022b). In Germany, maize (*Zea mays* L.) is the predominantly used bioenergy crop and grew in 2021 on 880,000 ha (Emmerling 2016; Frölich et al. 2016; FNR 2022b). However, its cultivation goes along with great ecological strains due to high application of machinery, fertilisers, and pesticides (Emmerling 2016; Frölich et al. 2016). Alternative crops are sought, which are more sustainable and environmentally friendly (Gansberger et al. 2015; Emmerling 2016; Frölich et al. 2016; Ruf et al. 2019).

One promising new bioenergy crop is the cup plant (*Silphium perfoliatum* L.). Native to eastern North America, it was introduced in Europe in the 18th century as ornamental plant (Stanford 1990). Since 2004, it is used as alternative bioenergy crop in Germany (Frölich et al.

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2016). In 2021, there were more than 10,000 ha cultivated with *S. perfoliatum* in Germany, nearly tripling the area in one year (FNR 2022a). This perennial, yellow-flowering herb belongs to the Asteraceae family. It develops shoots from the second year on and persists for many years (Stanford 1990). The cup plant can be harvested profitably for more than 15 years, requires less use of machinery, fertilisers, and pesticides compared to maize, and it has benefits for the microbial biodiversity and the biomass in the soil, as well as for pollinators due to its late and long flowering period (Burmeister and Walter 2016; Emmerling 2016; Frölich et al. 2016; Hartmann and Lunenberg 2016; Mueller and Dauber 2016). All these are essential ecological advantages over maize. However, because of its alien status, its high productivity, and reproductive potential (Stanford 1990; Frölich et al. 2016), there could be a risk of possible invasiveness. According to EU legislation, a species is classified as invasive if its spread threatens biodiversity (Article 3, No. 2 EU-Regulation No. 1 143/2014). A spread of the cup plant from its fields is already documented in northern Bavaria (Germany) (Ende and Lauerer 2022). Further spontaneous occurrences are noted in 15 of Germany's 16 federal states and in several other European countries, e.g. Belgium, Austria, Poland (Roskov et al. 2019; GBIF 2021). In the Netherlands, Ukraine, and Russia, the cup plant is already detected as potentially invasive (Matthews et al. 2015; Vinogradova et al. 2015; Zavialova 2017). Until now, an invasive behaviour was not reported in Germany. However, several studies suppose a certain invasive potential, because of its spread, its preference for moist habitats, which are often valuable for nature conservation, and its high competitiveness (Ende et al. 2021, 2023; Ende and Lauerer 2022). Another important trait that promotes the spread and thus the invasive behaviour of a plant species is the effective dispersal of the diaspores (Coutts et al. 2011). Until now, studies to dispersal vectors of the cup plant are completely missing. The seeds of the cup plant could be dispersed by wind due to their small wings (Kowalski and Wierciński 2004). A dispersal by water streams is conceivable because in its native range this species prefers habitats near rivers (Stanford 1990; Penskar and Crispin 2010; Gansberger et al. 2015). Wind and water both serve as long-distance dispersal vectors for many plants including invasive species (Skarpaas and Shea 2007; Landenberger et al. 2007; Jaquemyn et al. 2010; Zhang et al. 2022). It is known that rodents can also disperse plants seeds effectively and thus contribute to the spread of invasive plants (Wróbel and Zwolak 2013; Suselbeek 2014; Bieberich et al. 2016; Lichti et al. 2017; Kempter et al. 2018). Cup plant seeds have a similar fat content as those of sunflower (*Helianthus annuus* L.) (Kowalski and Wierciński 2004) what leads to the assumption that they are consumed by rodents. To provide insights into these characteristics of the cup plant that contribute to the evaluation of its invasive potential, we investigated the dispersal and persistence of cup plant seeds for the first time. We conducted four experiments at the Ecological Botanical Gardens of the University of Bayreuth (Germany) and its vicinity to answer the following questions:

Is wind a dispersal vector for cup plant seeds and how far are they dispersed by wind?

Can rodents serve as dispersal vectors for cup plant seeds?

How long do cup plant seeds retain their germination ability in water?

How long do cup plant seeds retain their germination ability in soil?

Studying the dispersal vectors of cup plant contributes to estimate the future settlement of this possibly invasive species in Central Europe; and the results are transferable to other regions with similar climate where the cup plant is cultivated. This study helps to alert farmers, conservationists, and other stakeholders to the possible invasiveness of the cup plant.

MATERIAL AND METHODS

Seed material

Cup plant fruits are flat achenes with two small wings and a thin pericarp (Kowalski and Wierciński 2004; Gansberger 2016) (Fig. 1). Each fruit contains one seed (Gansberger 2016). In the present study, for the purpose of simplicity, we occasionally use the term "seed" and mean by that "fruit" or "achene".

For all experiments of the present study, we used not-stratified seeds of the company Metzler & Brodmann Saaten GmbH, Ostrach, Germany. For each experiment, they were harvested by the company in the previous autumn. We stored them after receiving at about 6°C until start of the respective experiment. We selected ripe, undamaged seeds for each experiment. We characterised the selected seeds harvested in 2019, which were used for the wind and water experiments (Table 1). Seeds for the soil seed bank experiment were harvested in 2018, those for the rodent experiment in 2022. Due to the same origin, they are apparently similar characterised as the seeds of 2019 (Table 1).

Experimental setups and data collection

Wind experiment

The wind experiment was executed in June 2020 on several days with no precipitation. The experimental site was a 10 × 10 m area at the Ecological Botanical Gardens of the University of Bayreuth in Germany. It was located in a meadow that was mown, laid out with a tarpaulin, and filled up with a 3 cm layer of sand. In the centre of this area, we placed a pole of 2 m height, which corresponds to the height of a medium-sized shoot of a cup plant (Ende et al. 2021; Müller et al. 2021). Trees, houses, or other wind barriers were at least 70 m away in each direction.

Table 1. Characterisation of cup plant seeds harvested in 2019 by Metzler & Brodmann Saaten GmbH, Ostrach, Germany. Ripe, undamaged seeds were chosen. Given is the average ± standard deviation.

Parameter	n	Entire fruit	Portion of wings	Method
Area [cm²]	200	0.50 ± 0.10	0.18 ± 0.05 (37 %)	Seeds were scanned with HP Scanjet automatic document feeder and analysed using WinFOLIA 2013 for Leaf Analysis (Regent Instruments Canada Inc.)
Length [cm]	200	0.96 ± 0.10		
Width [cm]	200	0.69 ± 0.08	0.20 ±0.05 (29 %)	
Thickness [mm]	50	1.01 ± 0.15		calliper
Thousand grain weight [g]	20	18.06 ± 1.68		Weight of 20 × 10 seeds was measured using scales (AE240, Mettler) and extrapolated to 1000.

Twenty samples of each ten ripe and undamaged seeds with intact wings were prepared previously. For each experimental run, one sample was selected randomly. The ten seeds were placed distant to each other inside a closed petri dish with the lower part of the petri dish placed upside down on the pole. Between the lid and the lower part of the petri dish a spacer was placed that was glued to the lid. Next to the upper part of the pole, we measured wind with a hand anemometer (Anemo, Deuta-Werke Bergisch-Gladbach, Germany) with an accuracy of 0.5 $m.s^{-1}$. When the required wind speed was reached, the lid of the petri dish was removed, and the seeds were exposed to the wind for 10 s. The number of the seeds blown away was counted and the distance of each seed to the pole was measured with a measuring tape accurate to 1 cm. This procedure was repeated until each wind speed was repeated about ten times. The total number of repetitions was 122. The maximum measured wind speed was 7 $m.s^{-1}$. This corresponds to level 4 of the Beaufort scale that is a moderate breeze (Häckel 2021). The Beaufort scale is an international scale to classify wind strength (Häckel 2021). It ranges from 0 (no wind) to 12 (hurricane) (Häckel 2021). To make it easier to find seeds, that were blown away, they were previously marked with a pink marker (4000 creative, edding). The thousand grain weight of marked seeds was 18.99 ± 1.95 g and not significantly different to the thousand grain weight before marking (Table 1, t-test: $p = 0.116$).

Rodent experiment

The rodent experiment was executed for 21 consecutive days in October/November 2022. The experimental site was at and around a cup plant field in northern Bavaria in Germany (49°54’57.9”N, 11°33’09.3”E). We considered three habitats: (1) the cup plant field itself that was harvested three weeks before the start of the experiment, (2) a meadow that was mown in the week before the experiment and that is separated from the cup plant field by an agricultural path (49°54’57.4”N, 11°33’02.4”E), and (3) a sparse pine forest, also separated from the cup plant field by a pathway (49°55’00.7”N, 11°33’17.1”E). In each habitat, three boxes were placed in a line with 20 m distances between. The boxes were made of wood and had the following inside dimensions: 30 cm width, 30 cm depth, and 13 cm height. They had a removable lid and two opposite closed side walls. The other two sides were open but equipped with a 3 cm high wooden strip to prevent the seeds being blown away by wind. The boxes were filled with 30 seeds each. Every day at the same time (afternoon), seeds left over from the previous day were counted and removed, and 30 new seeds were placed in the boxes. We positioned wildlife cameras at each one of the three boxes of the habitats cup plant field and meadow, as well as at all the three boxes in the forest.

Water experiment

We stratified all the seeds for the water experiment using the following procedure: We soaked the seeds in water for three days by changing the water daily. Afterwards, we

Figure 1. Cup plant fruits are flat achenes with two small wings. Photo by Lukas Hummel.

stored them with quartz sand moistened with Previcur Energy (Bayer, 0.1% solution) in plastic bags for two weeks at 4°C. Then, we rinsed them with water and started the experiment on 20 Apr. 2020. Each ten seeds were placed in 48 glasses filled with 100 ml tap water and subjected to one of the two treatments: running water was simulated by a shaker (Gyrotory water bath shaker, G76 New Brunswick Scientific, 160 RPM). Standing water was simulated by a not-moving box similarly shaped to the shaker. The water-filled glasses with the seeds were placed in the shaker (running water treatment) resp. in the box (standing water treatment) and stored for three different durations: one week, two weeks, and four weeks. Each treatment and each duration had eight samples (n = 8). Evaporated water was filled up daily during the experiment. On 15 May 2020 (25 days after the start of the experiment), oxygen saturation was measured with an oxygen electrode (HQ 40d multi, HACH) three times in each of the eight remaining glasses and middled per glass. In the running water treatment, oxygen saturation was on average 100%. This was significantly higher than in the standing water treatment where the average was 81% (LM, Adjusted $R^2 = 0.86$, $p < 0.001$, n = 16).

The experiment was carried out in a greenhouse at the Ecological Botanical Gardens of the University of Bayreuth. The side walls and the roof of this greenhouse opened and closed automatically so that no precipitation could reach the experimental setup and the temperature in the greenhouse was similar to the outside temperature. During the experiment, outside temperature was on average 10.5 ± 2.6°C (weather station in the Ecological Botanical Gardens operated by the Micrometeorology group, BayCEER, University of Bayreuth).

To the end of the respective storage duration, number of seeds germinated in water was counted and not-germinated seeds were sown in pots in a greenhouse. Number of seedlings was counted daily until no seedling was added for seven days. Additionally, there was a control treatment of 8 × 10 seed (n = 8), which was not stored in water, and sown directly after stratification at the same time as the two-weeks treatment. The sum of seeds germinated in water and in the pots after sowing was considered as germination rate.

Soil seed bank experiment

Thirty seeds each were put in small sacks together with 20 g of sand (previously sterilised for 24 h at 120°C in an oven). These sacks were made from a piece of pantyhose (Kunert, Glatt & Softig 20) and knotted at both ends. These sacks were buried respectively stored in three soil depths (treatments): soil surface, 10 cm depth, and 30 cm depth, at the end of November 2018. The experimental site was a species-poor, flat meadow in the Ecological Botanical Gardens of the University of Bayreuth in Germany. The 10 cm and 30 cm treatments were buried by drilling a hole of the respective depth with a soil drill (3.5 cm diameter). The sacks were provided with a red ribbon, long enough to reach the soil surface to facilitate retrieval when the sacks were placed into the hole. The hole was filled up with the present soil and marked with a metal sign. A wire frame was placed on the sacks of the soil surface treatment and secured to the ground with pegs to prevent displacing of the sacks. Samples were placed 40 cm distant to each other in four blocks with each eight repetitions per treatment in randomised order. Per block and treatment, two samples were excavated with a spade and a shovel in spring (between the end of March and the beginning of April) of the following four years, resulting in n = 8 per treatment and year. After excavation, seeds germinated in the soil were counted. Not-germinated seeds were sown in pots in a greenhouse. Number of seedlings was counted daily until no seedling was added for seven days. With the excavation in the first spring, a control treatment (n = 8) was sown at the same time. For each sample of control treatment 30 seeds were stratified by the following procedure: seeds were soaked in water for three days, changing the water daily. Afterwards they were stored with moist quartz sand in plastic bags for three weeks at 4°C. Finally, they were stored outside in shade (in sand in plastic bags) for four days with alternating temperature (mean daytime temperature was 13.2°C, mean night-time temperature was 4.8°C, weather station at the Ecological Botanical Gardens operated by the Micrometeorology group, BayCEER, University of Bayreuth). The sum of seeds already germinated in the soil and after sowing in the pots was taken as germination rate in the respective year.

Data analysis

Statistical analysis and data visualisation were performed with R v.4.2.2 (R Core Team 2022). For statistical modelling and testing, we used linear models (LM) and checked the diagnostic plots. In case of non-normal distribution or heteroscedasticity of residuals, we transformed the parameters or used generalised linear models (GLM). Log-transformation was executed with the natural logarithm. Significant differences between the treatments were analysed using the Tukey's post-hoc test ("emmeans" of the R package "emmeans" v.1.8.5; Lenth 2023). If the diagnostic plots were still not satisfying, we used the non-parametric Kruskal-Wallis rank sum test with the post-hoc test multiple comparison test after Kruskal-Wallis (kruskalmc) of the R package "pgirmess" v.2.0.0 (Giraudoux 2022). We used the function "predict" of the R package "stats" (R Core Team 2022) to calculate confidence intervals of LM. For GLM, we used the function "add_ci" of the R package "ciTools" v.0.6.1 (Haman and Avery 2020). In the experiment for seed persistence in soil, we checked the influence of block with a Kruskal-Wallis rank sum test. Because it was not significant in each case, we eliminated the block for the final models. The level of significance was always 0.05. We used the function "ddply" of the R package "plyr" v.1.8.8 (Wickham 2011) to get the average values of particular treatments.

RESULTS

Seed dispersal via wind

The higher the wind speed, the more cup plant seeds were blown away (Fig. 2A, Table 2). At slow wind speeds of 3 m.s^{-1}, 30% (average) of seeds were blown away, whereas at the highest wind speed of 7 m.s^{-1}, 65% were blown away. The distance of the seeds also increased with increasing wind speed (Fig. 2B). At 3 m.s^{-1} they flew 1.1 m (average) far and at 7 m.s^{-1} they flew 3.2 m far. The furthest distance that a single seed flew was 6.6 m at a wind speed of 7 m.s^{-1}.

Seed removal by rodents

In the forest habitat, 100% of the exposed cup plants seeds were removed every day, whereas in the meadow and the cup plant field, no seed was removed (Fig. 3, Table 3). In the boxes in the forest, many leftovers from fruit pericarps and many faeces were frequently observed. This suggests that the rodents ate the seeds in the box, at least partially, instead of carrying them away. Indeed, several videos taken by the wildlife cameras in the forest show the bank vole (*Myodes glareolus* (Schreber, 1780)) eating cup plant seeds in the boxes (Fig. 4A). A few photos at night were also taken of the mouse genus *Apodemus*, of which the yellow-necked mouse (*Apodemus flavicollis*

Table 2. Effects of wind speed on the number and the distance of cup plant seeds blown away. For visualisation see Fig. 2.

Parameter	n	d.f.	F value	p	Model
Portion of seeds	122	1	160.05	< 0.001	GLM with Poisson distribution
Distance	386	1	291.84	< 0.001	GLM with Gamma distribution

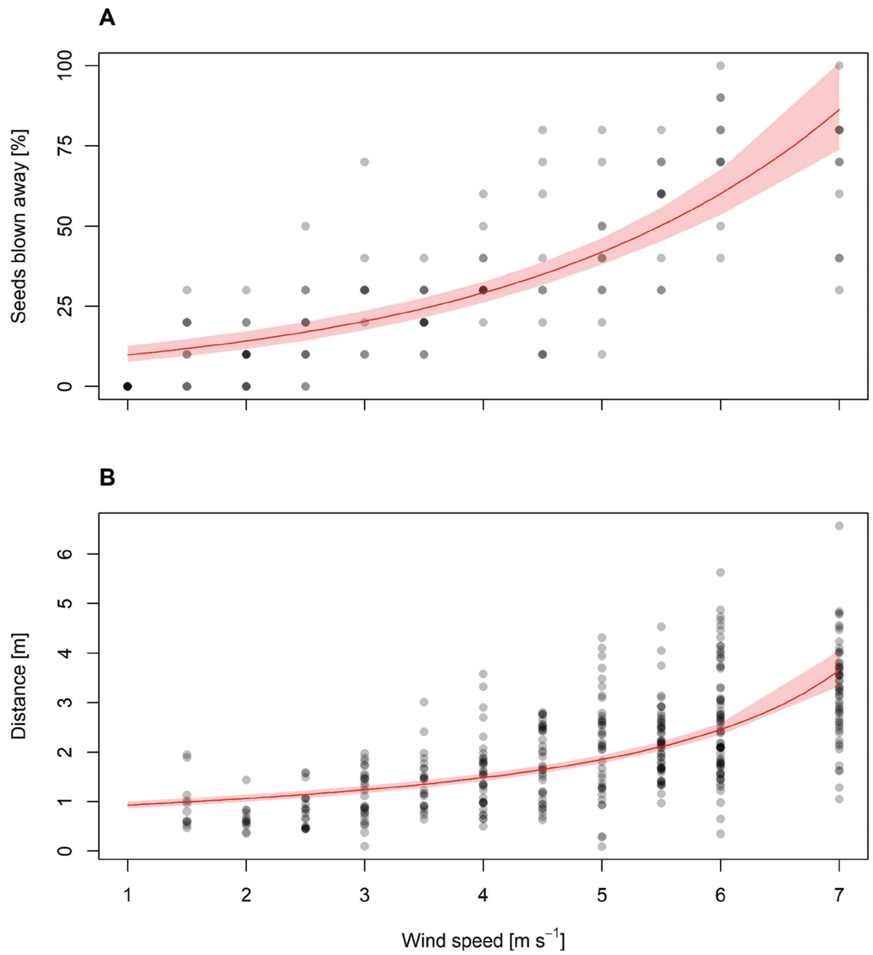

Figure 2. A. Cup plant seeds blown away by wind depending on wind speed; 100% corresponds to 10 seeds; n = 122. **B**. Distance of cup plant seeds blown away by wind depending on wind speed; seeds that were not blown away by wind were excluded; n = 386. The darker the dots are, the more dots are on top of each other. The red lines are fitted by the models in Table 2. The red ribbons show the 95% confidence intervals of the models.

Table 3. Effects of habitat on the removal rate of cup plant seeds. For visualisation see Fig. 3.

Parameter	n	d.f.	Chi²	p	Test
Removal rate	189	2	170.09	< 0.001	Kruskal-Wallis rank sum test

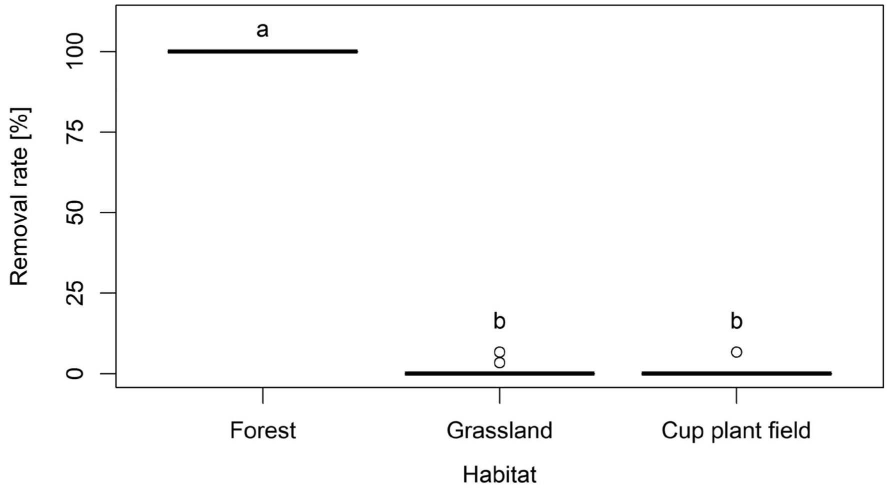

Figure 3. Removal rate of cup plant seeds depending on habitat. 100% corresponds to 30 seeds. Different letters indicate significant differences (kruskalmc test; Table 3). Data were collected for 21 days at three replicates per habitat resulting in n = 63.

(Melchior, 1834)) and the wood mouse (*Apodemus sylvaticus* (Linnaeus, 1758)) are possible species (Fig. 4B). In the meadow and the cup plant field, not a single rodent was photographed by the wildlife cameras. In the boxes in the forest, the bird species great tit (*Parus major* Linnaeus, 1758), was also seen several times.

Seed persistence in water

After one, two, and four weeks of storage in water, the total germination rate of cup plant seeds was on average 85% (Fig. 5B). There was no significant difference between the treatments running or standing water, the duration of storage in water, nor compared to the control (Table 4). However, many of the seeds already germinated in water. Germination rate in water was affected by both treatment and duration of storage in water (Table 4). In the running water treatment, the germination rate was 79% after two weeks and did not increase over the following two weeks (Fig. 5A). In the standing water treatment, the germination rate in water was 50% after two weeks and increased to 81% after four weeks. In both treatments, the seeds had already sunk to the bottom in the first three days. After germination, the seedlings looked fresh and vital in water until the end of the experiment.

Seed persistence in soil

In the first spring after the seeds were placed in the soil, the total germination rate was 95% on average (Fig. 6B).

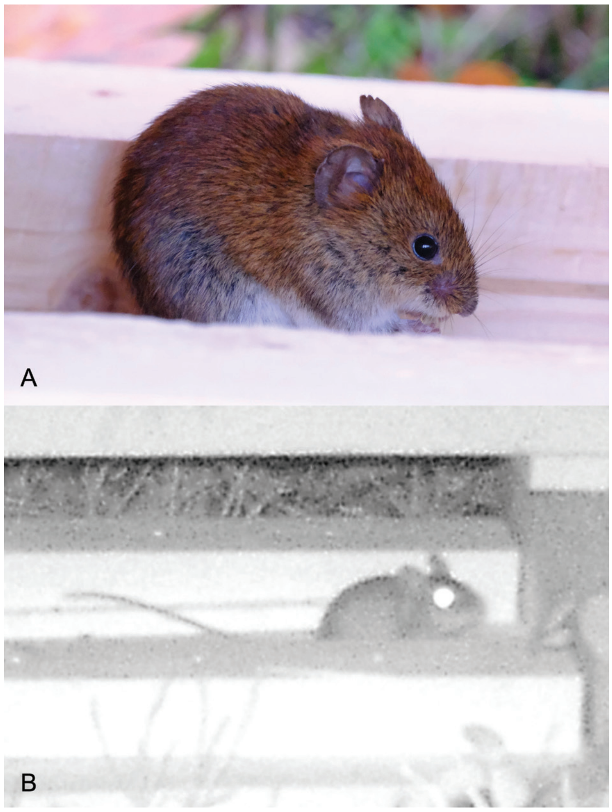

Figure 4. Rodents seen in the boxes with cup plant seeds in the forest habitat. **A**. Bank vole (*Myodes glareolus*) eating cup plant seeds. Photo by Lukas Hummel. **B**. *Apodemus* sp. Photo at night by Wildlife camera (Wild-Vision Full HD 5.0, SECACAM, Ven Trade GmbH, Köln, Germany).

Table 4. Effects on the germination rate of cup plant seeds already in water (upper part) and in total (lower part). For visualisation see Fig. 5.

Dependent variable	Parameter	d.f.	F value	p	Model
Germination rate already in water	treatment	1	7.75	0.008	LM, $p < 0.001$, Adjusted $R^2 = 0.75$, n = 48
	duration	2	67.79	< 0.001	
	treatment × duration	2	2.90	0.07	
Germination rate in total	treatment	2	1.27	0.289	LM, $p = 0.353$, Adjusted $R^2 = 0.02$, n = 56
	duration	2	1.79	0.178	
	treatment × duration	2	0.37	0.696	

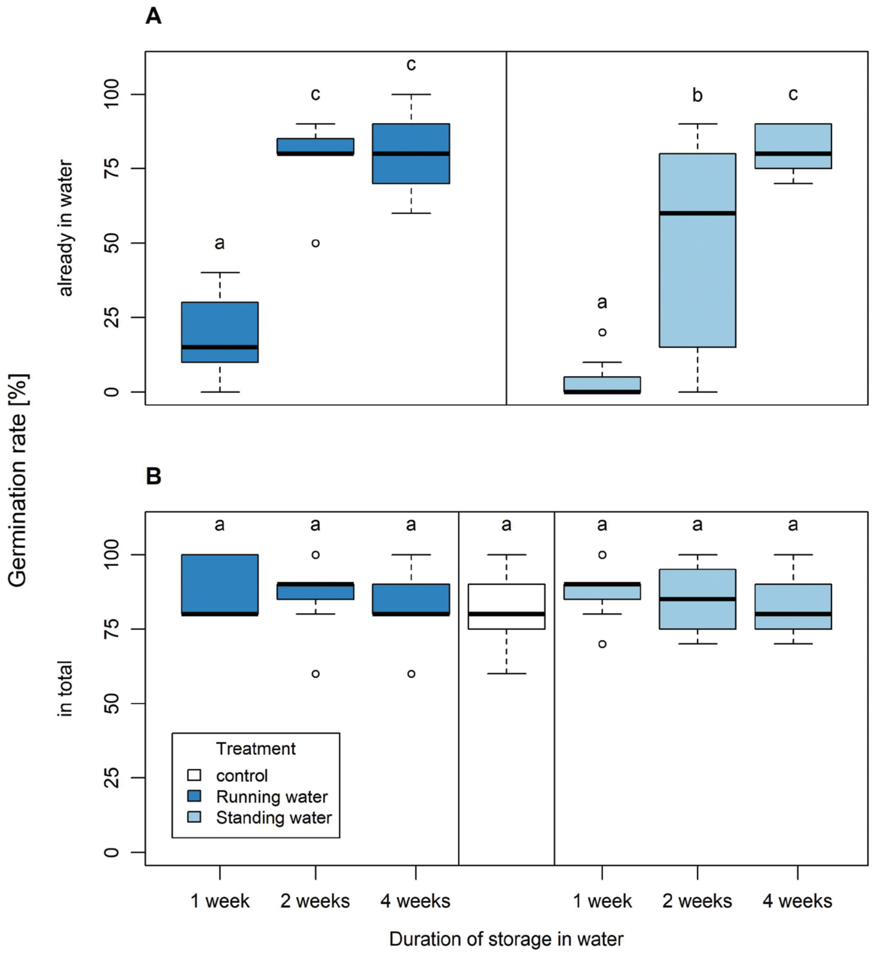

Figure 5. Germination rate of cup plant seeds (**A**) already in water and (**B**) in total, depending on treatment and duration of storage in water. Total germination rate was calculated as sum of seeds germinated in water and in the pots after sowing. 100% corresponds to 10 seeds. Different letters indicate significant differences (Tukey's post-hoc test; Table 2). n = 8.

It was the same for all treatments and not significantly different to the control. In the second year, germination rate was decreased differently in all treatments (Fig. 6B; Table 5). The seeds on the soil surface germinated to 19% on average in the second year, whereas germination ability of seeds buried at 10 cm depth was already completely extinguished. The seeds buried at 30 cm depth had the highest germination rate. There, 51% of the seeds germinated in the second year. In this treatment, germination rate decreased continuously to 37% in the fourth year. Our experiment observed only the first four years after placing the seeds in the soil. According to the mathematical model, the germination ability of the seeds stored at 30 cm depth would extinguish between the eighth and the 15th year (Fig. 7). On the soil surface no seeds germinated after the second year.

Especially in the 10 cm treatment, the reason for the missing germination in the second year was not the loss of germination ability. It was the complete germination of the seeds already in the soil in the first year of the experiment (Fig. 6A). On the soil surface and at 30 cm depth, on average 19% of the seeds had already germinated when

Table 5. Effects on the germination rate of cup plant seeds already in the soil (upper part) and in total (lower part). For visualisation see Fig. 6.

Dependent variable	Parameter	d.f.	Chi²/F value	p	Model
Germination rate already in the soil	treatment	2	1.73	0.421	Kruskal-Wallis rank sum test, n = 96
	duration	3	66.13	< 0.001	Kruskal-Wallis rank sum test, n = 96
Germination rate in total	treatment	3	35.16	< 0.001	LM, p < 0.001, Adjusted R^2 = 0.73, n = 104
	duration	1	176.11	< 0.001	
	treatment × duration	2	3.80	0.026	

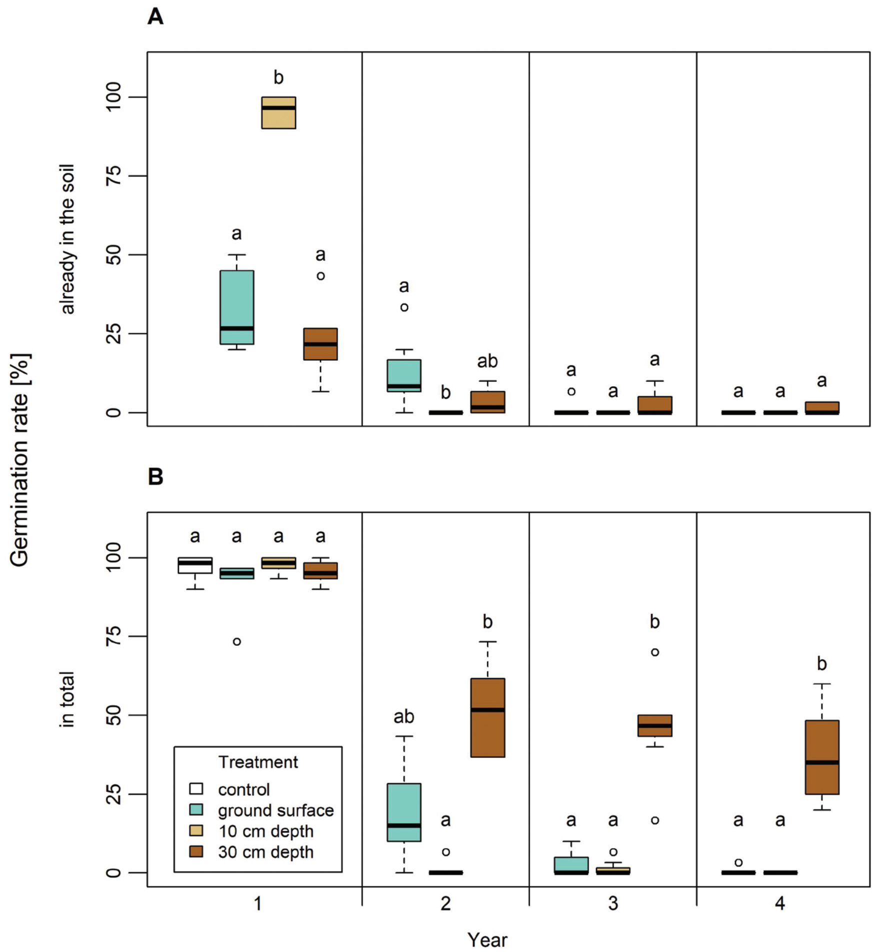

Figure 6. Germination rate of cup plant seeds (**A**) already in soil and (**B**) in total, depending on treatment and duration of storage in soil. Total germination rate was calculated as sum of seeds germinated in the soil and in the pots after sowing. 100% corresponds to 30 seeds. Different letters indicate significant differences within the respective year (kruskalmc tests; Table 5). n = 8.

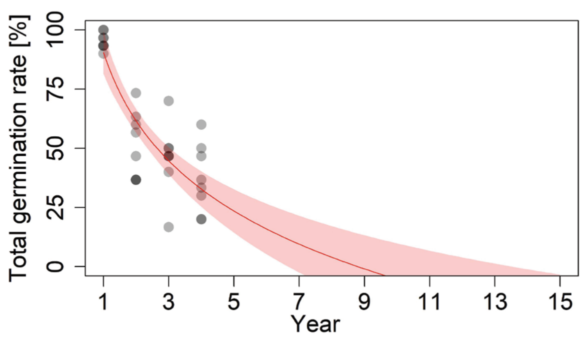

Figure 7. Total germination rate of cup plant seeds stored at 30 cm soil depth depending on duration of storage in soil. Total germination rate was calculated as sum of seeds germinated in the soil and in the pots after sowing. 100% corresponds to 30 seeds. The darker the dots are, the more dots are on top of each other. The red line is fitted by LM: y = 90.5 – 41.6*ln(x), Adj. R^2 = 0.72, p < 0.001. The red ribbon shows the 95% confidence interval of the model. n = 32.

they were excavated in the first year. A few single seeds at 30 cm depth germinated in the soil the following years.

DISCUSSION

In the present study, the dispersal and persistence of cup plant seeds were investigated for the first time. It provides valuable information for assessing the future spread of this possibly invasive species.

Wind serves as long-distance dispersal vector for many plant species, including invasive species such as the tree of heaven (*Ailanthus altissima* (Mill.) Swingle) or the Canada goldenrod (*Solidago canadensis* L.) (Landenberger et al. 2007; Zhang et al. 2022). Kowalski and Wierciński (2004) assumed the ability of the cup plant seeds to fly due to their small wings. Though, in the present study, cup plant seeds were dispersed by wind with a speed of up to 7 $m.s^{-1}$ only over a few meters. The positive relationship between dispersal distance and wind speed probably continues with higher wind speeds that were not investigated in the present study. Hence, higher distances are expected at higher wind speeds. However, the mean wind speed in inland Germany is only 2 to 4 $m.s^{-1}$ (Häckel 2021). Especially in the month September, when many cup plant fruits are ripe and when usually the harvest takes place (Gansberger et al. 2015; Gansberger 2016; Hartmann and Lunenberg 2016), a mean wind speed of 1.4 $m.s^{-1}$ was measured for the years 2018–2022 nearby the experimental site (weather station at the Ecological Botanical Gardens operated by the Micrometeorology group, BayCEER, University of Bayreuth). The maximum wind speed there per year in September was between 9.8 and 17.4 $m.s^{-1}$. Therefore, most of the time, the wind speed is too slow to disperse cup plant seeds over more than a few meters. Nonetheless, single strong gusts of wind could suffice to cause a further dispersal. It is also conceivable that the seeds are picked up from the ground by the wind and transported further. These processes as well as the dispersal of cup plant seeds at higher wind speeds could be investigated by a wind tunnel experiment to complement the results of the present field study. Until now, studies on the wind dispersal of the diaspores of cup plant are missing. The present study is the first in this respect. The related species compass plant (*Silphium laciniatum* L.) has similarly shaped fruits and was dispersed over 1.1 m on average (Pleasants and Jurik 1992). Spontaneously colonised cup plants were detected in a study in Germany at a mean distance of 2.1 m from their fields (Ende and Lauerer 2022). Altogether, we conclude that wind is not a vector to disperse cup plant seeds over long distances. It can only cause dispersal over short distances of a few meters. *Heracleum sosnowskyi* Manden., which is invasive in eastern Europe, had also an increasing dispersal distance with increasing wind speed (Chadin et al. 2021). However, it only covers short distances of a few meters, too (Chadin et al. 2021). This example shows that long-distance wind dispersal is not a precondition for successful invaders.

Many rodents hoard seeds and nuts in caches to survive periodic food scarcity, which is in Central Europe the winter season (Suselbeek 2014; Lichti et al. 2017). In this way, they contribute to plant dispersal when they do not use up their supply (Wróbel and Zwolak 2013; Suselbeek 2014; Lichti et al. 2017; Kempter et al. 2018). The dispersal of the seeds of invasive plants by rodents was proven for the red oak (*Quercus rubra* L.) and for the cutleaf coneflower (*Rudbeckia laciniata* L.) (Bieberich et al. 2016; Suzuki et al. 2016). The present study is the first to prove, that rodents – especially the bank vole and *Apodemus* sp. – eat cup plant seeds. In principle, these taxa also hoard (Vander Wall 2001; Suselbeek 2014; Bieberich et al. 2016; Kempter et al. 2018). But it is unclear whether they also hoarded cup plant seeds in the present study. Rodents are known to rather hoard seeds than eat them, when the seeds are less perishable and larger (Lichti et al. 2017). The seeds of cup plant survive the winter season (present study), which would qualify them for storage. Though, the seeds are relatively small compared to, for example, acorns or beech nuts, that are typically hoarded by rodents (Howe and Smallwood 1982; Jensen and Nielsen 1986; Wróbel and Zwolak 2013; Suselbeek 2014; Bieberich et al. 2016). In the present study, cup plant seeds were only removed, and rodents were only proven in the forest habitat. In the meadow or the cup plant field, no cup plant seeds were removed, and no rodent was seen. However, forests are less suitable habitats for the cup plant than open habitats (Ende and Lauerer 2022). Further studies are necessary to investigate whether rodents remove cup plant seeds also in open habitats and whether they displace and hoard them. When rodents displace seeds and nuts, they usually only disperse them over small distances of a few meters, rarely several tens of meters (Wróbel and Zwolak 2013; Kempter et al. 2018; Li et al. 2021). Endozoochorous seed dispersal by rodents after consumption can be neglected (Fischer and Türke 2016).

Occasionally, the great tit was also recorded in the boxes with cup plant seeds in the forest habitat in the present study. This species rarely stores food (Vander Wall 1990). Endozoochorous seed dispersal after consumption by birds is typical for fleshy fruits with persistent seeds inside (Howe and Smallwood 1982; Howe 1989). Therefore, we do not assume a dispersal of cup plant seeds by birds.

Water can be an effective long-distance dispersal vector for plant species and can facilitate the spread of exotic plants (Thébaud and Debussche 1991; Jacquemyn et al. 2010). Until now, it is unclear, whether cup plant seeds are dispersed by water. An important precondition for water dispersal is the maintenance of germination ability over a long duration in water. The present study is the first that experimentally investigated the germination rate of cup plant seeds after storage in water. The germination rate of cup plant seeds did not differ between standing and running water and was not reduced by storage in water for one, two, or four weeks. Thus, if the seeds are dispersed by water, they could travel large distances and establish new populations far away from their mother plants. Though, a high portion of seeds already germinated in the water. A precondition for successful settlement of those seeds that have already germinated in water is that the seedlings reach suitable habitats and quickly establish roots there. It was remarkable that the seedlings in water looked fresh and vital until the end of the experiment, although they had been completely submerged for two or three weeks. Nevertheless, we assume that the settlement is more successful if the seeds are not already germinated when they are washed ashore. During the first week in water, only a few seeds germinated. This duration could already be sufficient for the seeds to be spread over long distances via rivers and streams.

The present study was conducted in spring (April), when the seed dormancy is already broken in nature. Therefore, we have stratified the seeds before the experiment to simulate seed dormancy break, which explains why so many seeds germinated so quickly and already in the water. Our study practically simulated a spring flood. However, if the seeds get into water right after ripening in autumn before stratification, the proportion of seeds germinating already in water would probably be much lower. The seeds could thus travel considerably longer distances in the winter, until they are washed ashore on the riverbank and then germinate in spring.

In our study, the seeds sank within the first three days. Because of the previous stratification, the seeds were already saturated with water at the beginning of the experiment. The seeds reaching the water in a dry stage would probably float on the water surface for a longer period, hence dispersing over longer distance. Although floating on water is an advantage for water dispersal (Howe and Smallwood 1982), it is not a precondition to dispersal. Seeds could also be carried by water when they have sunk, especially in case of flooding. This is shown by the example of the invasive Himalayan balsam (*Impatiens glandulifera* Royle) (Lhotská and Kopecký 1966; Čuda et al. 2017). In a study with the invasive Bohemian knotweed (*Fallopia* × *bohemica* (Chrtek & Chrtková) J.P.Bailey), seed floatation correlated positively with the achene wing area (Lamberti-Raverot et al. 2017). Because the wings of cup plant fruits do not seem to promote wind dispersal (present study), maybe their function is improving flotation and water dispersal. To clarify this hypothesis, the study should be repeated with dry and not stratified cup plant seeds, and in autumn.

Dispersal by water would effectuate the cup plant to establish primarily in riverbanks. According to Ende et al. (2021), these habitats are particularly suitable for the cup plant, because the growth and reproductive potential was the highest under moist soil conditions. Spontaneous occurrences of the cup plant along rivers outside of its natural range are already documented in several European countries (Müller et al. 2021; Vladimirov 2021; Davydov 2022). Germination and successful establishment in riverbanks are therefore possible and increasingly to be expected in the future. Due to the high value for nature conservation of riparian fringes and floodplains (Finck et al. 2017), the possible dispersal of cup plant seeds by water courses and the associated colonisation of these habitats should be considered critically from an invasion biology perspective. Because of the high competitiveness of the cup plant – especially under moist conditions – a suppression of native species is conceivable there, and therefore a risk for biodiversity is possible (Ende et al. 2023). In some regions of Europe, dominance stocks of cup plant are already recorded (Brennenstuhl 2010; Zykova and Shaulo 2019; Vladimirov 2021; Shynder et al. 2022). Hence, cup plant should be cultivated far away from watercourses and moist ecosystems to prevent a dispersal by water and a colonisation of these ecosystems.

A persistent soil seed bank can enable species to re-establish new stands many years after seed formation. Whether and how long cup plant seeds retain their germination ability in the soil was unclear so far. In the present study, cup plant seeds were stored over four years in different soil depths to examine germination ability. All cup plant seeds stored on the soil surface or at 10 cm soil depth germinated in the first one or two years. However, at 30 cm depth, one third of the seeds retained their germination ability for four years. According to model calculations a retaining of a few seeds is to be expected for about ten years. Altogether, cup plant does not seem to be able to develop a long-term persistent seed bank, at least not in shallow soil depths. The seeds could get into deeper soil layers by ploughing or by rodents. Only in this case, cup plant seeds could develop new stands years later, if they reach the surface again. Although, a long-term persistent seed bank favours the invasiveness of an alien species (Gioria et al. 2012; Pyšek et al. 2015), there are also successful invasive species with only a transient or short-term persistent seed bank, e.g. the Himalayan balsam (Skálová et al. 2019) or the giant hogweed (*Heracleum mantegazzianum* Sommier & Levier) (Krinke et al. 2005).

Another long-distance dispersal vector for cup plant seeds could be agricultural machinery. However, no studies exist on this topic. The cup plant is usually harvested in September, when many seeds are ripe (Gansberger et al. 2015; Gansberger 2016; Hartmann and Lunenberg 2016). Both the trailer that transports the harvest and the harvester itself could lose seeds on their way away from the field. In Germany, spontaneously settled cup plants are documented at roadsides several hundred meters away from their fields, probably dispersed by agricultural machinery (Ende and Lauerer 2020 and further personal observations). Montagnani et al. (2022) identified machinery as dispersal vector for many invasive alien plant species (e.g. *Asclepias syriaca* L., *Heracleum mantegazzianum*, *Heracleum persicum* Fischer). To prevent a spreading of the possibly invasive cup plant, harvesters should be cleaned, and trailers should be covered well before leaving the field.

CONCLUSION

The present study is the first that investigated dispersal and persistence of the seeds of the possibly invasive cup plant. Cup plant seeds can be dispersed over short distances by wind and rodents. Longer distances could be covered by water and also by agricultural machines. These insights are valuable to assess further spreading of the cup plant and to contribute to the evaluation of its invasive potential. Further studies are needed to investigate dispersal by water, rodents, and agricultural machinery. Based on current knowledge, we assess the risk of cup plant spreading as low, especially if the preventive measures mentioned above are considered. However, it will increase with each additional cup plant field. A further expansion of the area cultivated with cup plants is to be expected, due to its ecological advantages over maize and its increasing area in recent years.

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SUPPLEMENTARY MATERIALS

Supplementary material 1
Dataset wind experiment.
https://doi.org/10.5091/plecevo.104640.suppl1

Supplementary material 2
Dataset rodent experiment.
https://doi.org/10.5091/plecevo.104640.suppl2

Supplementary material 3
Dataset water experiment.
https://doi.org/10.5091/plecevo.104640.suppl3

Supplementary material 4
Dataset soil seed bank experiment.
https://doi.org/10.5091/plecevo.104640.suppl4