Birgt der Hoffnungsträger unter den Bioenergiepflanzen ein invasives Potenzial?

Autökologie, Konkurrenzverhalten und Spontanvorkommen der Durchwachsenen Silphie (*Silphium perfoliatum*)

Dissertation

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Deckblattzeichnung: Paul Ende

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Dissertation

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Inhalt

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Zusammenfassung

Die Durchwachsene Silphie (*Silphium perfoliatum*) stammt aus dem Osten Nordamerikas und wird in Deutschland und anderen europäischen Ländern seit einigen Jahren als Bioenergiepflanze zur Gewinnung von Biogas genutzt. Inzwischen gilt sie wegen ihrer guten Erträge und ihrer ökologischen Vorteile gegenüber der primär genutzten Bioenergiepflanze Mais (*Zea mays*) als bewährte Alternative und wird auf 10.000 ha in Deutschland angebaut. Aufgrund ihrer Produktivität und ihres hohen Reproduktionspotenzials könnten sich Verwilderungen der gebietsfremden Silphie etablieren und ausbreiten, welche die heimische Biodiversität oder Ökosystemdienstleistungen gefährden könnten. Dieses mögliche invasive Potenzial wird in der vorliegenden Dissertation in vier Einzelstudien untersucht und bewertet.

Die derzeitige Spontanbesiedlung der Silphie wurde rund um elf Silphie-Felder in Nordbayern erfasst (Manuskript 1). Die Silphie hat sich im 15 m-Umkreis aller Felder und in verschiedenen Lebensräumen in insgesamt 224 Plots mit je 1 bis 60 Individuen spontan angesiedelt. Die Vorkommenswahrscheinlichkeit nahm mit sinkendem Abstand zum Feldrand und mit zunehmendem Alter der Silphie-Felder zu. Besonders günstig für ihre Ansiedlung waren Lebensräume ohne Strauch- oder Baumschicht mit einem Offenbodenanteil von 25%. Die Etablierung (Stängelbildung) wurde an wärmeren Standorten mit höherer Wuchshöhe der Krautschicht und mit zunehmendem Abstand zum Feldrand begünstigt.

In einem zweijährigen Wachstumsversuch wurden das Wachstum und das Reproduktionsvermögen der Silphie in Abhängigkeit von der Bodenfeuchte untersucht (Manuskript 2). Mit durchschnittlich 3 m Pflanzenhöhe und 1,5 kg Trockenbiomasse pro Pflanze das höchste Wachstum und mit etwa 350 Blütenköpfchen pro Pflanze das höchste Reproduktionsvermögen erzielte die Silphie unter feuchten Bodenbedingungen. Zum nassen und zum trockenen Bereich hin sanken diese Werte ab. Eine zukünftige Besiedlung von Lebensräumen mit feuchten Bodenverhältnissen ist demnach möglich, aber kritisch, da solche Lebensräume häufig von hohem naturschutzfachlichem Wert sind.

Die Konkurrenzstärke der Silphie gegenüber heimischen Arten wurde am Beispiel der Großen Brennnessel (*Urtica dioica*) in einem vierjährigen Feldversuch untersucht (Manuskript 3). Die Biomasse der Silphie wurde zwar stark von Konkurrenz durch die Brennnessel reduziert, dennoch konnte sie sich gut unter diesen heimischen Pflanzen etablieren. Die Silphie reduzierte ihrerseits das Höhenwachstum der Brennnessel im niederschlagsreichen Jahr um ein Viertel und schränkte die Projektionsfläche der Brennnessel mit dem Alter zunehmend ein. Die Fähigkeit der Silphie sich zwischen der als konkurrenzstark bekannten Brennnessel zu etablieren und deren Wachstum zu hemmen, führt zu der Annahme, dass sie das Potenzial hat, naturschutzfachlich wertvolle Arten, die häufig konkurrenzschwächer sind, unterdrücken oder sogar verdrängen zu können.

Für die Invasivität förderlich sind u. a. effektive Ausbreitungsvektoren und die Fähigkeit eine Samenbank aufzubauen. Diese Eigenschaften wurden in vier Einzelversuchen untersucht

(Manuskript 4). Wind transportierte die Silphie-Samen nur wenige Meter weit und spielt somit für die Fernausbreitung keine Rolle. Nagetiere (*Myodes glareolus* und *Apodemus* spec.) nehmen Silphie-Früchte an und könnten somit als Ausbreiter ihrer Samen fungieren. Da sie ihre Vorräte allerdings meist in nur wenigen Metern Entfernung zum Sammelort anlegen, ermöglichen auch sie mutmaßlich keine Fernausbreitung. Im Wasser lagernd konnten Silphie-Früchte ihre Keimfähigkeit über vier Wochen erhalten. Somit könnten die Samen über Fließgewässer große Distanzen zurücklegen. In 30 cm Bodentiefe lagernd erhielten ein Drittel der Samen ihre Keimfähigkeit über vier Jahre. Modellberechnungen zufolge erlischt sie zwischen dem achten und dem 15. Jahr. In 10 cm Bodentiefe und an der Bodenoberfläche keimten die Samen bereits in den ersten zwei Jahren vollständig aus. Somit ist die Silphie nur in tieferen Bodenschichten fähig eine Samenbank aufzubauen und Jahre später neue Spontanvorkommen zu bilden, wenn die Samen wieder in die Nähe der Bodenoberfläche gelangen.

Aus den Ergebnissen dieser Studien und einer umfangreichen Literaturrecherche wurde die Silphie nach der Methodik vom Bundesamt für Naturschutz als potenziell invasiv (Handlungsliste) eingestuft. Eine zukünftige Gefährdung der heimischen Biodiversität durch die Silphie ist damit nicht auszuschließen. Weitere Forschungen u. a. zum Konkurrenzverhalten gegenüber konkurrenzschwächeren Arten, zur Samenausbreitung im Wasser und über Erntemaschinen sowie zu geeigneten Bekämpfungsmaßnahmen in der freien Natur sind erforderlich. Zudem ist ein Monitoring im Umfeld bestehender Silphie-Felder, besonders an Gewässern und in naturschutzfachlich wertvollen Habitaten, zu empfehlen, um eine mögliche Ausbreitung der Silphie in diesen und in angrenzenden Lebensräumen rechtzeitig zu identifizieren und ggf. einzudämmen.

Summary

The cup plant (*Silphium perfoliatum*) is native to eastern North America and has been used for several years in Germany and other European countries as bioenergy crop to produce biogas. Because of its good yield and its ecological advantages compared to the primary used bioenergy crop maize (*Zea mays*), meanwhile it is considered a proven alternative. Currently it is cultivated on 10,000 ha in Germany. Due to its productivity and high reproductive potential, the non-native cup plant could become established and spread, which could endanger native biodiversity or ecosystem services. This possible invasive potential is investigated and evaluated in the present thesis in four studies.

The spontaneous colonization of the cup plant was recorded around eleven cup plant fields in northern Bavaria (Manuskript 1). The cup plant has settled spontaneously within a 15 m radius of all fields and in different habitats in a total of 224 plots of 1 to 60 individuals each. The probability of occurrence increased with decreasing distance to the field and with increasing age of the cup plant fields. Habitats without shrubs or trees with a portion of open ground of 25% were particularly favorable for cup plant settlement. The establishing (stem development) of cup plant was favored in warmer locations with a higher growth height of the herb layer and with increasing distance to the field.

In a two-year field experiment, the growth and reproductive potential of the cup plant depending on soil moisture were investigated (Manuskript 2). With an average plant height of 3 m and 1.5 kg dry biomass per plant, the cup plant achieved the highest growth and with around 350 flower heads per plant the highest reproductive potential under moist soil conditions. These values decreased towards the wet and towards the dry conditions. Future colonization of habitats with moist soil conditions is therefore possible, but critical, since such habitats are often of high nature conservation value.

The competitiveness of the cup plant compared to native species was investigated in a four-year field experiment using the common nettle (*Urtica dioica*) as model species (Manuskript 3). Although the biomass of the cup plant was greatly reduced by competition from the nettle, it was nevertheless able to establish among these native plants. The cup plant reduced the plant height of the nettle by a quarter in the year with high precipitation. Additionally, it increasingly restricted the projection area of the nettle with increasing age. The ability of the cup plant to establish among the competitive common nettle and to reduce its growth leads to the assumption that it has the potential to suppress valuable species that are often less competitive.

Effective dispersal vectors and the ability to establish a seed bank contribute to the invasiveness of a plant species. These traits were investigated in four individual experiments (Manuskript 4). Wind dispersed cup plant seeds only over a few meters and thus plays no role in long-distance dispersal. Rodents (*Myodes glareolus* and *Apodemus* spec.) accept cup plant fruits and thus could be dispersers of their seeds. However, since they usually hoard their food only a few meters away

from the place of collection, they presumably do not enable long-distance dispersal either. Stored in water, cup plant fruits were able to keep their germination ability for four weeks. Thus, the seeds could cover large distances via running water. Stored at a soil depth of 30 cm, one third of the seeds retained their ability to germinate for four years. According to model calculations, it expires between the eighth and 15th year. At a depth of 10 cm and on the soil surface, the seeds germinated completely in the first two years. Thus, the cup plant is only able to build up a seed bank in deeper soil layers to form new spontaneous occurrences years later when the seeds come close to the soil surface again.

Based on the results of these studies and an extensive literature search, the cup plant was classified as potentially invasive according to the methodology of the Federal Agency for Nature Conservation. Hence, a future threat to native biodiversity from the cup plant cannot be excluded. Further research on e. g. competitiveness behavior against less competitive species, seed dispersal in water and via harvesters, and appropriate control measures are required. In addition, monitoring in the vicinity of existing cup plant fields, especially near water bodies and in habitats that are valuable for nature conservation, is recommended. This is essential to identify and, if necessary, control a possible spread of the cup plant in these and adjacent habitats.

1 Einleitung

1.1 Aufbau der Dissertation

Die vorliegende Dissertation ist kumulativ und umfasst vier Einzelarbeiten, die in internationalen Online-Zeitschriften veröffentlicht sind. Die Studien wurden am Ökologisch-Botanischen Garten der Universität Bayreuth und in der umliegenden Region durchgeführt. Sie bieten eine gute Basis für eine Invasivitätsbewertung der Durchwachsenen Silphie (*Silphium perfoliatum* L.), welche in der vorliegenden Dissertation durchgeführt wird. Weiterhin werden Handlungsempfehlungen für den weiteren Umgang mit der gebietsfremden Silphie entwickelt. Da alle vier Manuskripte in Englischer Sprache geschrieben sind und damit deutschen Landwirt*innen und Naturschützer*innen möglicherweise weniger zugänglich sind, habe ich mich entschieden, die restlichen Teile der Dissertation in Deutsch zu verfassen. Darin enthalten sind auch deutsche Zusammenfassungen der vier Manuskripte. Letztendlich sind es nicht die Wissenschaftler*innen, die eine möglicherweise invasive Ausbreitung der Silphie verhindern können, sondern die Praktiker*innen.

1.2 Die Problematik gebietsfremder Arten

Die Globalisierung und die damit einhergehende Reise- und Transportaktivität des Menschen führt zu immer weiter vernetzten und verstärkten Korridoren, die die Ausbreitung von Arten außerhalb ihres ursprünglichen Verbreitungsgebietes ermöglichen (Bonnamour et al. 2021; Seebens et al. 2017; Hulme 2009). Ein kleiner Teil dieser Arten wird invasiv, indem sie sich in ihrem neuen Gebiet unkontrolliert ausbreiten und negative Auswirkungen auf die einheimische Natur, die Wirtschaft oder die menschliche Gesundheit haben (Nentwig 2010; Vitousek et al. 1996, für Begriffsdefinitionen s. Kasten 1). Invasive Arten sind weltweit verantwortlich für gravierende Ökosystemveränderungen und das Zurückdrängen oder sogar Aussterben von einheimischen Arten (Dueñas et al. 2021; Fei et al. 2014). Auch wenn vor allem Inseln mit ihren oft endemischen Arten von der Problematik der Neobiota besonders betroffen sind, richten invasive Arten auch in Mitteleuropa erhebliche ökologische, gesundheitliche und wirtschaftliche Schäden an (Dueñas et al. 2021; Russel et al. 2017; Nentwig 2010; Kowarik & Rabitsch 2010; Hulme 2007). So sind aktuell 41 gebietsfremde Gefäßpflanzenarten in der EU als invasiv gelistet **(**EU-Verordnung Nr. 1143/2014)**,** weitere 29 sind in Deutschland vom Bundesamt für Naturschutz als invasiv eingestuft worden (Nehring et al. 2013). Die meisten von ihnen wurden absichtlich als Zier- oder Nutzpflanzen nach Deutschland eingeführt, wie z. B. der Japanische Staudenknöterich (*Fallopia japonica*) (Nehring et al. 2013). Er wurde als Zier-, Futter- und Wildäsungspflanze genutzt, ist aber für die Verdrängung einheimischer Arten und für wasserwirtschaftliche Probleme verantwortlich (Nehring et al. 2013; Kowarik & Rabitsch 2010).

Trotz dieser möglichen Folgen gibt es in Deutschland kaum gesetzliche Bestimmungen zum Umgang mit gebietsfremden Arten, wenn noch keine negativen Auswirkungen von ihnen bekannt sind. Es gilt lediglich eine Genehmigungspflicht zum Ausbringen gebietsfremder Arten in die freie Natur, von der jedoch land- oder forstwirtschaftlich genutzte Pflanzenarten ausgenommen sind (§40 Abs. 1 BNatSchG). Das Bundesamt für Naturschutz gibt Empfehlungen zur Vorsorge und zur Früherkennung möglicher invasiver Arten (BfN 2023). Demnach sollten gebietsfremde Arten generell beobachtet und beforscht werden, um eine mögliche Invasivität zu erkennen, bevor die Arten weiter ausgebreitet werden (BfN 2023). Aufgrund fehlender gesetzlicher Verpflichtungen wird dies kaum durchgeführt. Die vorliegende Dissertation soll an dieser Stelle ansetzen: Für eine gebietsfremde, landwirtschaftlich genutzte Pflanzenart – die Durchwachsene Silphie (*Silphium perfoliatum*) – deren weitere starke Ausbreitung durch den Menschen abzusehen ist, soll Forschung zu einem möglichen Invasionspotenzial betrieben werden.

Kasten 1: Invasionsbiologische Begriffe

Einheimische/heimische Arten sind Arten, die das entsprechende Gebiet ohne menschliche Unterstützung besiedelt haben oder dort entstanden sind (Kowarik & Rabitsch 2010).

Endemische Arten sind Arten, die natürlicherweise ausschließlich in einem oft räumlich eng begrenzten Gebiet vorkommen (Trautner 2021).

Gebietsfremde/nichtheimische Arten sind Arten, die aus ihrem natürlichen Verbreitungsgebiet heraus direkt oder indirekt durch den Menschen in ein Gebiet gelangt sind (Art. 3 Nr. 1 EU-VO Nr. 1143/2014; Kowarik & Rabitsch 2010).

Invasive Arten sind gebietsfremde Arten, deren Einbringung oder Ausbreitung die Biodiversität und die damit verbundenen Ökosystemdienstleistungen gefährden oder nachteilig beeinflussen (Art. 3 Nr. 2 EU-VO Nr. 1143/2014). Oft verursachen sie auch ökonomische oder gesundheitliche Probleme (BfN 2023). Diese werden jedoch für die Bewertung der Invasivität nicht berücksichtigt (Nehring et al. 2015).

Neobiota (Neophyten) sind gebietsfremde (Pflanzen-)Arten die nach der Entdeckung Amerikas 1492 in ein Gebiet gelangt sind (BfN 2023; Nentwig 2010).

1.3 Biologie der Durchwachsenen Silphie

Die Durchwachsene Silphie oder Becherpflanze (*Silphium perfoliatum* L.) ist ein ausdauernder Hemikryptophyt aus der Familie der Korbblütengewächse (Asteraceae) (Müller et al. 2021, für Begriffsdefinitionen s. Kasten 2). Im ersten Wuchsjahr entwickelt sie nur eine Blattrosette (Abb. 1 D), ab dem zweiten Wuchsjahr dann mehrere Stängel, Blüten und Früchte (Abb. 1 A). Sie kann mehrere Jahrzehnte alt werden (Stanford 1990). Die Stängelblätter sind bis zu 30 cm lang, bis zu 20 cm breit und gegenständig so miteinander verwachsen, dass sie eine Art Becher bilden, in dem sich Wasser sammeln kann – deshalb der Name Becherpflanze (Abb. 1 B) (Stanford 1990; Hegi 1918). Charakteristisch und leicht unterscheidbar machen sie auch die vierkantigen Stängel (Abb. 1 B). Die Silphie wird 2-4 m hoch und bildet zahlreiche Blütenköpfchen, die einen Durchmesser von 5-8 cm haben und von Juli bis Oktober blühen (Abb. 1 A und E) (Müller et al. 2021; Mueller & Dauber 2016; Wrobel et al. 2013; Jabłoński & Kołtowski 2005; Stanford 1990; Hegi 1918). In der Mitte der Blütenköpfchen liegen die zwittrigen Röhrenblüten mit sterilen Narben (Stanford 1990). Außen herum sind weibliche, gelbe Zungenblüten angeordnet (Stanford 1990; Hegi 1918). Die Silphie wird durch Insekten selbst- oder fremdbestäubt (Gansberger et al. 2015). Pro Blütenköpfchen bilden sich 20-30 Früchte (Stanford 1990). Diese sind flache Achänen mit zwei kleinen Flügelchen am Rand und jeweils einem Samen (Abb. 1 C) (Kowalski & Wierciński 2004; Hegi 1918). Zur Ausbreitung der Früchte gibt es bisher keine Studien. Es werden Wind-, Tier- und Stoßausbreitung sowie Ausbreitung über landwirtschaftliche Maschinen vermutet (Müller et al. 2021; Stolzenburg & Monkos 2012; Kowalski & Wierciński 2004).

In ihrer Heimat, im östlichen und mittleren Nordamerika, wächst die Silphie vorwiegend in feuchten Prärien, aber auch an Flussufern, in Sümpfen und in lichten Auwäldern (Penskar & Crispin 2010; Stanford 1990). In Deutschland hat sie sich spontan in Staudenfluren an Flussufern sowie an frischen Ruderal- und Siedlungsflächen, an Ackerrainen sowie an Wegrändern angesiedelt (Müller et al. 2021; Schönfelder 2017; Siegel 2017; Siegel & Löbnitz 2014; Schönfelder 2012; Brandes 2003; Hardtke & Ihl 2000). Die Silphie toleriert Temperaturen von bis zu -30 °C und Überflutungen von 15 Tagen (Stanford 1990).

Kasten 2: Botanische Begriffe

Achänen sind einsamige Früchte, die aus unterständigen Fruchtknoten gebildet werden. Sie öffnen sich nicht bei Reife (Schließfrüchte). Die Fruchtwand (Perikarp) und die Samenschale (Testa) sind miteinander verwachsen (Gemeinholzer 2018; Heß 2005).

Hemikryptophyt (Oberflächenpflanzen) sind ausdauernde Pflanzen, deren Sprossachse in der ungünstigen Jahreszeit (Winter) abstirbt und deren Erneuerungsknospen sich durch Erde oder Pflanzenteile geschützt in Bodennähe befinden (Thomas 2018).

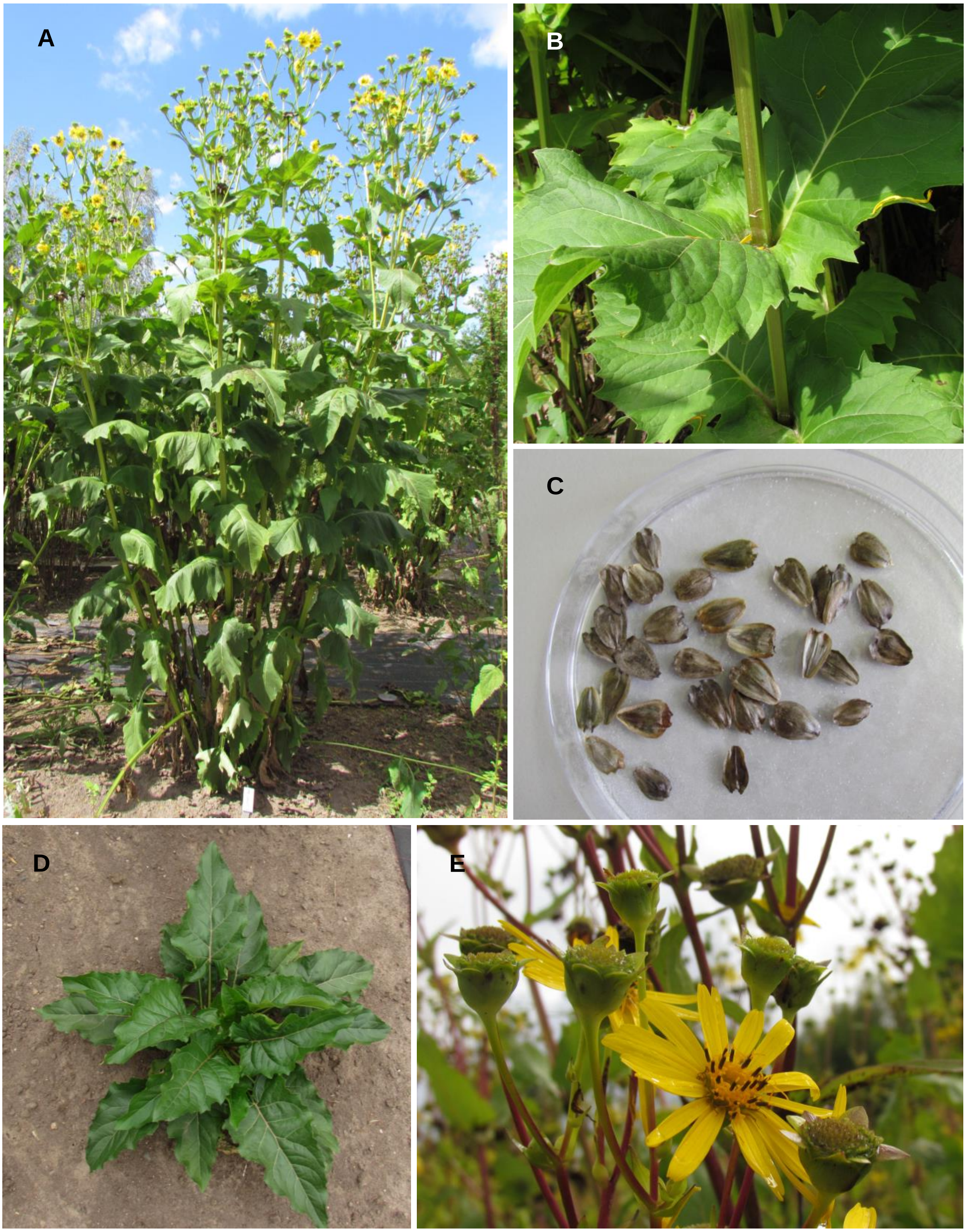

Abb. 1: Die Durchwachsene Silphie (*Silphium perfoliatum*). **A:** Gesamte Pflanze. **B:** Becherartig verwachsene Stängelblätter und vierkantiger Stängel. **C:** Flache Achänen (Früchte) mit zwei kleinen häutigen Flügeln. **D:** Blattrosette im ersten Wuchsjahr. **E:** Blütenköpfchen und Fruchtstände. Fotos: L. Marie Ende.

1.4 Verbreitung der Durchwachsenen Silphie

Die Durchwachsene Silphie (*Silphium perfoliatum*) stammt aus dem Osten Nordamerikas (Stanford 1990). Dort ist sie in den zentralen USA von den Bundesstaaten Texas bis North Dakota und dem kanadischen Ontario bis hin zur Ostküste nach Massachusetts und im Süden bis North Carolina heimisch (Hassler 2019). Außerhalb ihres natürlichen Verbreitungsgebietes kommt die Silphie spontan in ganz Mitteleuropa, tlw. auch in West-, Nord- Ost- und Südeuropa sowie vereinzelt in Asien vor (Abb. 2).

Nach Europa wurde die Silphie im 18. Jahrhundert als Zierpflanze eingeführt, wo sie 1762 erstmalig im Botanischen Garten von Montpellier (Frankreich) dokumentiert wurde (Stanford 1990). Im Jahr 1779 tauchte sie zum ersten Mal in einem deutschen Lehrbuch auf (Gesellschaft von Gelehrten 1779), weshalb davon ausgegangen werden kann, dass sie zu diesem Zeitpunkt auch schon in Deutschland kultiviert wurde. Der älteste Nachweis eines Spontanvorkommens der Silphie in Deutschland stammt aus dem Jahr 1880 aus Dresden (Wobst 1880). Diese große Zeitspanne zwischen Ersteinbringung und Erstnachweis einer Verwilderung ist nicht ungewöhnlich, da von vielen gebietsfremden Arten Latenzphasen (time lags) zwischen dem Zeitpunkt der Einbringung und dem ersten spontanen Auftreten in ihrem neuen Gebiet bekannt sind (Nehring et al. 2013; Kowarik et al. 1995).

In den 1980er Jahren wurde die Silphie in der DDR und anderen mitteleuropäischen Ländern als Frischfutterpflanze für Kaninchen angebaut, wodurch erstmals ein Anbau auf größeren Flächen stattfand (Frölich et al. 2016). Wahrscheinlich ist das auch der Grund dafür, dass im Jahr 2013 die spontanen Vorkommen der Art in Deutschland überwiegend in den neuen Bundesländern lagen und bis heute dort ihr Verbreitungsschwerpunkt ist (Griebl 2020; BfN 2013). Seit 2004 wird die Silphie als Bioenergiepflanze in Deutschland angebaut (Frölich et al. 2016). Die Anbaufläche steigt seither stark an: 2015 lag sie noch bei 400 ha, im Jahr 2020 schon bei 3.500 ha und verdreifachte sich dann in einem Jahr auf 10.000 ha in 2021 (FNR 2023). Inzwischen kommt sie in fast allen Bundesländern Deutschlands verwildert vor (Wörz et al. 2023; Müller et al. 2021; Griebl 2020). Hessen ist das einzige Bundesland ohne gesicherten Nachweis von Spontanvorkommen (Gregor 2023). Allerdings gibt es auch dort bereits Fundpunkte, von denen unbekannt ist, ob es sich um kultivierte oder spontane Vorkommen handelt (GBIF 2023).

Auch in anderen europäischen Ländern, wie Österreich, Polen und der Tschechischen Republik, sowie in Ostasien (China und Japan) und Südamerika (Chile) wird die Silphie seit einigen Jahren als Bioenergie- oder Futterpflanze kultiviert (Peni et al. 2020; Siwek et al. 2019; Ustak & Munoz 2018; Gansberger et al. 2015; Mayr et al. 2013; Pichard 2012; Pan et al. 2011).

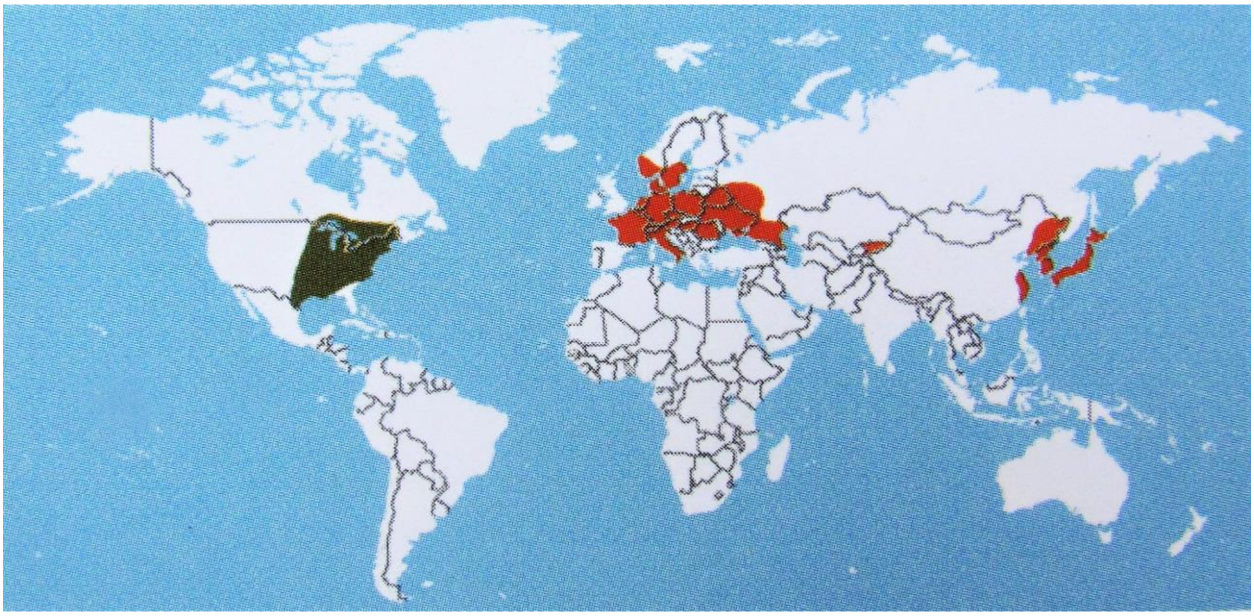

Abb. 2: Globale Verbreitung der Durchwachsenen Silphie (*Silphium perfoliatum*). Grün: Natürliches Verbreitungsgebiet; Rot: Wildvorkommen als Neophyt (Griebl 2020).

1.5 Die Durchwachsene Silphie als alternative Bioenergiepflanze

Die derzeit in Deutschland am meisten angebaute Bioenergiepflanze für die Erzeugung von Biogas ist Mais (*Zea mays* L.) mit 0,88 Mio ha Anbaufläche (FNR 2022). Auf weiteren 1,77 Mio. ha wird Mais als Futter- und Nahrungspflanze kultiviert (FNR 2022). Der Maisanbau verursacht erhebliche Umweltbelastungen durch hohen Pflanzenschutzmittel-, Dünger- und Maschineneinsatz (Grunwald et al. 2020; Boardman et al. 2009). Bodenerosion und -verdichtung sowie Eutrophierung der umliegenden Ökosysteme sind nur einige der umweltschädlichen Auswirkungen des Maisanbaus (Montemayor et al. 2019; Vogel et al. 2016; Szulc et al. 2015; Nevens & Reheul 2003). Deshalb ist das politische Ziel, den Getreidekorn- und Maisanteil in neu bezuschussten Biogasanlagen bis zum Jahr 2026 auf 30% zu reduzieren (§39i Abs. 1 EEG). Im Jahr 2023 liegt diese Grenze noch bei 40% (§39i Abs. 1 EEG). Aus diesem Grund werden alternative Bioenergiepflanzen getestet, die ausreichend hohe Erträge liefern und dabei im Anbau umweltfreundlicher als Mais sind.

Die Durchwachsene Silphie (*Silphium perfoliatum*) wurde in Deutschland seit 2004 zur Gewinnung von Biogas getestet (Frölich et al. 2016). Inzwischen gilt sie als bewährte, alternative Bioenergiepflanze und wurde im Jahr 2021 auf 10.000 ha angebaut (FNR 2023; Frölich et al. 2016). Zu Beginn der Nutzung der Silphie als Biogaspflanze wurde sie noch als Jungpflanzen im Feld ausgepflanzt, was sehr hohe Etablierungskosten verursachte (Biertümpfel et al. 2018; Conrad & Biertümpfel 2010). Inzwischen wird die Silphie meist direkt im Feld gesät (Cossel et al. 2020). Die Silphie wächst im ersten Jahr nur als Blattrosette, sodass keine Biomasse geerntet werden kann (Cossel et al. 2020; Conrad & Biertümpfel 2010). Um trotzdem schon im ersten Jahr auf diesen Feldern Erträge zu erzielen, wird die Silphie mitunter gemeinsam mit Mais gesät (Heimler et al.

2021; Frölich et al. 2016). Ab dem zweiten Jahr kann dann über mindestens 10 bis15 Jahre hinweg Silphie-Biomasse geerntet werden, ohne dass sich der Ertrag mindert (Frölich et al. 2016; Dauber et al. 2016; Gansberger et al. 2015). Seit einigen Jahren laufen Untersuchungen, die Silphie auch stofflich zur Papierherstellung oder zur Produktion von Dämmstoffen zu nutzen (Kyriakis et al. 2023; Höller et al. 2021; Frase et al. 2019; Höller et al. 2016).

Die Silphie gilt als trockentolerant, weil sie bis zu 2,40 m tief wurzeln und somit an tiefliegende Wasserressourcen gelangen kann (Schoo et al. 2017; Schoo et al. 2013). Zudem weist sie eine hohe Wassernutzungseffizienz auf, die in trockenen Jahren sogar die von Mais überschreiten kann (Franzaring et al. 2014; Pan et al. 2011). Der Trockenmasseertrag der Silphie liegt je nach Standort bei 11 bis 22 t/ha, was in etwa dem von Mais entspricht (Gansberger et al. 2015). Der Methanertrag ist neben dem Standort stark vom Erntezeitpunkt abhängig und liegt bei 70 bis 100% des Mais-Ertrags (FNR 2022; Gansberger et al. 2015). Diesen möglichen Einbußen stehen langfristig Kosteneinsparungen durch geringeren Maschinen-, Dünger- und Pflanzenschutzmitteleinsatz gegenüber (Gerstberger et al. 2016).

Hinzu kommen ökologische Vorteile des Silphie-Anbaus gegenüber dem Maisanbau: Die Bodenruhe durch jahrelange ausbleibende Bodenbearbeitung, die cellulosereichere Streu sowie der höhere Wurzelanteil an der Gesamtbiomasse der Pflanze können positiv auf den Humusaufbau, die Gefügestabilisierung und damit auf den Erosionsschutz sowie auf die Biomasse und Diversität der Bodenlebewesen wirken (Rummel et al. 2020; Grunwald et al. 2020; Schorpp et al. 2016; Emmerling 2016; Schorpp & Schrader 2016; Emmerling 2014). Die Silphie muss weniger gedüngt werden als Mais und kann schnell große Stickstoffmengen aufnehmen, was zu geringerer Stickstoffauswaschung und zu geringerem Restnitrat im Boden nach der Ernte führt (Stolzenburg et al. 2021; Grunwald et al. 2020; Frölich et al. 2016). Die Silphie ist kaum anfällig für Krankheiten und Schädlinge und gedeiht ab dem zweiten Jahr i. d. R. ohne Pestizideinsatz (Cossel et al. 2020; Frölich et al. 2016). Herbizide sind meist nur im ersten Wuchsjahr notwendig, danach ist die Silphie so konkurrenzstark, dass Ackerunkräuter von ihr unterdrückt werden (Cossel et al. 2020; Gansberger et al. 2015). Die Silphie bildet zahlreiche Blütenköpfchen, die von Juli bis Oktober blühen (Müller et al. 2021; Wrobel et al. 2013; Jabłoński & Kołtowski 2005). Damit bieten sie in einer Zeit, wo in Mitteleuropa das Blütenangebot gering ist, vielen blütenbesuchenden Insekten Nahrung durch Nektar und Pollen (Dauber et al. 2016; Mueller & Dauber 2016; Burmeister & Walter 2016; Schorpp et al. 2016). Untersuchungen haben gezeigt, dass außer den Blütenbesuchern auch die Abundanz und Diversität weiterer Arthropoden und Ackerwildkräuter durch den Silphie-Anbau gefördert werden können (Burmeister et al. 2023; Häfner et al. 2023; Heine et al. 2019; Glemnitz & Brauckmann 2016; Kelm 2013). Es gibt allerdings auch Argumente gegen den Silphie-Anbau: Wegen ihrer Anspruchslosigkeit könnte die Silphie vermehrt auch auf Grenzertragsstandorten angebaut werden, die bisher landwirtschaftlich wenig interessant waren. Dadurch, so die Befürchtung, könnten natur- und artenschutzfachlich wertvolle Habitate verloren gehen (Schmid-Egger & Witt 2014).

1.6 Wissensstand zur Invasivität der Durchwachsenen Silphie

Ein invasives Verhalten der Durchwachsenen Silphie (*Silphium perfoliatum*) im Sinne von Beeinträchtigungen der heimischen Biodiversität oder der menschlichen Gesundheit sowie der Verursachung von wirtschaftlichen Problemen ist bisher noch nicht nachgewiesen worden. Allerdings sind für Bioenergiepflanzen wünschenswerte Eigenschaften häufig auch solche, die ein invasives Potenzial fördern können (Raghu et al. 2006). Hierzu gehören u. a. langandauernde Bodenbedeckung, schnelles Wachstum im Frühjahr, das zur Unterdrückung konkurrierender Pflanzen führt sowie eine hohe Wassernutzungseffizienz, welche alle auch auf die Silphie zutreffen (Cossel et al. 2020; Gansberger et al. 2015; Franzaring et al. 2014; Pan et al. 2011; Raghu et al. 2006). Hinzu kommt ihr Potenzial eine hohe Anzahl an Samen zu entwickeln, welches ebenfalls eine Invasivität begünstigen kann (Mueller & Dauber 2016; Moravcová et al. 2010; Jabłoński & Kołtowski 2005; Kolar & Lodge 2001; Stanford 1990).

Inzwischen kommt die Silphie in ganz Europa, sowie in West- und Südostasien verwildert vor (Griebl 2020). Systematische Bewertungen ihres Invasionspotenzials existieren bisher aber nur für zwei Länder. Und auch diese stützen sich auf eine geringe Datenlage, da bisher keine invasionsbiologischen Untersuchungen an der Silphie durchgeführt wurden. In den Niederlanden wird ihr Invasionsrisiko als „mittel“ eingestuft und eine Besiedlung naturschutzfachlich wertvoller Habitate sowie ihr Einfluss auf heimische Arten und Ökosystemfunktionen als „wahrscheinlich“ bewertet (Matthews et al. 2015). In Österreich ist die Silphie unbeständig verwildert, wird jedoch nicht als invasiv bewertet (Essl & Rabitsch 2002).

Weitere Studien geben Einschätzungen zur Invasivität der Silphie, ohne sich dabei auf eine Bewertungsmethode oder auf wissenschaftliche Untersuchungen zu stützen: In Litauen wird das Invasionsrisiko der dort spontan vorkommenden Silphie als gering angesehen (Gudžinskas & Taura 2020). In der Ukraine kommt sie verwildert vor und wird als potenziell invasiv betrachtet (Shynder et al. 2022; Zavialova 2017). In Bulgarien bildet sie Dominanzbestände von bis zu 90% Deckung und gilt als eingebürgert, aber als nicht-invasiv (Vladimirov 2021). Auch in Russland ist sie lokal eingebürgert (Zykova & Shaulo 2019). Da sie an manchen Standorten undurchdringliche Monodominanzbestände bildet, wird sie als potenziell invasiv bewertet (Zykova & Shaulo 2019; Vinogradova et al. 2015). Bemerkenswert ist zudem, dass aus den USA Beobachtungen vorliegen, denen zufolge die Silphie in ihrem natürlichen Areal in der Lage ist, durch die Bildung von Dominanzbeständen koexistierende Arten zu verdrängen (Czarapata 2005).

In Deutschland kommt die Silphie fast in allen Bundesländern unbeständig vor und gilt lokal als eingebürgert (Wörz et al. 2023; Müller et al. 2021; Griebl 2020; BfN 2013; Hardtke & Ihl 2000). Es gibt etliche Florennachweise, die aber meist nur Informationen zum Fundort enthalten. Etwas ausführlicher dokumentierte Brennenstuhl (2010) über mehrere Jahre einen spontan etablierten Dominanzbestand der Silphie auf einer trockenen Ruderalfläche, der keine Begleitflora zuließ. Über Florennachweise hinaus gibt es bisher keine Studien, die die Standortbedingungen für die

Ansiedlung, die Etablierung oder die weitere Ausbreitung der Spontanvorkommen der Silphie sowie deren Einflüsse auf die einheimische Flora untersuchen. Auch bezüglich ihrer Diasporenausbreitung, der Keimfähigkeit ihrer Samen nach natürlicher Stratifikation sowie ihrer aktuellen Verbreitung ist bisher wenig bekannt. Aufgrund der geringen Datenlage wurde von Seiten des Bundesamts für Naturschutz auch noch keine Bewertung ihrer Invasivität durchgeführt, obwohl die Verantwortlichen dort bereits auf das mögliche invasive Potenzial dieser Art aufmerksam geworden sind (Nehring pers. Mitt.). Von manchen Autor*innen wird das Invasionsrisiko der Silphie in Deutschland – ohne zugrundeliegende Bewertungsmethodik – als gering eingeschätzt (Biertümpfel et al. 2018; Haag et al. 2015; Aigner et al. 2012). Andere weisen auf ein mögliches invasives Potenzial hin (Schümann 2013; Stolzenburg & Monkos 2012).

2 Synopsis

2.1 Zielsetzung der Dissertation

Ziel der vorliegenden Dissertation ist es, bisher fehlende Untersuchungen zu invasionsbiologisch relevanten Eigenschaften der Durchwachsenen Silphie (*Silphium perfoliatum*) durchzuführen, um zum Verständnis des Ausbreitungs- und Etablierungsprozesses, in dem sich die Silphie gerade befindet, beizutragen. Aus den gewonnenen Erkenntnissen soll erstmalig eine naturschutzfachliche Invasivitätsbewertung der Silphie für Deutschland sowie Handlungsempfehlungen für den weiteren Umgang mit ihr abgeleitet werden. Die Ziele der vier Manuskripte der Dissertation sind:

(1) die aktuelle Verbreitung der Silphie rund um Silphie-Felder zu erfassen sowie ihre Standortansprüche für die Ansiedlung und die Etablierung zu untersuchen;

(2) das Wachstum und das Reproduktionsvermögen der Silphie in Abhängigkeit von der Bodenfeuchte zu untersuchen;

(3) die Konkurrenzstärke der Silphie gegenüber heimischen Pflanzenarten am Beispiel der Großen Brennnessel (*Urtica dioica*) zu untersuchen;

(4) die Ausbreitung der Silphie-Früchte über die Vektoren Wind, Wasser und Nagetiere sowie den Erhalt der Keimfähigkeit nach Lagerung im Wasser und im Boden zu untersuchen

2.2 Ausführliche Zusammenfassung der Manuskripte

2.2.1 Manuskript 1: Spreading of the cup plant (*Silphium perfoliatum*) in northern Bavaria (Germany) from bioenergy crops

Essenziell für die Invasivität einer Pflanzenart ist deren Ansiedlung und Etablierung in Habitaten, wo sie nicht aktiv vom Menschen ausgesät oder gepflanzt wurde. Ziel dieser Studie war es deshalb, festzustellen, inwieweit sich die Silphie angrenzend an ihre Felder bereits spontan angesiedelt hat und welche Standortbedingungen auf die Ansiedlung und die Etablierung einen Einfluss haben. Dafür wurden die Umgebungen von elf Silphie-Feldern in Nordbayern untersucht. Um jedes dieser zwischen zwei und elf Jahre alten Silphie-Bestände wurde der 15 m-Umkreis nach spontan angesiedelten Silphie-Pflanzen abgesucht. Um gefundene Exemplare wurde in einem 1 m x 1 m-Plot 15 verschiedene Standortparameter erhoben. Zum Vergleich wurden die selben

Standortparameter bei zufällig gewählten Plots erhoben, an denen sich die Silphie nicht angesiedelt hat. Insgesamt wurden 325 nicht-besiedelte (uninvaded) und 224 besiedelte (invaded) Plots untersucht. Mit logistischen Regressionsmodellen wurden die Standortparameter herausgefiltert, die einen Einfluss auf die Ansiedlung bzw. Etablierung der Silphie hatten.

Die Silphie hat sich bereits außerhalb aller untersuchten Felder in insgesamt 224 Plots mit je 1 bis 60 Individuen spontan angesiedelt. Die Vorkommenswahrscheinlichkeit der Silphie sank deutlich mit zunehmendem Abstand zum Feldrand, in den ersten 3 m bereits um die Hälfte. Allerdings wurden bis zum Rand des untersuchten Feldumkreises von 15 m Abstand zum Feldrand immer noch vereinzelt Silphie-Pflanzen dokumentiert. Im Mittel hatten die Spontanvorkommen der Silphie einen Abstand von 2,1 m zum Feldrand. Mit zunehmendem Alter der Silphie-Felder wurden mehr Spontanvorkommen nachgewiesen. Da die Silphie eine ausdauernde Art ist, kann sie – einmal angesiedelt – über mehrere Jahrzehnte bestehen. Zusätzlich können mit jedem weiteren Bestandsjahr des Feldes weitere Spontanvorkommen hinzukommen, womit die Zahl der angesiedelten Silphie-Pflanzen um die Felder mit der Zeit zunimmt, wie diese Studie bestätigt.

Die Silphie besiedelte spontan sehr unterschiedliche Lebensräume (Abb. 3). Bevorzugt wurden offene Biotope und Siedlungsbiotope, weniger häufig besiedelt wurden gehölzdominierte Biotope. An Gewässern, die allerdings nur selten im Kartiergebiet vorkamen, konnten keine Spontanvorkommen nachgewiesen werden. Als besonders günstig für die Silphie-Ansiedlung hat sich ein Offenbodenanteil von etwa 25% erwiesen (Abb. 3 A). Auf Böden mit dichter Vegetation und/oder mit dichter Streuauflage ist die Ansiedlung offenbar erschwert (Abb. 3 C). Höhere Offenbodenanteile sind ebenfalls weniger geeignet, mutmaßlich da in diesen Fällen die Böden oft stark verdichtet (z. B. auf unbefestigten Wegen) oder durch Gehölze beschattet waren.

Spontan angesiedelte Silphie-Pflanzen, die bereits einen Stängel gebildet hatten, also mindestens im zweiten Wuchsjahr standen, wurden in dieser Studie als etabliert angesehen. Solche Pflanzen wurden im Umkreis aller elf untersuchten Felder und insgesamt in 59% aller besiedelten Plots gefunden (Abb. 3 B). Förderlich für die Etablierung waren wärmere Standorte mit höherer Wuchshöhe der Krautschicht und überraschenderweise mit größerer Entfernung zum Feldrand. Grund für die beiden letztgenannten Parameter könnte sein, dass die Silphie insbesondere auf selten oder nicht gemähten Flächen, wo die Krautschicht größere Wuchshöhen erreicht, Stängel entwickeln kann und solche Flächen mit zunehmendem Abstand zum Feldrand häufiger werden.

Die genannten Ergebnisse wurden mit denen von Kartierungen, die drei Jahre zuvor um die selben Silphie-Felder durchgeführt wurden (Ende & Lauerer 2020), verglichen. Die Anzahl etablierter Silphie-Pflanzen hat sich in dieser Zeit mehr als versechsfacht. 20 Individuen wurden über diese vier Jahre hinweg jährlich aufgesucht. Alle haben diese Zeitspanne überlebt, zudem ist ihre Stängelzahl signifikant gestiegen. In dieser kurzen Zeitspanne von vier Jahren wurde somit bereits ein steigendes Reproduktionspotenzial der spontan angesiedelten Silphie-Pflanzen nachgewiesen.

Abb. 3: Spontanvorkommen der Durchwachsene Silphie (*Silphium perfoliatum*). **A:** Jungpflanzen in einem Ackerrandstreifen mit 25% Offenbodenanteil in Hessenreuth. **B:** Etablierte Pflanze in einem mäßig artenreichen Saum bei Plech. **C:** Einzelne Jungpflanze in dichter Streuschicht in einem Ahornforst bei Unterkonnersreuth. **D:** Pflanze mit beginnender Stängelbildung in einem Bordstein in Speichersdorf. Fotos: L. Marie Ende.

2.2.2 Manuskript 2: Possibly Invasive New Bioenergy Crop *Silphium perfoliatum*: Growth and Reproduction Are Promoted in Moist Soil

Gewässerränder und andere Feuchtlebensräume waren in der in Manuskript 1 dargestellten Studie unterrepräsentiert. Die Silphie tritt in ihrer nordamerikanischen Heimat und auch in Mitteleuropa jedoch häufig spontan in Lebensräumen mit feuchten oder nassen Böden auf (Müller et al. 2021; Siegel 2017; Schönfelder 2017; Penskar & Crispin 2010; Stanford 1990). Ziel dieser Studie war es, das Wachstum und das Reproduktionsvermögen der Silphie – beides wichtige Eigenschaften für die Etablierungschancen einer Art und damit für die Fähigkeit invasiv zu werden – in Abhängigkeit von der Bodenfeuchte systematisch zu untersuchen. Dafür wurde ein zweijähriger Wachstumsversuch in sogenannten Hohenheimer Grundwasserbecken angelegt. In diesen Becken wachsen die Pflanzen auf gleichmäßig geneigten Böden in unterschiedlichem Abstand zum Grundwasserspiegel und dadurch entlang eines kontinuierlichen Bodenfeuchtegradienten (Abb. 4).

Mit durchschnittlich 3 m Pflanzenhöhe und 1,5 kg Trockenbiomasse pro Pflanze das höchste Wachstum und mit etwa 350 Blütenköpfchen pro Pflanze das höchste Reproduktionsvermögen erzielte die Silphie unter feuchten Bedingungen (50-60 cm Abstand zwischen Bodenoberfläche und Grundwasserspiegel). Zum nassen und zum trockenen Bereich hin sanken diese Werte ab und waren bei 100 cm Abstand zum Grundwasser nur noch ein Drittel bis halb so hoch. Die Anzahl der Stängel pro Pflanze und die Anzahl der Früchte pro Blütenköpfchen wurden nicht von der Bodenfeuchte beeinflusst.

Das höhere Wachstum und das höhere Reproduktionsvermögen unter feuchten Bodenverhältnissen führt zu der Vermutung, dass feuchte Lebensräume besonders gut für die weitere spontane Ansiedlung und Etablierung der Silphie geeignet sind. Diese Eigenschaft der Silphie ist kritisch zu bewerten, da feuchte Lebensräume häufig naturschutzfachlich wertvoll sind und viele von ihnen auf der Roten Liste der gefährdeten Biotoptypen stehen (Finck et al. 2017) bzw. nach §30 BNatSchG geschützt sind. Eine Besiedlung durch die Silphie könnte dort zu Ökosystemveränderungen und zu einer Verdrängung heimischer Arten führen. Trockene Lebensräume, die häufig ebenfalls einen hohen naturschutzfachlichen Wert haben, sind nach den Ergebnissen dieser Studie nicht gefährdet, von der Silphie besiedelt zu werden.

Abb. 4: Grundwasserbecken in der Seitenansicht im August des zweiten Wuchsjahrs der Durchwachsenen Silphie (*Silphium perfoliatum*). Von rechts nach links verkleinert sich der Abstand zum Grundwasserspiegel, wodurch der Boden feuchter wird. Foto: L. Marie Ende.

2.2.3 Manuskript 3: Competitiveness of the exotic *Silphium perfoliatum* against the native *Urtica dioica*: A field experiment

In dieser Studie wurde untersucht, wie konkurrenzstark die Silphie gegenüber potenziell koexistierenden einheimischen Arten ist. Dabei sollte einerseits abgeschätzt werden, inwieweit sich die Silphie in bestehender Vegetation etablieren kann; und andererseits wie stark sie heimische Arten im Wachstum hemmen oder sogar verdrängen kann, was in Manuskript 2 zuletzt als mögliche von der Silphie ausgehende Gefahr genannt wurde. Als Konkurrenz-Modellart wurde die weit verbreitete Große Brennnessel (*Urtica dioica*) ausgewählt, weil diese wie die Silphie mehrjährig und an Standorten, die auch für die Besiedlung durch die Silphie geeignet sind, konkurrenzstark ist (Hejda et al. 2021; Weber 2008; Grime 2001). Beide Arten wurden in einem Feldversuch unterschiedlichen Konkurrenzsituationen ausgesetzt. Dabei wurde jeweils eine Pflanze der Silphie bzw. der Brennnessel ohne Konkurrenz (Kontrolle) oder umgeben von acht Pflanzen der eigenen (intraspezifische Konkurrenz) bzw. der anderen Art (interspezifische Konkurrenz) gepflanzt. Über vier Jahre wurden bei beiden Arten verschiedene Wachstums- und Reproduktionsparameter erhoben.

Die Silphie konnte sich nach dem Auspflanzen inmitten von Brennnessel-Pflanzen gut etablieren, ihre oberirdische Biomasse wurde aber erheblich durch konkurrierende Brennnessel-Pflanzen reduziert (Abb. 5 A). Die Projektionsfläche (die maximale horizontale Ausdehnung der Pflanze) und die Wuchshöhe der Silphie sowie die Anzahl ihrer Blütenköpfchen wurden durch interspezifische Konkurrenz durch die Brennnessel ähnlich oder sogar weniger stark reduziert als durch intraspezifische Konkurrenz. Im niederschlagsreichen dritten Wuchsjahr wurde keine signifikante Reduktion der Projektionsfläche der Silphie durch Konkurrenz der Brennnessel nachgewiesen. Die Anzahl der Früchte pro Silphie-Blütenköpfchen war unabhängig von der Konkurrenzsituation.

Brennnessel-Pflanzen entwickelten sich auch bei Konkurrenz durch die Silphie insgesamt gut (Abb. 5 B). Ihre Wuchshöhe wurde nur wenig sowohl durch intra- als auch durch interspezifische Konkurrenz beeinflusst. Im niederschlagsreichen dritten Wuchsjahr wurde diese jedoch signifikant um ein Viertel im Vergleich zu den Kontrollpflanzen aufgrund von Konkurrenz durch die Silphie reduziert. Die Projektionsfläche der Brennnessel wurde über die Jahre gleichmäßig stark durch intraspezifische Konkurrenz reduziert. Interspezifische Konkurrenz durch die Silphie verminderte die Projektionsfläche der Brennnessel mit jedem Wuchsjahr stärker und erreichte im vierten Wuchsjahr 82% Reduktion im Vergleich zu den Kontrollpflanzen, was einer ähnlichen Reduktion wie durch intraspezifische Konkurrenz entsprach.

Die Ergebnisse zeigen, dass die Silphie offenbar in der Lage ist, sich in Beständen heimischer Pflanzen zu etablieren und in einem gewissen Ausmaß ihrerseits durch Konkurrenz das Wachstum heimischer Arten zu hemmen. Dabei handelte es sich in dem Experiment als heimische Art um die konkurrenzstarke Große Brennnessel. Anzunehmen ist, dass die Silphie in Beständen von Arten, die weniger konkurrenzstark als die Brennnessel sind, umso stärker das Wachstum koexistierender heimischer Arten hemmen kann. In sensiblen Lebensräumen mit naturschutzfachlich wertvollen Arten könnte die Silphie somit zum Problem werden.

Abb. 5: Durchwachsene Silphie (*Silphium perfoliatum*) und Große Brennnessel (*Urtica dioica*) in unterschiedlichen Konkurrenzsituationen im Juni des zweiten Wuchsjahres. **A:** Silphie umgeben von acht Brennnessel-Pflanzen. **B:** Brennnessel umgeben von acht Silphie-Pflanzen. Fotos: L. Marie Ende.

2.2.4 Manuskript 4: Dispersal and persistence of cup plant seeds (*Silphium perfoliatum*): do they contribute to potential invasiveness?

In den Manuskripten 1-3 wurden Ansiedlungs- und Etablierungschancen der Silphie in der freien Natur, besonders unter feuchten Bodenbedingungen, nachgewiesen. Eine weitere wichtige Eigenschaft für das invasive Potenzial einer Pflanzenart ist das Ausbreitungsvermögen ihrer Diasporen und deren Überdauerung im Boden als Voraussetzung für den Aufbau einer Samenbank. Es wurde deshalb in vier Einzelversuchen geprüft inwieweit die Vektoren Wind, Wasser und Nagetiere für die Samenausbreitung der Silphie in Frage kommen und wie lange die Keimfähigkeit der Samen im Boden erhalten bleiben kann.

Um die anemochoren Ausbreitungsdistanzen zu ermitteln, wurden Silphie-Früchte auf einem 2 m hohen Pfahl dem Wind bei unterschiedlichen Windgeschwindigkeiten ausgesetzt und die Entfernung der verwehten Früchte gemessen. Je höher die Windgeschwindigkeit war, desto mehr Früchte wurden ausgebreitet und desto größer war die Transportdistanz. Bei der höchsten im Versuch gemessenen Windgeschwindigkeit von 7 m/s, was einer mäßigen Brise entspricht (Häckel 2021), wurden die Früchte durchschnittlich 3,2 m weit verfrachtet. Wind spielt also offenbar für eine Fernausbreitung der Silphie keine Rolle.

Ein zweiter Versuch sollte die Frage klären, ob Nagetiere Silphie-Früchte sammeln und dadurch zur Ausbreitung beitragen. Die Früchte der Silphie wurden in einem Silphie-Feld und in dessen Umgebung in drei verschiedenen Biotoptypen (Silphie-Feld, Wald und Wiese) in Holzkisten angeboten, die durch Wildkameras überwacht wurden. Diese Kisten hatten eine Grundfläche von 30 cm x 30 cm und waren 13 cm hoch. Sie waren an zwei Seiten offen und oben geschlossen, sodass sie eine Art Tunnel ergaben, in dem die Nagetiere vor Räubern geschützt waren. Über drei Wochen hinweg wurde täglich die Zahl der entnommenen Früchte gezählt und 30 neue Früchte ausgelegt. Im Wald wurden jeden Tag 100% der Früchte entnommen. Es wurden die Rötelmaus (*Myodes glareolus*) und eine Art der Gattung Waldmäuse (*Apodemus*) in den Kisten im Wald nachgewiesen. Die Rötelmaus wurde zudem beim Fressen der Früchte dokumentiert. Rötelmäuse und Waldmäuse sind bekannt dafür, dass sie Vorräte aus gesammelten Früchten und Samen anlegen (Kempter et al. 2018; Vander Wall 2001). Somit können sie als potenzielle Ausbreiter für Silphie-Samen gelten. Allerdings ermöglichen auch sie keine Fernausbreitung, da sie ihre Vorräte meist nur in einer Entfernung von wenigen Metern zum Sammelort anlegen (Kempter et al. 2018; Wróbel & Zwolak 2013). In den Biotoptypen Wiese und Silphie-Feld wurden keine Silphie-Früchte von Nagetieren entnommen.

In einem dritten Versuch wurde getestet, ob die Samen der Silphie im Wasser lagernd keimfähig bleiben, als Voraussetzung dafür, dass sie im Wasser hydrochor ausgebreitet werden können. Dazu wurden die Früchte in Wassergläsern gelagert und nach ein, zwei und vier Wochen ausgesät. Die Samen blieben auch nach vier Wochen Lagerung im Wasser keimfähig. Dabei keimten zwar die meisten Samen bereits innerhalb der ersten zwei Wochen im Wasser, die Keimlinge blieben aber bis zum Versuchsende nach vier Wochen vital (Abb. 6 A). Relevant für die Beurteilung der hydrochoren Samenausbreitung ist die Beobachtung, dass die Früchte bereits in den ersten zwei Tagen auf den Boden sanken, was eine Wasserausbreitung in der Natur erschweren würde. Allerdings wurden die Früchte direkt vor Versuchsbeginn über zwei Wochen nass stratifiziert, was ihr frühes Absinken und die frühe Keimung erklären könnte. Möglicherweise bleiben Früchte, die im Herbst trocken ins Wasser gelangen, länger an der Wasseroberfläche und keimen später aus. Diese Studie erbrachte den Nachweis, dass die Samen der Silphie längere Zeit im Wasser keimfähig bleiben und somit eine Voraussetzung für eine hydrochore Ausbreitung über längere Distanzen in Fließgewässern erfüllt ist.

Ein viertes Experiment sollte klären, wie lange die Samen der Silphie im Boden lagernd ihre Keimfähigkeit behalten. Dazu wurden die Früchte in unterschiedlichen Bodentiefen eingelagert und eine mögliche Keimung im Boden bzw. der Erhalt der Keimfähigkeit nach ein, zwei, drei und vier Jahren durch Aussaat getestet. Samen, die an der Bodenoberfläche und in 10 cm Bodentiefe gelagert waren, keimten innerhalb der ersten zwei Jahre vollständig im Boden aus. Bei Lagerung in 30 cm Bodentiefe sank die Keimfähigkeit nach jedem Jahr, betrug aber im vierten Jahr immer noch 37%. Mit einem linearen Modell wurde berechnet, dass die Keimfähigkeit erst zwischen dem achten und dem 15. Jahr vollständig erlischt. In einer Bodentiefe von 30 cm ist die Silphie somit fähig eine Samenbank anzulegen. Dies ist eine Voraussetzung dafür, dass die Samen, wenn sie durch Bodenbearbeitung oder Nagetiere in tiefere Bodenschichten gelangen auch nach Jahren Spontanvorkommen bilden können, wenn sie wieder in die Nähe der Bodenoberfläche gelangen.

Als ein weiterer möglicher Ausbreitungsvektor für die Samen der Silphie werden in diesem Manuskript Erntemaschinen diskutiert. Es sind bereits Spontanvorkommen entlang von Transportwegen in mehreren hundert Metern Entfernung zum Silphie-Feld nachgewiesen worden, die mutmaßlich durch Ausbreitung der Samen durch Erntefahrzeuge entstanden sind (Ebner 2022; Ende & Lauerer 2020; weitere eigene Beobachtungen). Zudem wurde eine große Menge an Häckselgut inkl. Silphie-Früchten im Schneidwerk einer Erntemaschine nach der Silphie-Ernte beobachtet, die auf dem weiteren Weg der Maschine leicht verloren werden und somit zur Ausbreitung beitragen können (Abb. 6 B, eigene Beobachtungen).

Abb. 6: **A:** Keimlinge der Durchwachsenen Silphie (*Silphium perfoliatum*), die innerhalb der zweiten Woche im Wasser gekeimt sind und insgesamt seit vier Wochen im Wasser lagern. **B:** Erntemaschine nach der Silphie-Ernte mit großen Mengen Silphie-Früchten im Schneidwerk. Fotos: L. Marie Ende.

2.3 Naturschutzfachliche Invasivitätsbewertung für die Durchwachsene Silphie in Deutschland

Das Bundesamt für Naturschutz hat eine Methodik zur naturschutzfachlichen Invasivitätsbewertung für gebietsfremde Arten entwickelt, mit der bereits 80 Gefäßpflanzenarten, die in Deutschland wild vorkommen, bewertet wurden (Nehring et al. 2015; Nehring et al. 2013). Die Durchwachsene Silphie wurde bisher noch nicht bewertet, weil keine ausreichenden Daten vorlagen (Nehring pers. Mitt.). Die Ergebnisse der Manuskripte dieser Dissertation ermöglichen nun eine erstmalige Invasivitätsbewertung, die im Folgenden durchgeführt wird. Der Aufbau des Artensteckbriefs sowie die einzelnen Kriterien und deren Bewertungen richten sich nach der Methodik des Bundesamts für Naturschutz (Nehring et al. 2015, BfN-Skript 401). Die naturschutzfachliche Invasivitätsbewertung für die Silphie wurde von L. Marie Ende durchgeführt und von Stefan Nehring überprüft.

Naturschutzfachliche Invasivitätsbewertung

Silphium perfoliatum – Durchwachsene Silphie

Systematik und Nomenklatur:	***Silphium perfoliatum* L., 1759**
	Durchwachsene Silphie, Becherpflanze
	Synonyme: *Resinocaulon perfoliatum*, *Silphium conjunctum*, *Silphium erythrocaulon*, *Silphium hornemannii*, *Silphium petiolatum*, *Silphium quadrangulum*, *Silphium scabrum*, *Silphium tetragonum* (Hassler 2019)
	Spermatophyta, Asteraceae
Lebensraum:	Terrestrischer Lebensraum
Status:	Unbeständig

Gilt momentan noch als unbeständig, jedoch gibt es erste, sich etablierende Vorkommen (AG Flora von Bayern 2023; Ende & Lauerer 2022; BfN 2013; Hardtke & Ihl 2000).

Ursprüngliches Areal:	östliches Kanada, zentrale nördliche USA, nordöstliche USA, zentrale südliche USA, südöstliche USA (Hassler 2019)
Einführungsweise:	Absichtlich
Einfuhrvektoren:	Botanischer Garten, Gartenbau (Stanford 1990)
Ersteinbringung:	1762-1779

Frühester Nachweis in Europa: 1762 in Frankreich (Stanford 1990). 1779 erste Erwähnung in einem deutschen Lehrbuch (Gesellschaft von Gelehrten 1779). Die von Brennenstuhl (2010) genannte Ersteinbringung nach Deutschland im Jahr 1762 wurde nicht durch weitere Literatur bestätigt.

Erstnachweis:	1880

1880 in Pillnitz bei Dresden (Sachsen) nachgewiesen (Wobst 1880).

Einstufungsergebnis:

Potenziell invasive Art – Handlungsliste

Vergebene Wertstufe

A) Gefährdung der Biodiversität

Interspezifische Konkurrenz — Begründete Annahme

Im Feldversuch wurde eine hohe Konkurrenzstärke der Silphie nachgewiesen (Ende et al. 2023). Sie verdrängt heimische Arten durch Ausbildung monodominanter Bestände auf trockener Ruderalfläche in Deutschland (Brennenstuhl 2010) sowie in Schluchtwäldern in Russland in der Region Oblast Nowosibirsk (Zykova & Shaulo 2019). In Bulgarien bildet sie an Flussrändern Dominanzbeständen von bis zu 90% Deckung (Vladimirov 2021). In ihrer Heimat in den USA ist sie ebenfalls in der Lage durch Bildung von Dominanzbeständen heimische Arten zu verdrängen (Czarapata 2005). In kultivierten Beständen unterdrückt sie Ackerunkräuter ab dem zweiten Wuchsjahr selbstständig ohne Hilfe mechanischer oder chemischer Unkrautbekämpfung (Cossel et al. 2020). Eine Gefährdung heimischer Arten wird für Feuchtlebensräume angenommen (Ende et al. 2023; Ende et al. 2021).

Prädation und Herbivorie — nicht beurteilt

Hybridisierung — Nein

Zum gegenwärtigen Zeitpunkt ist keine Gefährdung heimischer Arten durch Hybridisierung bekannt. Eine Hybridisierung mit heimischen Arten ist nicht zu erwarten, da es keine heimischen Vertreter der Gattung *Silphium* gibt.

Krankheits- und Organismenübertragung — Nein

Die Silphie ist u. a. Wirt der weit verbreiteten Pilze *Sclerontia* spp., *Fusarium* spp., *Alternaria* spp. und *Botrytis* spp. (Gansberger et al. 2015; Aigner et al. 2012). Es wurde zudem eine neue Pilzart in Österreich an ihr entdeckt: *Ascochyta silphii* sp. nov. (Bedlan 2014). Sie verursacht Blattschäden in Form von braunen Flecken. Zum gegenwärtigen Zeitpunkt ist keine Gefährdung durch Übertragung von Pathogenen der Silphie auf heimische Arten bekannt.

Negative ökosystemare Auswirkungen — Unbekannt

Veränderungen der Vegetationsstruktur sind aufgrund ihres hohen und dichten Wuchses denkbar.

B) Zusatzkriterien

Aktuelle Verbreitung — Großräumig

In ganz Deutschland zerstreut, Verbreitungsschwerpunkt in Sachsen, Sachsen-Anhalt und Thüringen (Wörz et al. 2023; Müller et al. 2021; Griebl 2020). Vorkommen in angrenzenden Ländern (u. a. in Österreich, Schweiz, Polen) (Griebl 2020; Hassler 2019).

Maßnahmen — Vorhanden

Verhinderung absichtlicher Ausbringung (Landwirt*innen, Imker*innen), Mechanische Bekämpfung von Jungpflanzen (Ausstechen) und chemische Bekämpfung denkbar. Verhinderung der unabsichtlichen Ausbreitung durch Anpassung von Anbauvorschriften, z. B. Pufferzonen zu Gewässern und Schutzgebieten (Ende & Lauerer 2022; Ende et al. 2021; Ende et al. 2024), regelmäßige Entfernung in der Nähe von Schutzgebieten; systematisches Monitoring in der Nähe von gefährdeten Lebensräumen, Sonstiges (Öffentlichkeitsarbeit). Für den Silphie-Umbruch auf landwirtschaftlichen Flächen hat sich Fräsen mit anschließendem Herbizideinsatz als am wirkungsvollsten erwiesen, auch wenn damit keine vollständige Beseitigung bewirkt werden konnte (Parzefall et al. 2022).

C) Biologisch-ökologische Zusatzkriterien

Vorkommen in natürlichen, naturnahen und sonstigen naturschutzfachlich wertvollen Lebensräumen **Ja**

Nachweise an Gewässerrändern (Müller et al. 2021; Schönfelder 2017; Siegel 2017; Brandes 2003; Hardtke & Ihl 2000). Zudem höheres Wachstum und höheres Reproduktionsvermögen unter feuchten Bodenbedingungen nachgewiesen (Ende et al. 2021). Zukünftige Besiedlung von Sümpfen, Quellfluren und weiteren Gewässerufern somit denkbar.

Reproduktionspotenzial **Hoch**

Unter günstigen Bedingungen ist eine Produktion von mehr als 8000 Samen pro Pflanze möglich (Ende et al. 2023; Ende et al. 2021). Hohes Etablierungspotenzial durch klonales Wachstum (Stanford 1990).

Ausbreitungspotenzial **Hoch**

Die Silphie wird aktuell zunehmend als Bioenergiepflanze genutzt und ist im Handel außerdem als Zierpflanze verfügbar. Eine Fernausbreitung über Gewässer ist denkbar (Ende et al. 2024).

Aktueller Ausbreitungsverlauf **Expansiv**

Es ist eine starke Zunahme der Anbaufläche der Silphie in den letzten Jahren dokumentiert (FNR 2023). Die Anzahl der Fundpunkte der Silphie hat in Deutschland ebenfalls in den letzten Jahren stark zugenommen (GBIF 2023).

Monopolisierung von Ressourcen **Ja**

Das starke und schnelle Wachstum der Silphie ermöglichen die Bildung von Dominanzbeständen und somit eine Monopolisierung der Ressourcen Licht, Wasser, Nährstoffe und Raum (Ende et al. 2023; Brennenstuhl 2010). Die hohe Anzahl der Blütenköpfchen (Ende et al. 2021) ermöglicht zudem die Monopolisierung der Bestäubung.

Förderung durch Klimawandel **Ja**

Wegen ihrer tiefen Wurzeln gilt die Silphie als trocken- und hitzeresistent und sie kann gut unter voller Sonneneinstrahlung wachsen (Gansberger et al. 2015; Stanford 1990). Die Etablierung wird an wärmeren Standorten begünstigt (Ende & Lauerer 2022). Eine Förderung durch den Klimawandel wird angenommen.

D) Ergänzende Angaben

Negative ökonomische Auswirkungen **Unbekannt**

Als negative Auswirkungen auf die Landwirtschaft evtl. Auftreten bei Folge- oder Nachbarkulturen und deren Beeinträchtigung möglich.

Positive ökonomische Auswirkungen **Ja**

Landwirtschaft (Energiepflanze, Futterpflanze), Gartenbau (Zierpflanze), Sonstiges (Bienenweide)

Negative gesundheitliche Auswirkungen **Keine**

Wissenslücken und Forschungsbedarf **Ja**

Verbreitung in Deutschland, Diasporenausbreitung über Wasser, Auswirkungen in naturschutzfachlich wertvollen Lebensräumen

Anmerkungen: Bewertungsmethode nach Nehring et al. (2015)

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Bearbeitung und Prüfung

L. Marie Ende & Stefan Nehring
2024-02-14

2.4 Ausblick und Handlungsempfehlungen

Als ein wichtiges Ergebnis der vorliegenden Dissertation wird die Durchwachsene Silphie (*Silphium perfoliatum*) als potenziell invasive Art (Handlungsliste) eingestuft. Eine zukünftige Gefährdung der heimischen Biodiversität durch die Silphie ist damit nicht auszuschließen. Derzeit folgen daraus jedoch keine rechtlich bindenden Maßnahmen. Bis zum Jahr 2017 mussten potenziell invasive Arten noch beobachtet werden (§40 Abs. 2 BNatSchG i. d. F. v. 25.11.2016). Dieser Absatz ist in der aktuellen Fassung des BNatSchG nicht mehr vorhanden. Laut dem Bundesamt für Naturschutz sollten für Arten der Handlungsliste eine Überwachung ihrer Bestandsentwicklung und der von ihr ausgehenden Gefahr sowie vorbeugende Maßnahmen umgesetzt werden (Rabitsch & Nehring 2022). Dies ist auch nach meiner Meinung unbedingt erforderlich. Zudem gibt es neben dem Konkurrenzverhalten gegenüber konkurrenzschwächeren Arten, der Samenausbreitung im Wasser und über Erntemaschinen sowie geeigneten

Bekämpfungsmaßnahmen in der freien Natur noch viele weitere offene Fragen, die beforscht werden sollten. Ein Monitoring im Umfeld bestehender Silphie-Felder, besonders an Gewässern und in naturschutzfachlich wertvollen Habitaten, ist zu empfehlen, um eine mögliche Ausbreitung der Silphie in diesen und in angrenzenden Lebensräumen rechtzeitig zu identifizieren und ggf. einzudämmen.

Die derzeit in Deutschland angebauten Silphie-Felder sind größtenteils auf Saatgut ähnlicher Herkünfte zurückzuführen (Wever et al. 2021; Wever et al. 2019). Die genetische Variabilität dieser Art ist hier in Deutschland somit zwar verglichen mit anderen, züchterisch intensiv bearbeiteten Kulturpflanzen groß, verglichen mit den Populationen in ihrer Heimat jedoch sehr gering (Wever et al. 2021). Es gibt Bestrebungen eine größere Vielfalt an Herkünften für die Bioenergiegewinnung zu testen und daraus züchterisch Verbesserungen zu entwickeln (Wever et al. 2021; Blüthner et al. 2016; Biertümpfel & Conrad 2013). Damit würde allerdings auch die Wahrscheinlichkeit steigen, dass Genotypen mit stärkerem invasivem Potenzial nach Mitteleuropa eingeführt werden – gerade weil die für Bioenergiepflanzen gewünschten Eigenschaften häufig jene sind, die auch auf invasive Arten zutreffen (Raghu et al. 2006). Die Gefahr, dass durch die Selektion produktiver, konkurrenzstarker Saatgutherkünfte und die züchterische Optimierung das invasive Potenzial zukünftig bei uns angebauter Silphie gesteigert wird, ist groß. Deshalb ist aus invasionsbiologischer Sicht davon abzuraten, weitere Herkünfte nach Europa einzuführen.

Aufgrund der zunehmenden Beliebtheit und Bekanntheit der Silphie als Bioenergiepflanze und der vorgeschriebenen Reduktion des Maisanteils in Biogasanlagen (§39i Abs. 1 EEG) ist zudem mit einer weiteren starken Zunahme des Silphie-Anbaus und damit einhergehend auch mit einer Zunahme der spontanen Ansiedlungen zu rechnen. Mit jedem weiteren Silphie-Feld steigt allerdings die Wahrscheinlichkeit einer invasiven Ausbreitung der Art (Kowarik 2003). Umso wichtiger ist es, dass bei der Flächenauswahl für den Silphie-Anbau auf einen Abstand von mindestens 15 m zu Gewässern und naturschutzfachlich wertvollen Lebensräumen geachtet wird, um eine Fernausbreitung über Fließgewässer und eine Besiedlung dieser Lebensräume zu verhindern. Großes Augenmerk sollte auch auf die Vorbeugung der Ausbreitung über Erntemaschinen gelegt werden. Hänger mit Erntegut sollten nicht überladen und sorgfältig abgedeckt werden und Erntemaschinen vor dem Verlassen des Feldes abgefegt werden, um eine Fernausbreitung durch im Häckselgut enthaltene Samen zu verhindern. Aus invasionsbiologischer Sicht ist zudem eine möglichst frühe Biomasseernte zu empfehlen, um den Anteil ausgereifter und damit potenziell zur Ausbreitung beitragender Samen gering zu halten.

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4 Eigenanteil an den Manuskripten

Manuskript 1

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

Autoren: L. Marie Ende, Marianne Lauerer

Status: publiziert

Zeitschrift: NeoBiota 79: 87–105. https://doi.org/10.3897/neobiota.79.94283

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Eigenbeitrag: Konzept und Studiendesign: 90%, Datenerfassung: 100%, Datenanalysen: 100%, Manuskripterstellung: 100%, Manuskriptüberarbeitung: 80%, korrespondierende Autorin

Die Studie wurde von L.M.E. und M.L. konzipiert. L.M.E. führte die Datenerfassungen durch, analysierte die Daten, erstellte die Abbildungen und Tabellen und schrieb den ersten Entwurf des Manuskripts. Die Überarbeitung des Manuskripts wurde von L.M.E. und M.L. durchgeführt.

Manuskript 2

Titel: Possibly Invasive New Bioenergy Crop *Silphium perfoliatum*: Growth and Reproduction Are Promoted in Moist Soil

Autoren: L. Marie Ende, Katja Knöllinger, Moritz Keil, Angelika J. Fiedler, Marianne Lauerer

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Die Studie wurde von L.M.E. und M.L. mit Unterstützung von Andreas Schweiger konzipiert. K.K., M.K., A.J.F. and L.M.E. führten mit Unterstützung von Frederik Werner und Gudrun Hauschulz die Datenerfassungen durch. Der Grundwasserstand wurde durch eine Installation von Messtechnik durch Oliver Archner und Stefan Holzheu (beide Bayreuth Center of Ecology and Environmental Research BayCEER) automatisch erfasst. Laboranalysen des Bodens wurden von K.K. mit Unterstützung von Ursula Bundschuh durchgeführt. L.M.E. analysierte die Daten, erstellte die Abbildungen und Tabellen und schrieb den ersten Entwurf des Manuskripts. Die Überarbeitung des Manuskripts wurde von L.M.E., M.L., K.K., A.J.F. und Elisabeth Schaefer durchgeführt.

Manuskript 3

Titel: Competitiveness of the exotic *Silphium perfoliatum* against the native *Urtica dioica*: A field experiment

Autoren: L. Marie Ende, Sophie-Juliane Schwarzer, Alexandra Ebner, Marianne Lauerer

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Die Studie wurde von L.M.E. und M.L. konzipiert. L.M.E., S.-J.S. and A.E. führten mit Unterstützung von Jana Kaufmann, Angelika Fiedler, Katja Knöllinger, Gudrun Hauschulz und Hannah Bayha die Datenerfassungen durch. L.M.E. analysierte die Daten, erstellte die Abbildungen und Tabellen und schrieb den ersten Entwurf des Manuskripts. Die Überarbeitung des Manuskripts wurde von L.M.E., M.L., S.-J.S. und A.E. durchgeführt.

Manuskript 4

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

Autoren: L. Marie Ende, Lukas Hummel, Marianne Lauerer

Status: publiziert

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Die Studie wurde von L.M.E. und M.L. konzipiert. L.H. und L.M.E. führten mit Unterstützung von Carolin Lidola und Jana Kaufmann die Datenerfassungen durch. L.M.E. analysierte die Daten, erstellte die Abbildungen und Tabellen und schrieb den ersten Entwurf des Manuskripts. Die Überarbeitung des Manuskripts wurde von L.M.E., M.L. und L.H. durchgeführt.

5 Manuskripte

5.1 Manuskript 1

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

Autorinnen: L. Marie Ende, Marianne Lauerer

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Zusatzmaterial: Das Zusatzmaterial 1 und 2 des Manuskripts ist in der vorliegenden Arbeit angefügt. Das Zusatzmaterial 3 und 4 enthält die Daten, auf die sich die Auswertungen des Manuskripts beziehen und ist unter den folgenden Links online verfügbar:
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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

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 subgroups 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.

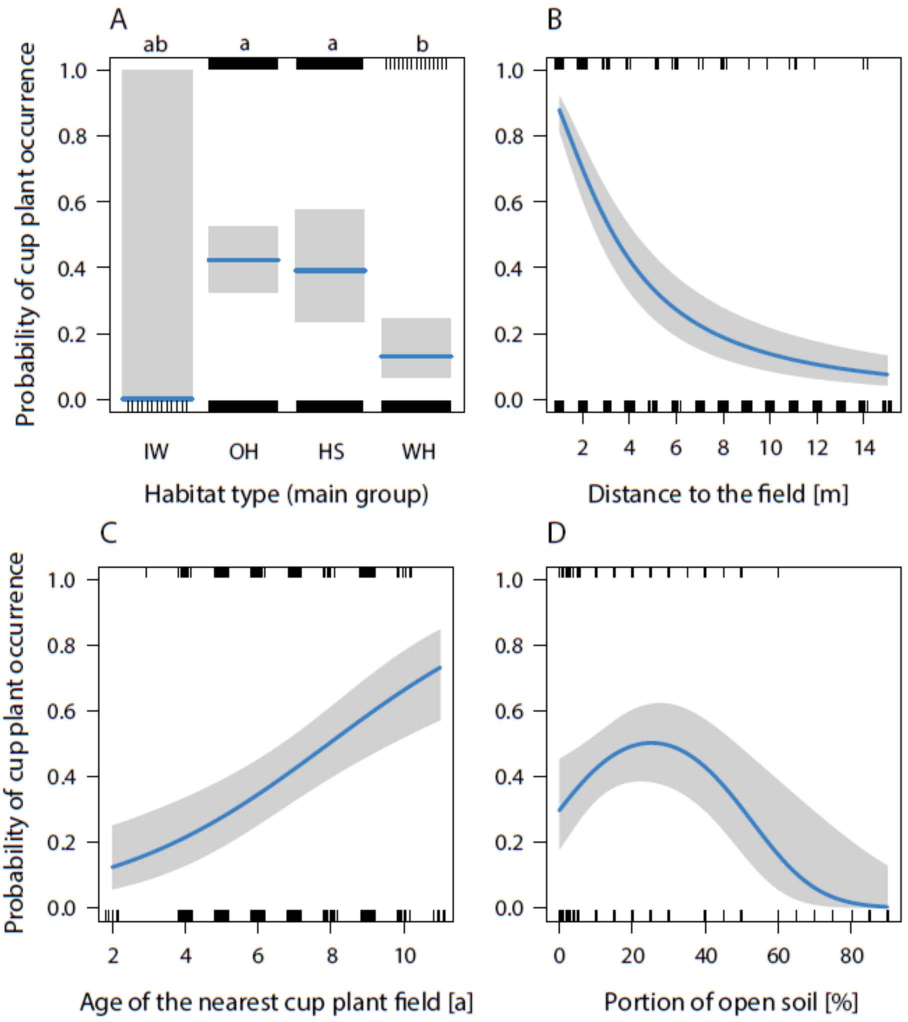

Figure 1. Probability of cup plant occurrence depending on the significant parameters of the final model (Table 2) **A** habitat type (main groups). Abbreviations: IW = Inland waters, including riparian areas, OH = Open habitats, HS = Human settlement areas, WH = Woody habitats (shrubs, trees and forests) **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**

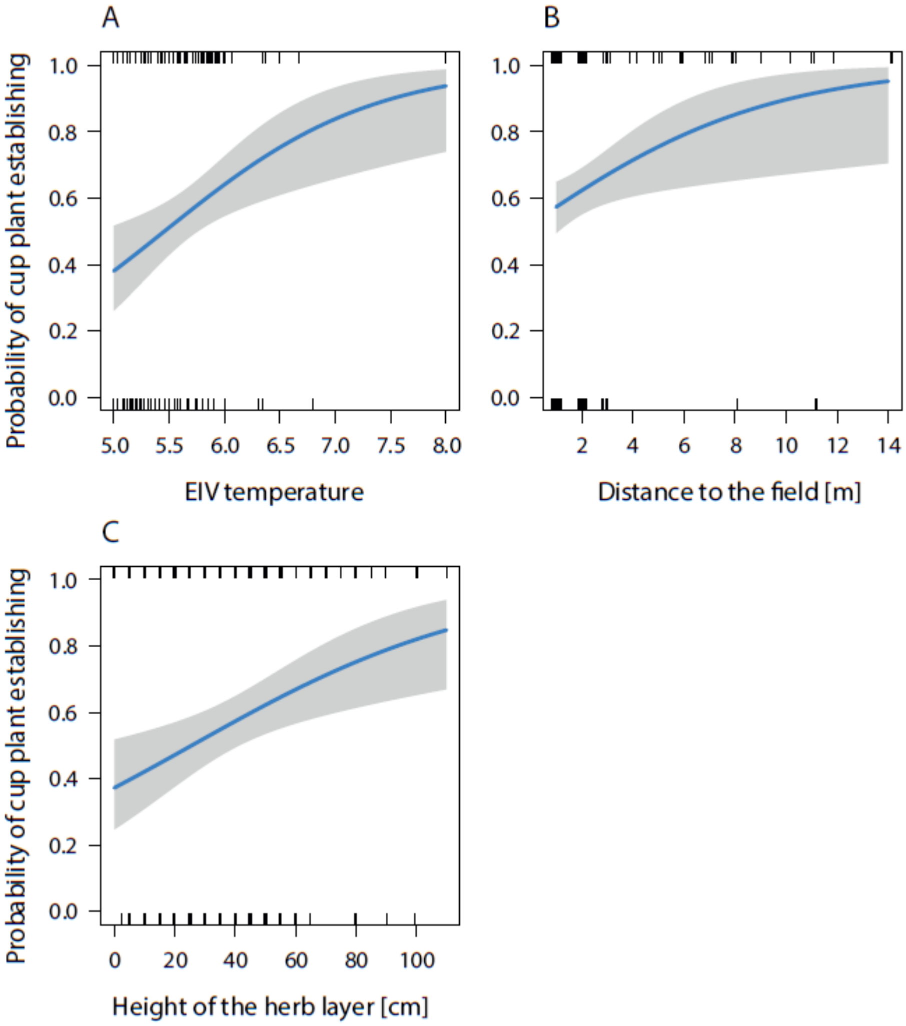

Figure 2. Probability of cup plant establishing depending on the significant parameters of the final model (Table 4) **A** EIV temperature. Abbreviation: EIV = Ellenberg indicator value **B** distance to the field **C** height of the herb layer. Parameters were fitted by the final model (Logistic regression, 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

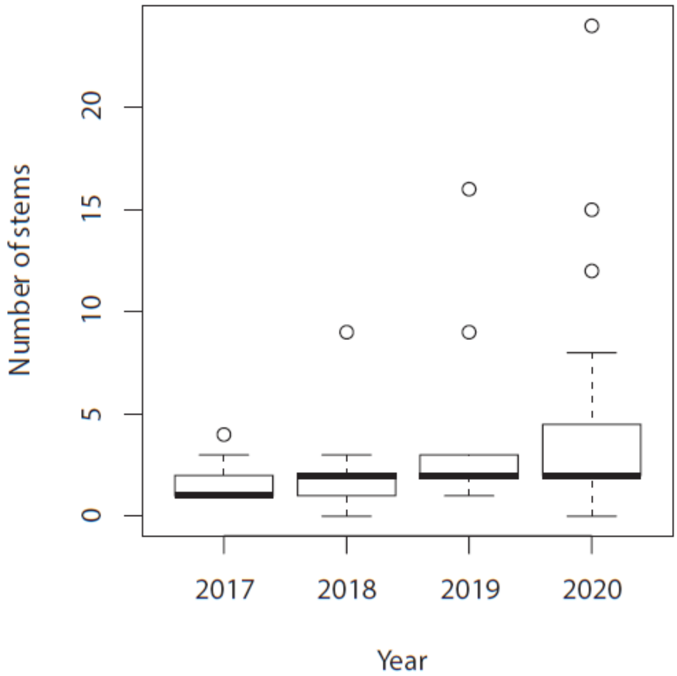

Figure 3. Number of stems of the establishing individuals monitored over the years. (n = 20, except in 2018 n = 19).

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)

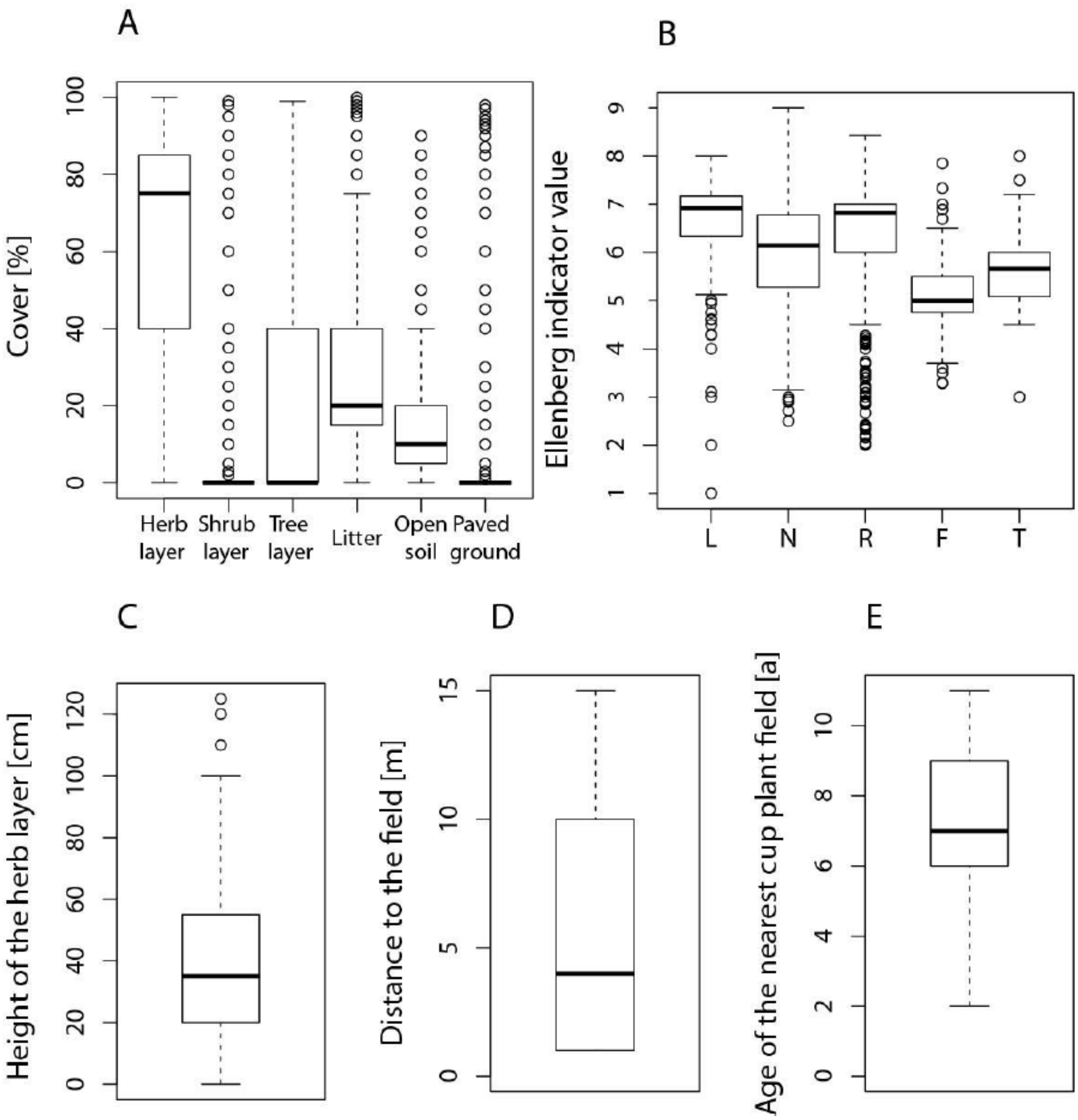
Link: https://doi.org/10.3897/neobiota.79.94283.suppl3

Supplementary material 4

Dataset establishing cup plants
Authors: L. Marie Ende, Marianne Lauerer
Data type: table (csv document)
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/neobiota.79.94283.suppl4

Supplementary material I. Characteristics of cup plant fields around which data were collected. Field names were given according to the nearest locality. Fields where more than one field age is given consist of diverse parcels of different years. Abbreviations: μ = mean per parameter, Σ = sum per parameter.

Field name	**GPS-coordinates (DMS)**	**Field age [a]**	**Field area [ha]**	**Investigated area within 15 m radius [ha]**	**Number of plots (invaded/ uninvaded)**
Geigenreuth	49.9301; 11.5302	8, 11	0.01	0.07	20 (12/8)
Bayreuth Wilhelminenaue	49.9467; 11.6049	5, 6	0.13	0.47	61 (16/45)
Bayreuth Tierheim	49.9271; 11.5564	2, 3, 5	0.52	0.07	15 (3/12)
Hessenreuth	49.8071; 11.9685	9	0.27	0.38	52 (21/31)
Unterkonnersreuth	49.9845; 11.5317	6	0.38	0.46	52 (10/42)
Speichersdorf	49.8745; 11.7836	5, 8, 9	0.43	0.13	32 (27/5)
Hollfeld	49.9448; 11.2872	7	0.46	0.20	43 (23/20)
Bayreuth Bezirkslehrgut	49.9290; 11.5531	8, 11	0.39	0.20	18 (1/17)
Ebermannstadt	49.7956; 11.1586	7	0.57	0.48	59 (19/40)
Plech	49.6587; 11.4819	6, 7	0.89	0.57	78 (30/48)
Gottersdorf	50.2087; 11.7672	4, 9	2.02	0.60	119 (62/57)
		μ =6.8	μ = 0.56	Σ = 3.63	Σ = 549 (224/325)



Supplementary material 2. Distribution of parameters in all plots independent whether invaded or uninvaded. **A** Cover of herb, shrub and tree layer, litter, open soil and paved ground ($n = 549$) **B** Ellenberg indicator values (EIV) for light availability (L, $n = 527$), soil nutrients (N, $n = 515$), soil reaction (R, $n = 477$), soil moisture (F, $n = 494$) and temperature (T, $n = 482$) **C** Height of herb layer ($n = 549$) **D** Distance between plot center and field margin ($n = 549$) **E** Age of the nearest cup plant field ($n = 549$). Shown is the median (line in the box) with the interquartile range (box), the values within 1.5 times interquartile range (whiskers) and the values outside this range (circles).

5.2 Manuskript 2

Possibly Invasive New Bioenergy Crop *Silphium perfoliatum*: Growth and Reproduction Are Promoted in Moist Soil

Autor*innen: L. Marie Ende, Katja Knöllinger, Moritz Keil, Angelika J. Fiedler, Marianne Lauerer

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Article

Possibly Invasive New Bioenergy Crop *Silphium perfoliatum*: Growth and Reproduction Are Promoted in Moist Soil

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Abstract: The cup plant (*Silphium perfoliatum*) is a new and promising bioenergy crop in Central Europe. Native to North America, its cultivation in Europe has increased in recent years. Cup plant is said to be highly productive, reproductive, and strongly competitive, which could encourage invasiveness. Spontaneous spread has already been documented. Knowledge about habitat requirements is low but necessary, in order to predict sites where it could spontaneously colonize. The present experimental study investigates the growth and reproductive potential of cup plant depending on soil moisture, given as water table distance (WTD). In moist soil conditions, the growth and reproductive potential of cup plant were the highest, with about 3 m plant height, 1.5 kg dry biomass, and about 350 capitula per plant in the second growing season. These parameters decreased significantly in wetter, and especially in drier conditions. The number of shoots per plant and number of fruits per capitulum were independent of WTD. In conclusion, valuable moist ecosystems could be at risk for becoming invaded by cup plant. Hence, fields for cultivating cup plant should be carefully chosen, and distances to such ecosystems should be held. Spontaneous colonization by cup plant must be strictly monitored in order to be able to combat this species where necessary.

Keywords: bioenergy crop; cup plant; groundwater; growth; invasive potential; reproductive potential; *Silphium perfoliatum*; soil moisture; water table distance

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1. Introduction

In Europe, biogas is being increasingly produced as a renewable energy source to replace fossil fuels [1]. Currently maize (*Zea mays* L.) is the most dominant biogas crop, though its cultivation goes along with great ecological damage from the high application of machines, fertilizer, and pesticides. Therefore, alternative bioenergy crops are being sought that are more ecologically agreeable [2–5].

One promising alternative crop in this context is the cup plant (*Silphium perfoliatum* L.) [2]. This perennial, yellow-flowering C3-plant belongs to the Asteraceae family. It develops stems and flowers from the second year onwards and persists many years [6]. Native in the prairies of eastern North America, cup plant was introduced to Europe in the 18th century as an ornamental plant [6]. Since 2004 it has been used as a bioenergy crop in Germany [2], and as of 2019 about 4500 ha have been cultivated there [7]. Many other European countries are cultivating this crop for bioenergy as well [3].

Cup plant has many ecological advantages over maize [2]: It can be harvested profitably for more than 15 years [8], and the application of machines and pesticides is much lower compared to maize, an annual plant [2]. In soil, higher portions of microbial biomass, higher microbial diversity, and higher biological activity comparative to maize have been proven [4]. Benefits for many pollinator species have also been detected: Insects are strongly attracted to the flowers of cup plant, which have a long flowering period relatively late in the year when most other floral resources have already finished blooming [9–11].

Furthermore, cup plant is easy to cultivate, highly productive with a high biogas yield, and it is competitive and very reproductive [2,6]. These traits make it an attractive bioenergy crop. However, in combination with the fact that harvest in agriculture usually takes place after flowering, they carry the risk of spontaneous spreading and settlement out from the fields. Spontaneous colonization was already documented in Upper Franconia (Germany) [12] and other parts of Germany as well as in other European countries (e.g., Austria, Switzerland, Poland) [13–16]. In the Netherlands and Russia, cup plant has already been graded as "potentially invasive" [17,18]. Studies on the invasive potential of this species are essential and should be of interest for all involved stakeholders before cup plant is cultivated on a large scale.

For this purpose, comprehensive knowledge about site requirements is necessary to allow predictions about where cup plant might establish itself. However, little is known about its site preferences in Europe, especially regarding soil moisture. It is assumed that cup plant prefers soils with good moisture provision but is also fairly drought tolerant [3,5,19,20]. So far, there are mainly empirical data or assumptions and only few experimental studies about the yield of cup plant in Central Europe depending on soil moisture. In its native range in North America, cup plant colonizes moist bottomlands and floodplains near streambeds [6]. Assuming that cup plant grows and reproduces in Central Europe in the same way that it does in its native range, it carries a special risk of invasion on moist sites. It is known that these are often ecosystems of high value for nature conservation in Central Europe. To assess the risk of these ecosystems becoming colonized by cup plant, we executed a growth experiment with cup plant over two years in tanks similar to those of Ellenberg's Hohenheimer groundwater table experiment [21–23] at the Ecological Botanical Gardens of the University of Bayreuth, Germany. The question was: How do growth and reproductive potential of cup plant differ depending on groundwater level? This study will not only provide insights into the demands and autecology of cup plant for the first time; the approach is also innovative because the findings are of great interest for nature conservation as well for agriculture.

2. Materials and Methods

2.1. Experimental Setup

The experiment was carried out from May 2018 to September 2019 in tanks similar to those of Ellenberg's Hohenheimer groundwater table experiment [21–23] at the Ecological Botanical Gardens of the University of Bayreuth (Germany, Bavaria). Temperature in the first growing season (May to August 2018) ranged from 1 °C to 35 °C (mean 18 °C) and precipitation sum was 151 mm, and in the second growing season (May to August 2019) between −3 °C and 37 °C (mean 17 °C) and 195 mm, respectively. Seeds of cup plant (Metzler & Brodmann Saaten GmbH, Ostrach, Germany, harvested 2016, pretreated) were sown on 5 March 2018. Seedlings were pricked out three weeks later and cultivated in a greenhouse. On 7 May 2018 the experiment started by planting the saplings into four tanks. For pricking and planting we chose vital plants of equal and mean size.

Each of the four tanks was a south-exposed, 6.4° inclined concrete tank (8 m × 4 m), with a constant soil depth of 90 cm (Figure 1). Substrate was a homogeneous mixture of 40% native soil, 40% compost and 20% quartz sand. In the lower part of each tank water was supplied via a garden hose and a perforated plastic pipe. Excess water could drain through a hole in the tank wall (Figures 1 and 2). The water table was held constant by hand in the first season and automatically by a float switch in the second growing season. Therefore, the plants in the tanks had different water table distances (WTD). In each tank, plants were arranged in nine rows indicating different WTD and in each row, there were nine plants. Distance between rows was 90 cm and between plants in a row 30 cm. For data collection we excluded all margin plants, resulting in seven rows of 28 plants each, divided across the four tanks. After the first growing season, we harvested in each row and in each tank the aboveground biomass of the second, the fourth and the sixth plant (seen from west), resulting in $n = 12$ per treatment (= row) (Figure 2). Afterwards, we removed the central part of the rootstock of these three and of the eighth plant. Consequently, in the second growing season five plants per row were left with distances of 60 cm between the plants. Excluding the margin plants, we had $n = 12$ per treatment (=row) again.

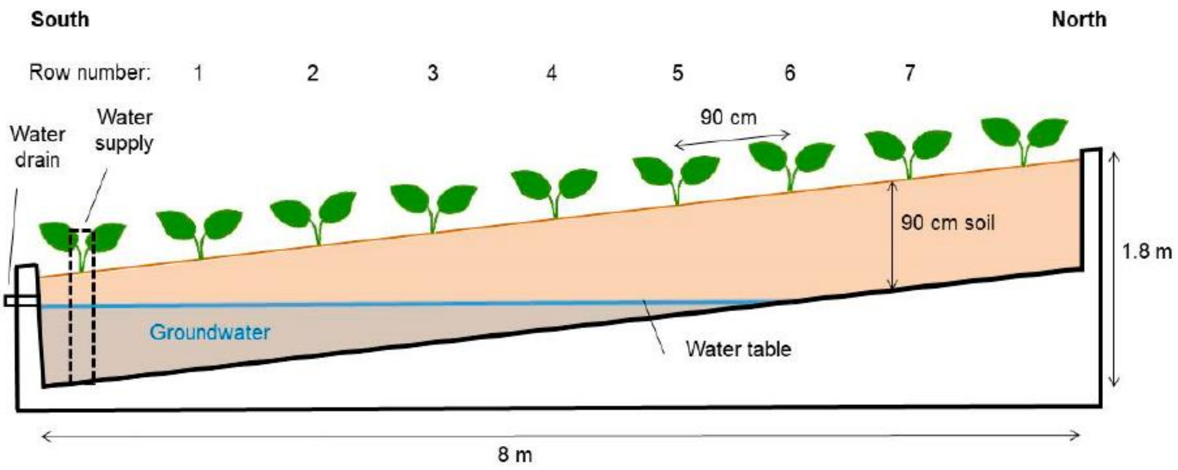

Figure 1. Scheme of a groundwater tank in longitudinal section.

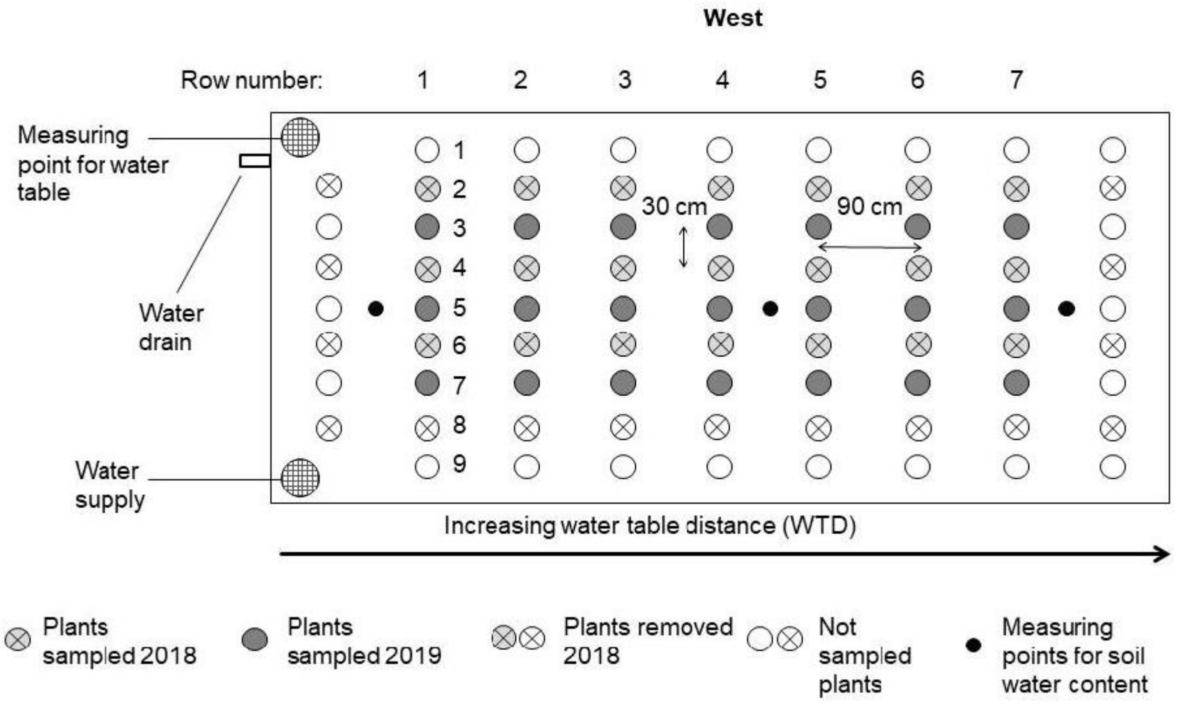

Figure 2. Top view of a groundwater tank indicating the plant arrangement, the harvesting scheme, and the measuring points for soil water content and water table.

2.2. Data Collection

In the first year, we harvested the living aboveground biomass on 9 August 2018, dried it in an oven at 70 °C until weight was constant, and measured the biomass with scales (PM 4600 Delta Range, Mettler-Toledo GmbH, Greifensee, Switzerland, same scales for all further weight measurement unless otherwise noted). Two samples of two different treatments had to be discarded because of plant material loss; consequently, the sample number for biomass of the first growing season was 82 instead of 84. In November 2018, the number of shoots higher than 15 cm of the individuals left in the tanks was counted.

In the second year, sampling and harvesting were carried out between 10 and 13 September 2019. We measured plant height by calculating the mean of the five highest shoots. The number of shoots higher than 50 cm was counted for each plant and was assigned to one of the three stages (1) dead, when more than 50% of biomass was brown, (2) vegetative, without capitula or with buds less than 1 cm in diameter, and (3) generative, with buds of at least 1 cm diameter or flowering or fruiting capitula, respectively. We harvested a representative subsample of the shoots, noting the shoot stages of the subsample, which included at a minimum one-third of the shoots from the original sample. Rosette leaves and shoots lower than 50 cm were harvested completely. The subsamples of the shoots higher than 50 cm were split in compartments of dead and living biomass whose fresh weights were measured. If necessary, again a subsample was taken and its fresh weight was measured before the biomass was dried in an oven at 90 °C until constant weight. Dry weight of biomass was measured and extrapolated to total biomass per plant. Before drying, capitula of the subsets were counted, assigned to the three phenological stages (1) budding, from a diameter of 1 cm on, (2) flowering, when ray florets were visible, and (3) fruiting, when ray florets were fallen off (comprising beginning of fruit development until fallen-off fruits) and extrapolated to the whole plant.

Additionally, we harvested three ripe capitula of the remaining shoots of each plant and dried them separately in paper bags at room temperature. We counted their number of fruits and weighed them with scales (AE 240, Mettler-Toledo GmbH, Greifensee, Switzerland).

Since 12 July 2018, water table was automatically recorded in a perforated pipe in the lower part of each of the four tanks (Figure 2) every 10 minutes by a pressure sensor (BayEOS HX711 Board, BayCEER, Bayreuth, Germany). For data analyses, we averaged water table for the time from the beginning of the water table measurement to particular data sampling for each tank. WTD was calculated using the mean water table, the inclination of the tanks (6.4°), and the distances to water table sensor for each row of each tank. Because soil depth was only 90 cm, plants with a calculated WTD larger than 90 cm had no vertical water access.

Soil water content was measured weekly in the second growing season (May to September 2019) with a TDR probe (TRIME®-FM3, IMKO Micromodultechnik GmbH, Ettlingen, Germany) in plastic pipes on three positions (Figure 2) and two depths (5–25 cm and 40–60 cm) in each tank. In November 2019, we took soil samples in 30 cm soil depth on two positions of each tank to assess the relationship between soil water content and soil water tension. We took an undisturbed soil sample with a core cutter of 100 cm^3 and a disturbed soil sample of about 200 cm^3. The undisturbed soil samples were saturated with water over five days and afterwards dried in an oven at 105 °C until constant weight. The disturbed soil samples were filled each in two sampling rings of 20 cm^3, placed in a pressure pot for 26 days at −15,000 hPa (pF = 4.2), and dried until constant weight. Before and between these steps, all soil samples were weighed each time (PB 3002 DeltaRange, Mettler-Toledo GmbH, Greifensee, Switzerland). After these steps, soil samples were weighed again (PG 503-S DeltaRange, Mettler-Toledo GmbH, Greifensee, Switzerland).

Meteorological data were obtained by a weather station in the Ecological Botanical Gardens 310 m away from the experimental site operated by the Micrometeorology group, Prof. Dr. Thomas, BayCEER, University of Bayreuth.

The data on which calculations in this study are based are available in the supplementary materials (Tables S1–S7).

2.3. Statistics

Data analysis and plot presentation were executed with R version 3.6.1 [24]. Calculating means of data by treatment, we used the function "ddply" from the R package "plyr" version 1.8.4 [25]. To read climate data and groundwater level data we used the R package "bayeos" version 1.4.6 [26]. We used linear models (LM) and checked the diagnostic plots. In case of non-normal distribution or heteroscedasticity of residuals we tried generalized linear models (GLM). If both LM and GLM were not possible, we executed Spearman's rank correlation analysis or the Kruskal–Wallis rank sum test (Kruskal test) with the post-hoc test multiple comparison test after Kruskal–Wallis (KruskalMC) of the R package "pgirmess" version 1.6.9 [27]. The four tanks were considered as four blocks in a block design. We checked the influence of block (tank) with an LM respectively a GLM. In case of non-significance we eliminated the block for the final model. In case of a significant effect of block we exerted a mixed effect model with block as random factor using the R package "lme4" version 1.1–21 [28]. Fits of mixed effect models were built using the mean of intercepts. Level of significance was always 0.05.

3. Results

3.1. Soil Water Conditions

The treatments of the experiment created by the rows in the tanks with increasing water table distance (WTD) described a wide range of soil water conditions (Table 1). Because soil depth was only 90 cm the two driest rows (6 and 7, Figure 1) had no direct vertical access to water table. Logically, soil water content decreased with increasing WTD, as well near soil surface as in deep soil layer. Water content of waterlogged soil was 50 ± 2% vol (mean ± standard deviation). Permanent wilting point (pF-value = 4.2) was reached at 9 ± 2%vol water content.

Table 1. Soil water conditions depending on the treatments. Row number in tank is counted from the bottom up (Figure 2). Water table distance (WTD) is given as mean ± standard deviation for both years separately. Soil depth was 90 cm. Soil water content was measured weekly only in the second growing season (year 2019) at three positions in the tanks (see Figure 2). Given values for each row were calculated by the models described in Figure 3.

Row Number in Tank	First Year (2018)	Second Year (2019)			Classification
	WTD (cm)	WTD (cm)	Soil Water Content (%vol) in Depths		
			5–25 cm	40–60 cm	
1	41 ± 7	40 ± 11	38	57	wet
2	51 ± 7	50 ± 11	31	48	very moist
3	61 ± 7	60 ± 11	26	40	slightly moist
4	71 ± 7	70 ± 11	22	33	fresh
5	81 ± 7	80 ± 11	18	28	slightly dry
6	91 ± 7	90 ± 11	15	23	medium dry
7	101 ± 7	101 ± 11	12	19	rather dry

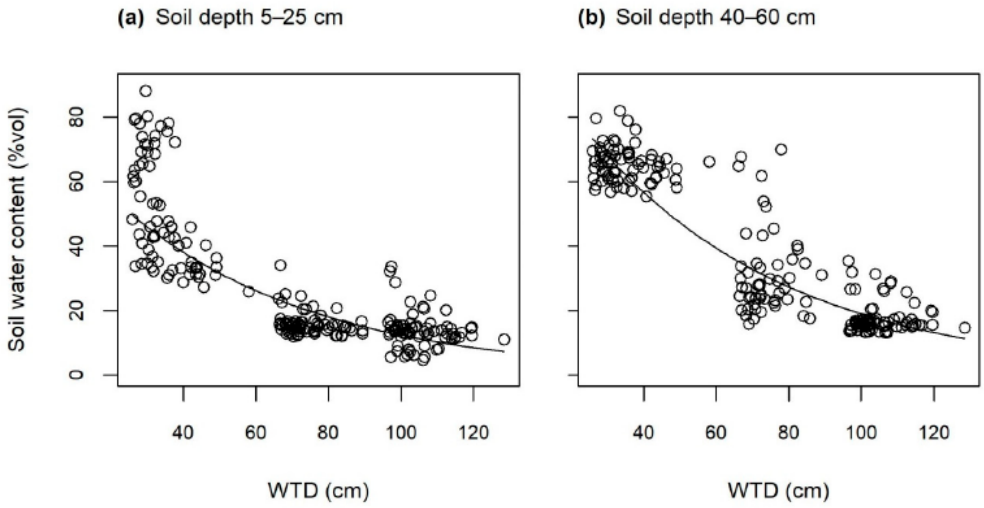

Figure 3. Soil water content in 5–25 cm (**a**) and 40–60 cm (**b**) soil depths depending on water table distance (WTD). Data were collected weekly in the second growing season from May to September 2019 at three positions in each tank (Figure 2). Lines are fitted by mixed effect LM: random effect = tank number (**a**): $\ln(y) = 4.39 - 0.02\,x$, $p < 0.001$, $n = 216$; (**b**): $\ln(y) = 4.77 - 0.02\,x$, $p < 0.001$, $n = 197$.

3.2. Growth and Aboveground Biomass

WTD had a significant effect on living aboveground biomass per plant in both years, although this effect was much smaller in the first than in the second year (Figure 4). Biomass was the highest at a WTD of around 50 to 60 cm (very to slightly moist soil) and achieved 167 ± 49 g in the first and 1491 ± 410 g in the second year (means ± standard deviation, dry weight). The latter was more than three times as high as in the driest treatment where only 458 g (mean, dry weight) living aboveground biomass per plant was measured. Living aboveground biomass was significantly determined by plant height (Spearman's rho = 0.75, $p < 0.001$) and not by number of shoots (Spearman's rho = 0.14, $p = 0.209$), considering the second year. Therefore, plant height was similarly affected by WTD as the living aboveground biomass and was between 135 and 335 cm (Figure 5). Plant height also reached its maximum at a WTD of around 50 to 60 cm (very to slightly moist soil) with 299 ± 18 cm in mean. Under wetter and drier soil conditions, plant height decreased.

Usually cup plant does not develop shoots before the second year [6]. However, in our experiment some individuals (34 of 84) had already developed one or more shoots (mean 1.6 ± 1.0) in the first growing season. This mainly occurred under moist soil conditions. Indeed, there was a significant correlation between number of shoot-developing individuals and row number of tank (Spearman's rho = −0.92, $p = 0.003$). In the second growing season, each individual independent of WTD developed from 8 to 32 shoots per plant (mean 18 ± 5). There was no significant effect of WTD on shoot number per plant (LM, $p = 0.714$).

All plants of all treatments grew and survived the two years of investigation in the experiment. However, at the end of the second growing season, a high portion of dead biomass in the three dry treatments was evident. There was in mean 23% and up to 73% (maximum) dead biomass in contrast to 6% (mean) in the wet, moist, and fresh treatments (Figure 6). There was a significant effect of WTD on the percentage of dead biomass.

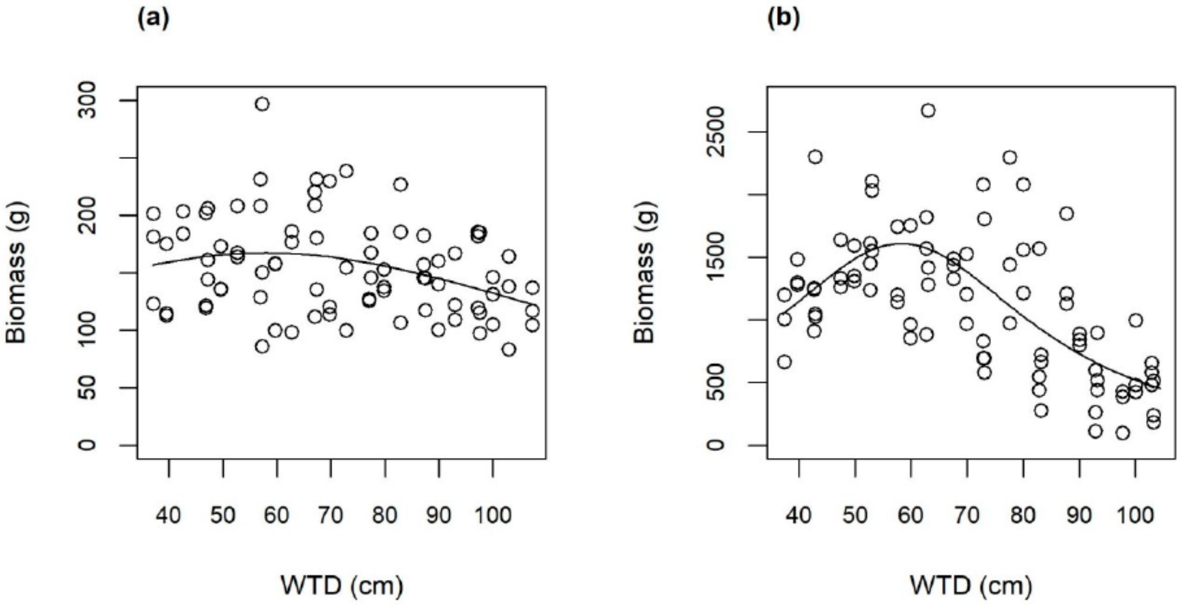

Figure 4. Living aboveground biomass (dry mass) per plant of cup plant, harvested (**a**): at the end of the first growing season (August 2018) and (**b**): at the end of the second growing season (September 2019) depending on water table distance (WTD). GLM: Gamma-distributed residuals, square function, (**a**): $p = 0.007$, $n = 82$; (**b**): $p < 0.001$, $n = 84$.

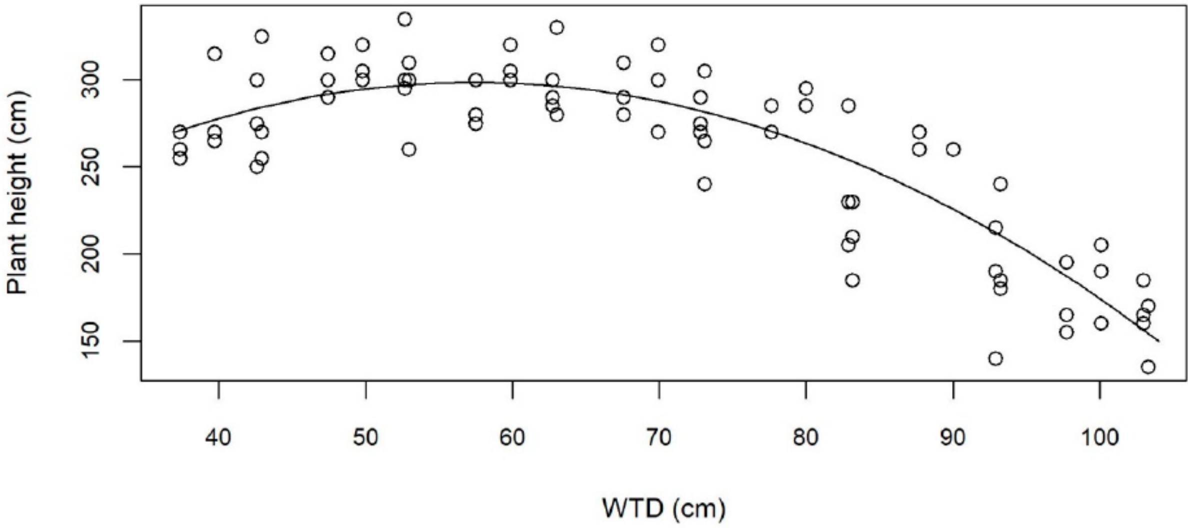

Figure 5. Plant height of cup plant at the end of the second growing season (September 2019) depending on water table distance (WTD). Mixed effect LM: random effect = tank number, square function, $n = 84$.

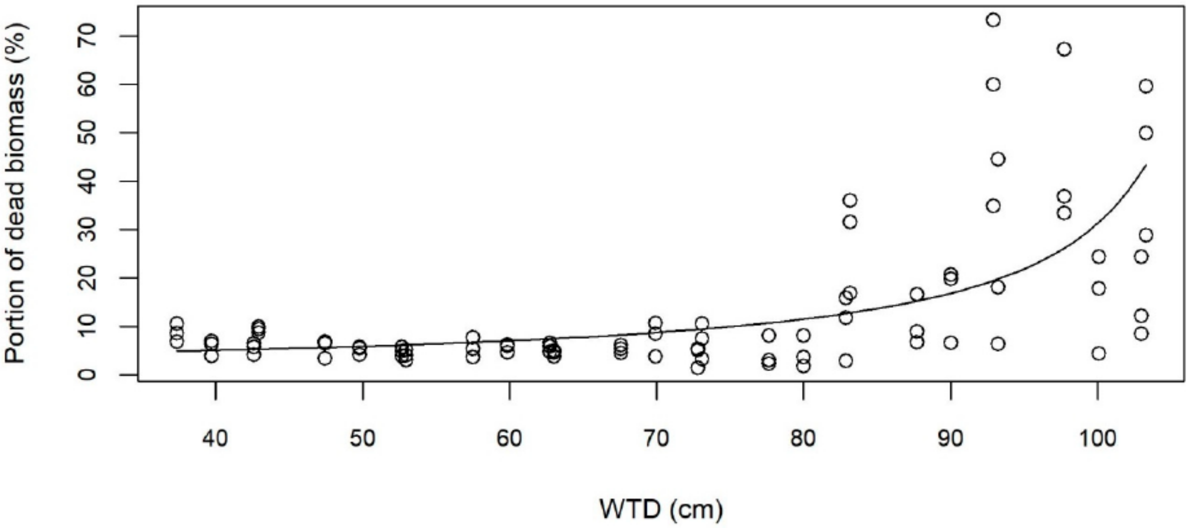

Figure 6. Portion of dead biomass of cup plant at the end of the second growing season (September 2019) depending on water table distance (WTD). GLM: Gamma- distributed residuals, $p < 0.001$, $n = 84$.

3.3. Reproductive Potential

There was a significant effect of WTD on the number of capitula at the end of the second growing season (Figure 7). The plants grown in very moist soil conditions (WTD around 50 cm) had the most capitula (mean ± standard deviation was 349 ± 156), whereas in wet soil conditions they developed slightly less (322 ± 143) and in rather dry soil conditions only a fifth (66 ± 115). In maximum one single plant developed 841 capitula (Figure 7). The number of fruits per capitulum was not affected by WTD (LM, $p = 0.734$) and was in mean 27 ± 4. The thousand grain weight was also not affected by WTD (mixed effect LM, $p = 0.115$) and was in mean 18.1 ± 3.9 g. Summing up, the plants grown in very moist to fresh soil conditions had a higher reproductive potential than those in dry or wet soil conditions because of a higher number of capitula. The number of capitula was significantly correlated with plant height (Spearman's rho = 0.64, $p < 0.001$) and not with number of shoots (Spearman's rho = −0.02, $p = 0.849$).

In September 2019, more than 90% of capitula of the plants grown in wet to fresh soil conditions had completed their flowering period and were already developing fruits (Figure 8). There was no significant difference between these four treatments regarding developmental stages of capitula (KruskalMC, $p > 0.05$). With increasing WTD the development slowed down. The drier the soil, the lower was the portion of fruiting capitula at the time of harvest and the higher was the portion of budding and flowering capitula. Regarding all treatments, there were significant correlations between row in tank and the portion of the three developmental stages of capitula (Spearman's rho for budding = 0.40, flowering = 0.68, fruiting = −0.76, p always < 0.001). Thus, plants on drier soil conditions not only produced less capitula (Figure 7) but took also longer to develop them.

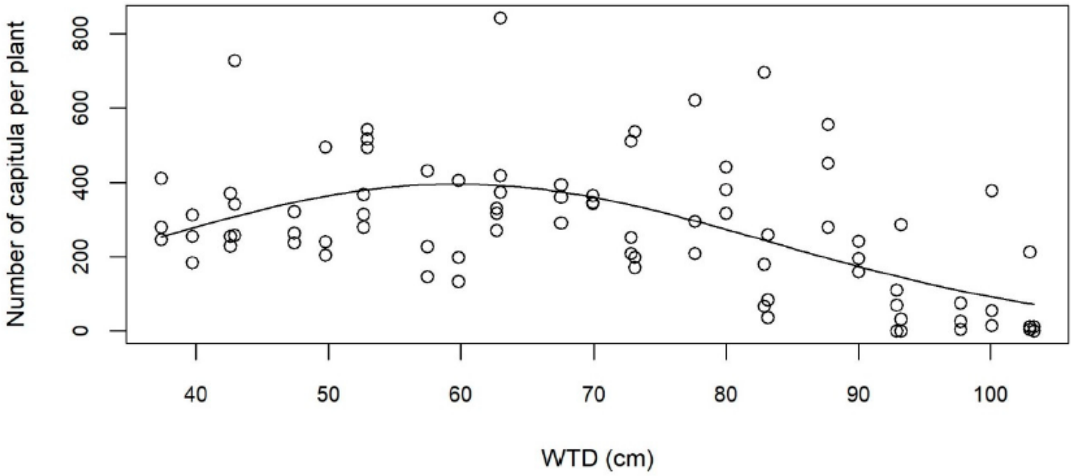

Figure 7. Number of capitula per plant of cup plant, regardless of their developmental stage, depending on water table distance (WTD). Data were collected at the end of the second growing season (September 2019). GLM: Poisson-distributed residuals, square function, $p < 0.001$, $n = 84$.

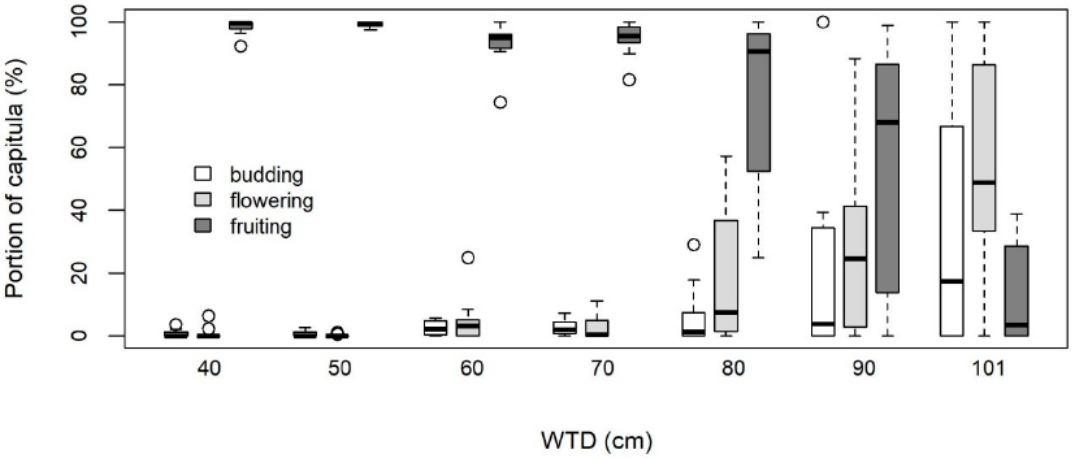

Figure 8. Portion of budding, flowering and fruiting capitula per plant of cup plant depending on water table distance (WTD, given as mean for each row of the four tanks). Data were collected at the end of the second growing season (September 2019). Note that the three different phenological stages of a treatment are always shown next to each other with a slight offset. $n = 12$ (in 90 cm WTD $n = 11$; in 101 cm WTD $n = 10$, because these three plants did not develop any capitulum at that time).

4. Discussion

4.1. Highest Yield on Moist Soil

Soil moisture conditions determined by water table distance (WTD) had a significant impact on growth and development of cup plant. Plant height and living aboveground biomass were the highest on moist soil with about 3 m and 1500 g dry weight per plant and decreased on wetter and especially on drier soil. Therefore, the plant height measured in our study reached the maximum published values for this species [19,29,30], indicating that optimal growth conditions were included in our study.

Several field studies and one pot experiment in Central Europe confirm our results that highest growth is achieved in periodically waterlogged or well-irrigated soil conditions [5,31,32]. In general, highest yields of cup plant are described on soils with good soil moisture; hydromorphic soils are unsuitable [3,6]. Cup plant is able to reach deep water resources with its roots; therefore it is considered as certainly drought-tolerant [3]. Because of the limited soil depth in the present study, deep rooting was prevented and cup plant suffered considerable damage in the dry treatments. The number of shoots per plant was in mean 18 and not affected by soil moisture. This value is quite high compared to other studies, which indicated 3.5 to 6.6 shoots per plant in the second growing season [33,34]. Essential for this parameter are stand density and age of the plants [33,34]. The fact that cup plant develops shoots already in the first year, as shown in our study, has not been published so far. We assume that reasons are the sowing early in spring and the precultivation under optimal conditions in the greenhouse before planting into the experimental tanks.

A high yield of cup plant under moist soil conditions, as demonstrated in our study, is desirable from the farmers' point of view. However, from the perspective of invasion biology, this might carry the risk that spontaneously grown and established cup plants could also become such vigorous plants and might compete with native species. Studies are lacking but necessary to assess the competitiveness of cup plant and its possible risk of suppression of native species in case of spontaneous settlement. A species could be classified as invasive if its spread threatens biodiversity (Article 3 No. 2 EU-Regulation No. 1 143/2014).

4.2. High Reproduction and Rapid Development on Moist Soil

In the present study, cup plant produced the most capitula with about 350 on moist soil, and their development there was faster in comparison to drier soil conditions. Another study in Germany confirms our results, where the number of flowering capitula of cup plant was higher under irrigated than under rainfed conditions [35]. This study also agrees with ours concerning an independence of number of disc florets per capitulum in respect to watering. Although fruits of cup plant are developed from ray florets and not from disc florets [6], this agreement of results confirms that the composition of capitula is independent of soil moisture conditions. The number of fruits per capitulum was about 27 in the present study and therefore in the upper range or even above the values of other studies (10–20 or 20–30) [3,6]. Thousand grain weight varies widely in the literature (14 to 21.5 g [3] and up to 23 g [6]). Our values are with a mean of about 18.1 g rather in the middle.

The rapid development of fruits on moist soils leads to a high proportion of ripe fruits at harvesting time. Together with the high fruit production under these conditions, there is a higher risk of cup plant spreading from the fields—presupposed germination and saplings' establishment are likewise successful.

4.3. Consequences and Recommendations for Nature Conservation

Spontaneous occurrences of cup plant have already been documented in seven federal states of Germany and in other European countries as well [13–16]. From the view of nature conservation, the indication of colonized sites is important to assess the risk for protected or otherwise valuable ecosystems. In its native range in eastern North America, cup plant colonizes moist bottomlands, river valleys, and lakesides [3,6]. This is in line with our results and confirms a possible risk that cup plant could colonize moist habitats in Germany, too. So far, observations of spontaneous occurrences of cup plants in Germany have shown a broader range of habitats. In addition to ruderal places and woody structures, however, even moist ecosystems as perennial fields on river banks as well as bottomland woods are colonized [12,36,37]. This circumstance holds together with the high growth and reproductive potential on moist soils, as shown in our study a particular risk for nature conservation. Moist ecosystems—such as riparian fringes, alluvial forests, fens, and swamps—are valuable for nature conservation, because they are endangered according to the German red list of threatened habitats [38] and protected according to §30 BNatSchG.

Thus, an adequate distance of cup plant fields to moist ecosystems should be kept strictly to prevent their spontaneous colonization by cup plant. Dispersal distance of cup plant is 6 m in median but could be more than 10 m [12]. Therefore, we recommend for cup plant fields distances of several 10 m from valuable ecosystems to preclude fruit dispersal even under extreme wind events. However, dispersal vectors and distances of cup plant fruits are not investigated, and studies are urgently required to be able to give more precise recommendations for minimizing the risk of spreading. So far, it is also unknown whether cup plant fruits can be spread by watercourses and remain viable. As long as this is not examined, it is important to keep a sufficiently large distance to streams, even if they are strongly anthropogenic shaped and not valuable for nature conservation. In order to prevent fruit dispersal by agricultural machines, they should be cleaned before leaving the field and the crop should be covered during transport.

Additionally, the number and size of cup plant fields play a decisive role for the invasion potential because each newly cultivated field enhances the risk for further spontaneous spreading [12,39]. In Germany, more than 1000 ha are newly cultivated with cup plant in each of the recent years, while the older fields remain cultivated [40]. Consequently, further spreading of cup plant is to be expected and needs to be observed. The areas surrounding the cup plant fields and the roads from the fields to the farms should be continuously screened for spontaneous occurrences of cup plant to be able to combat this species where necessary.

5. Conclusions

In Central Europe, cup plant is a promising bioenergy crop that can achieve high yields, especially on moist soils. Wetter and drier soils are less suitable, but cup plant is able to survive on a wide range of soil moisture conditions.

However, a caution in respect to a possible invasiveness of cup plant is advised. The highest risk for spontaneous colonization by cup plant is—similar to the highest yield—supposed for ecosystems with moist soils, which are often valuable for nature conservation in Germany. To assess the actual invasive potential of cup plant, more studies about habitat requirements, competitiveness, and dispersal vectors of cup plant are urgently needed. If precautionary measures are observed, cup plant can take a place in the Central European agricultural landscape and make a valuable contribution to the conservation of biodiversity.

Supplementary Materials: The following tables contain the data on which calculations and figures of the present study are based. They are available online at https://www.mdpi.com/2077-0472/11/1/24/s1: Table S1: Weather conditions during the experiment; Table S2: Soil water content over time; Table S3: Soil water content of soil samples; Table S4: Growth of cup plant at the end of the first growing season (August 2018); Table S5: Shoot development of cup plant at the end of the first growing season (November 2018); Table S6: Growth of cup plant at the end of the second growing season (September 2019); Table S7: Explanation of column names of the Tables S1–S6.

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5.3 Manuskript 3

Competitiveness of the exotic *Silphium perfoliatum* against the native *Urtica dioica*: A field experiment

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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

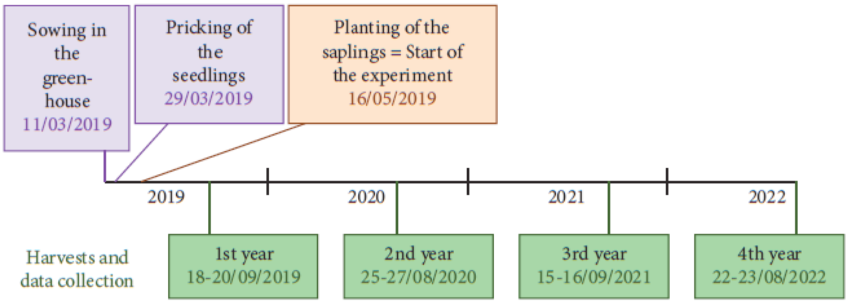

Figure 1: Timeline of the experiment. Dates are given as day/month/year.

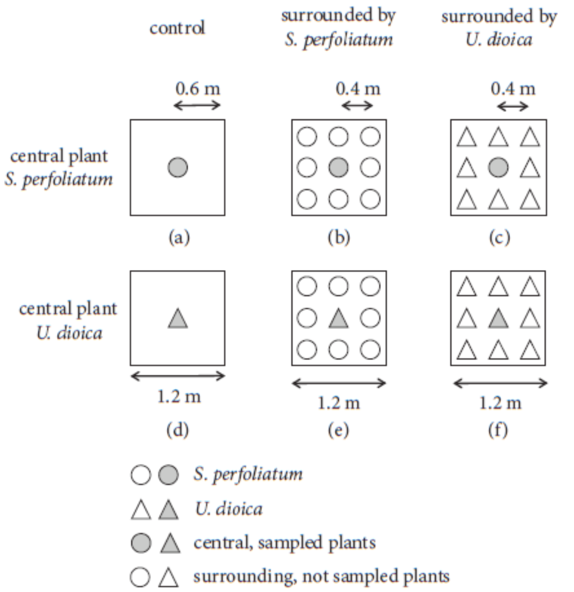

Figure 2: Treatments of *S. perfoliatum* and *U. dioica*. Both species were planted as control without competition (a, d), surrounded by eight plants of *S. perfoliatum* (b, e) and surrounded by eight plants of *U. dioica* (c, f). Distances between surrounding plants and to the respective central plant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

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):

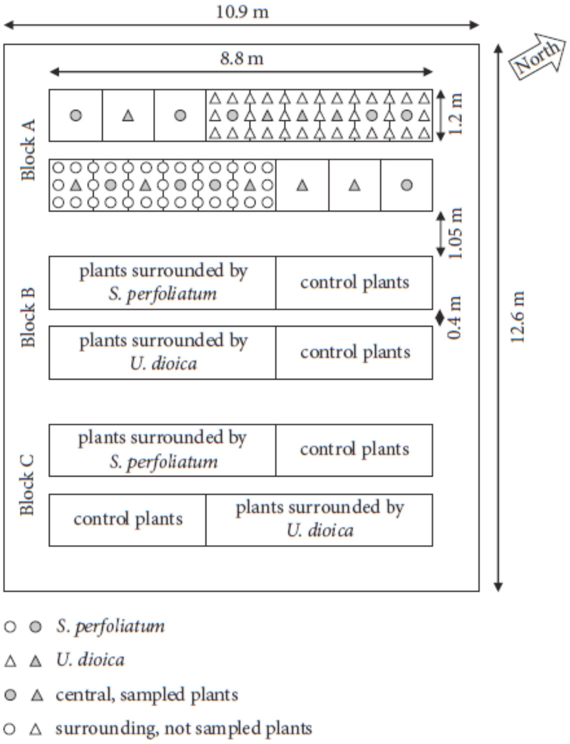

Figure 3: Experimental setup in the field at the Ecological Botanical Gardens of the University of Bayreuth (Germany). In each block, competition treatments per surrounding species were placed next to each other, with two adjacent plots sharing three surrounding plants. The order of treatments and the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

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

In equation (1), x is the parameter with the higher value: $\text{parameter}_{\text{control}}$ or $\text{parameter}_{\text{competition}}$. 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).

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 $n = 52$.

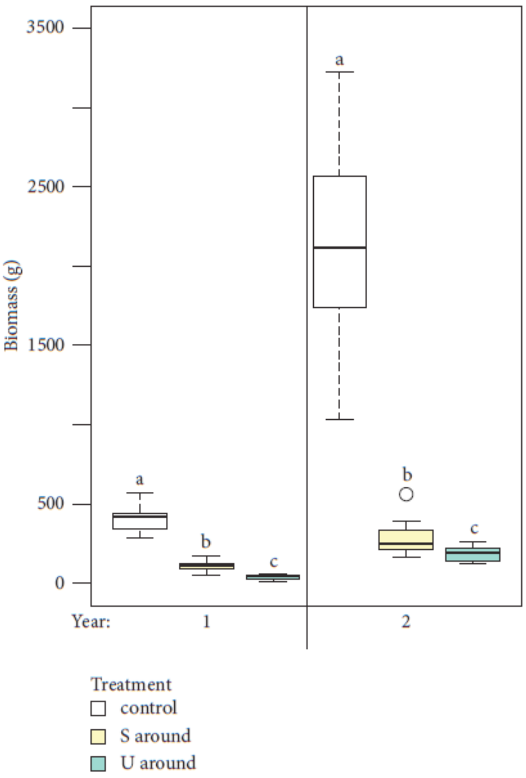

Figure 4: Living aboveground dry biomass per plant of *S. perfoliatum* depending on treatment: control without surrounding plants (white box), surrounded by *S. perfoliatum* (S around, yellow box), and surrounded by *U. dioica* (U around, green box). $n = 9$ (except U around $n = 8$). Different letters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

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 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*.

		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 $n = 81$		
Parameter	*Df*	Estimate	*F* value	*p*	Estimate	*F* value	*p*
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

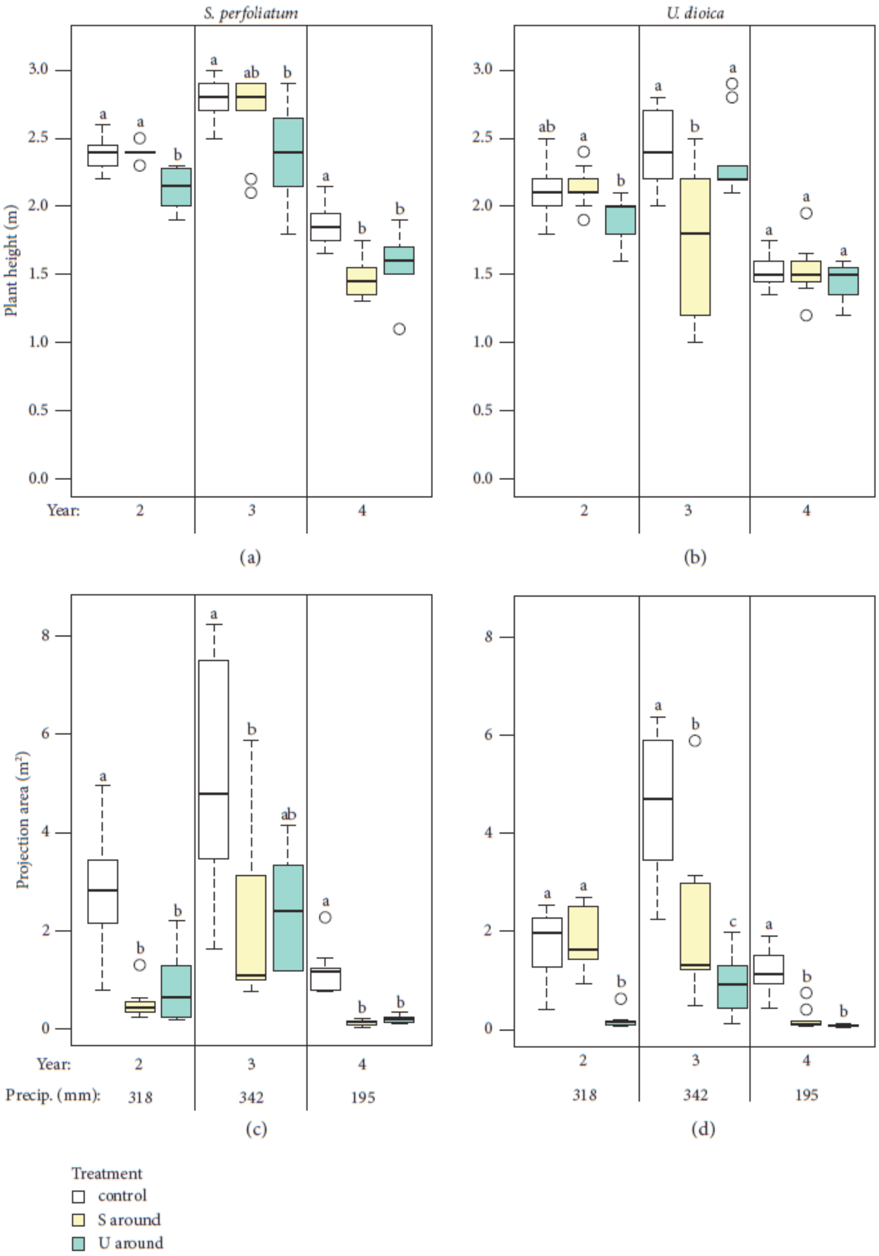

FIGURE 5: Plant projection area (a, b), plant height (c, d) of *S. perfoliatum* (a, c), and *U. dioica* (b, d) depending on the treatment: control without surrounding plants (white box), surrounded by *S. perfoliatum* (S around, yellow box), and surrounded by *U. dioica* (U around, green box). Precipitation 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.

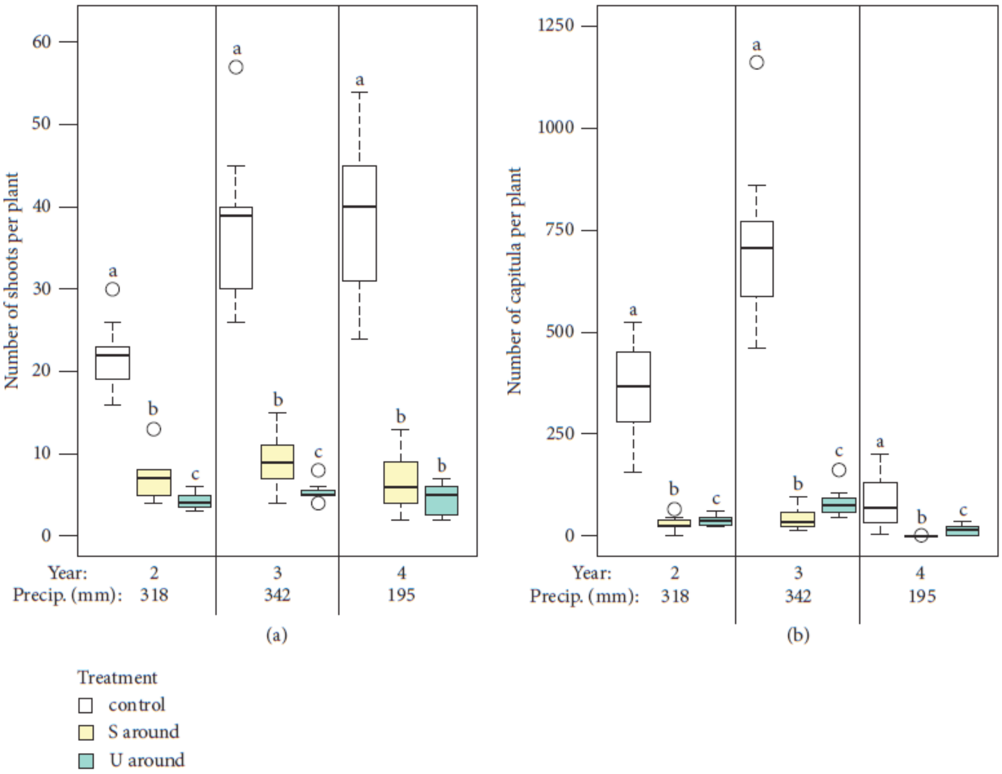

FIGURE 6: Number of living shoots (a) and number of capitula (b) per plant of *S. perfoliatum* depending on the treatment: control without surrounding species (white box), surrounded by *S. perfoliatum* (S around, yellow box), and surrounded by U. dioica *U. dioica* (U around, green box). Precipitation 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 ± 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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5.4 Manuskript 4

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

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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

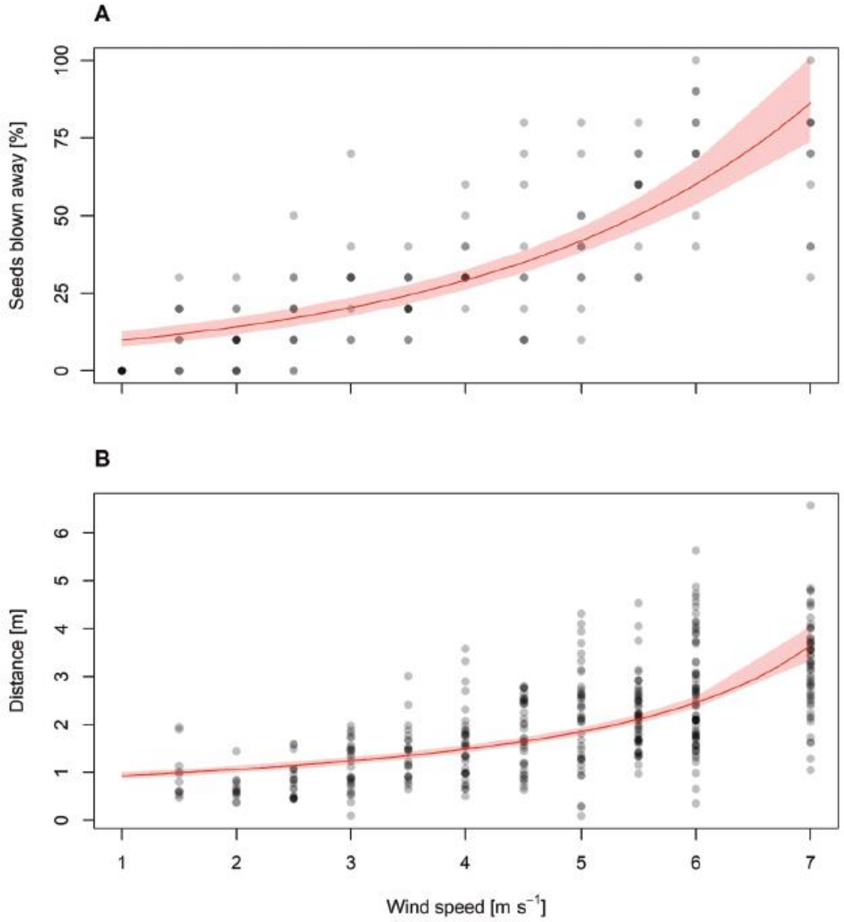

Figure 2. A. Cup plant seeds blown away by wind depending on wind speed; 100% corresponds to 10 seeds; n = 122. **B.** Distance of cup plant seeds blown away by wind depending on wind speed; seeds that were not blown away by wind were excluded; n = 386. The darker the dots are, the more dots are on top 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.	Chi^2	p	Test
Removal rate	189	2	170.09	< 0.001	Kruskal-Wallis rank sum test

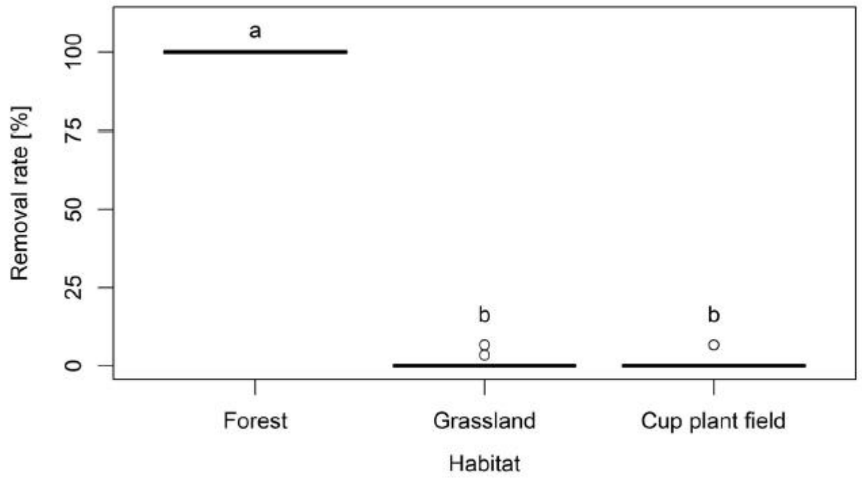

Figure 3. Removal rate of cup plant seeds depending on habitat. 100% corresponds to 30 seeds. Different letters indicate significant differences (kruskalmc test; Table 3). Data were collected for 21 days at three replicates per habitat resulting in n = 63.

(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).

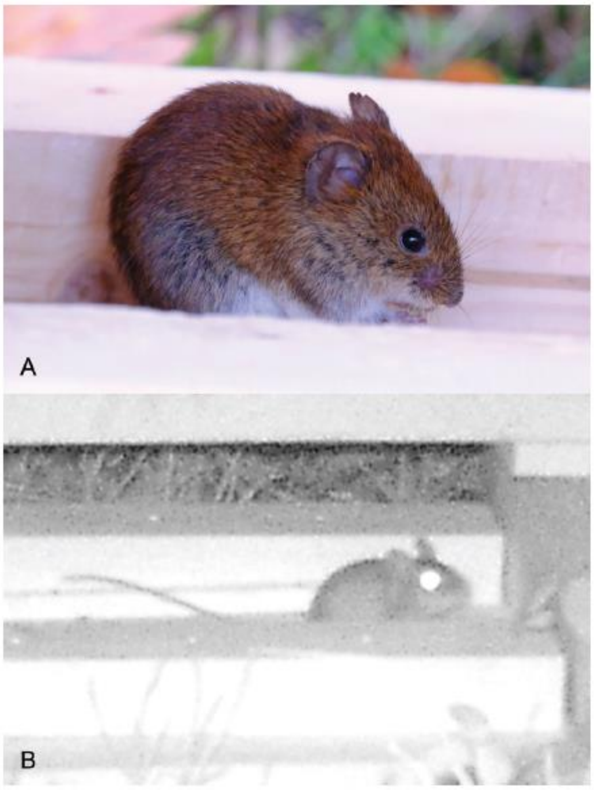

Figure 4. Rodents seen in the boxes with cup plant seeds in the forest habitat. **A.** Bank vole (*Myodes glareolus*) eating cup plant seeds. Photo by Lukas Hummel. **B.** *Apodemus* sp. Photo at night by Wildlife camera (Wild-Vision Full HD 5.0, SECACAM, Ven Trade GmbH, Köln, Germany).

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	

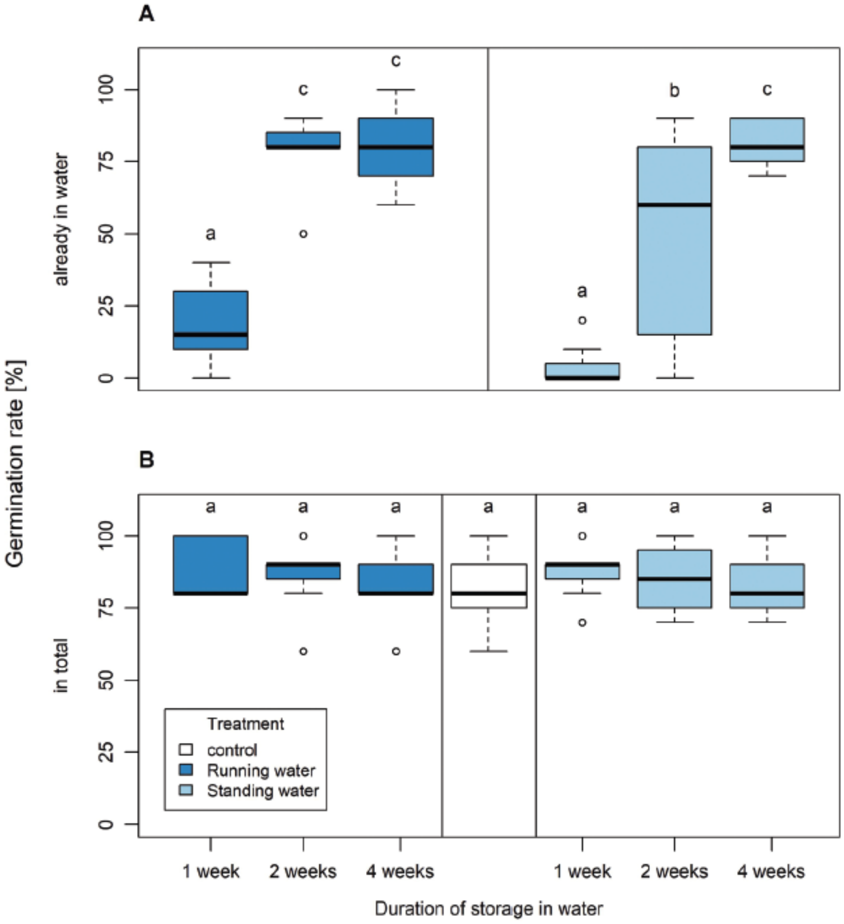

Figure 5. Germination rate of cup plant seeds (A) already in water and (B) in total, depending on treatment and duration of storage in water. Total germination rate was calculated as sum of seeds germinated in water and in the pots after sowing. 100% corresponds to 10 seeds. Different letters indicate 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	

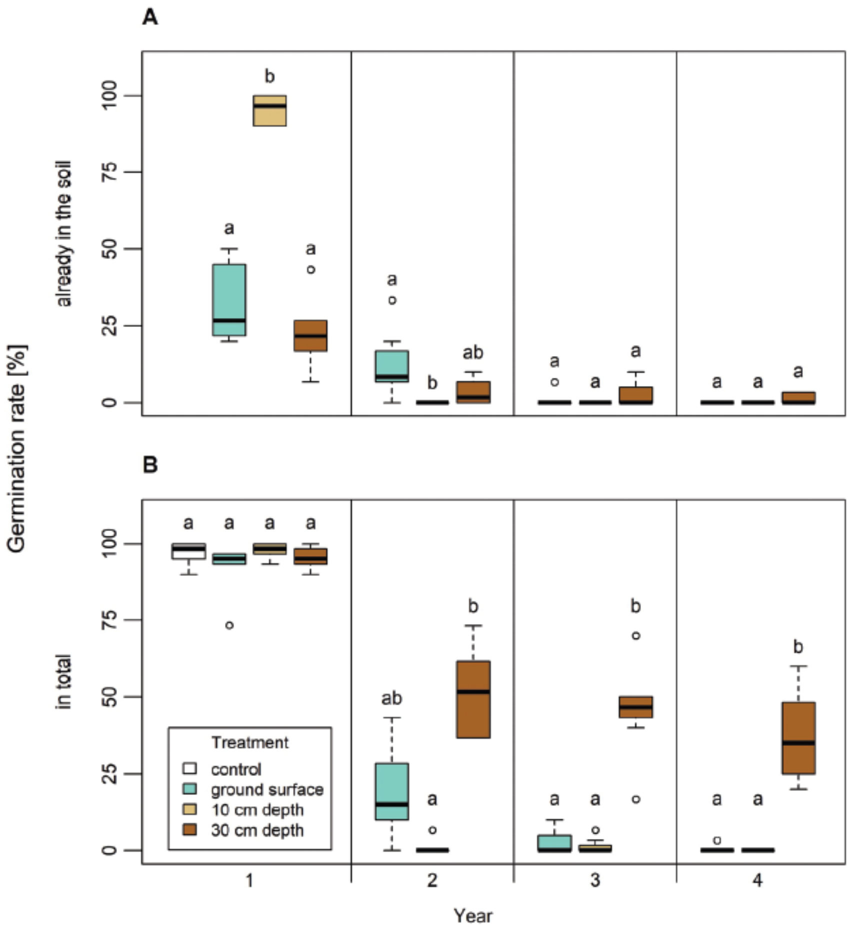

Figure 6. Germination rate of cup plant seeds (A) already in soil and (B) in total, depending on treatment and duration of storage in soil. Total germination rate was calculated as sum of seeds germinated in the soil and in the pots after sowing. 100% corresponds to 30 seeds. Different letters indicate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

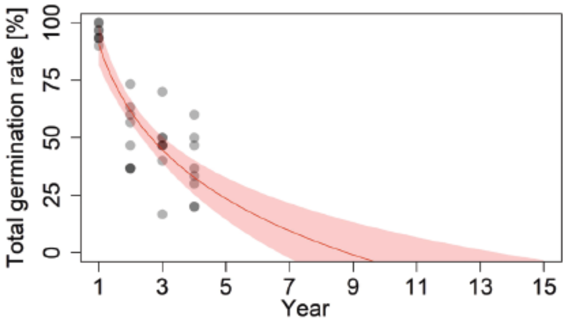

Figure 7. Total germination rate of cup plant seeds stored at 30 cm soil depth depending on duration of storage in soil. Total germination rate was calculated as sum of seeds germinated in the soil and in the pots after sowing. 100% corresponds to 30 seeds. The darker the dots are, the more dots are 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

6 Publikationsliste

Publikationen dieser Dissertation:

Ende L.M., Knöllinger K., Keil M., Fiedler A.J., Lauerer M. (2021) Possibly Invasive New Bioenergy Crop *Silphium perfoliatum*: Growth and Reproduction Are Promoted in Moist Soil. Agriculture 11 (1): 24. doi: 10.3390/agriculture11010024.

Ende L.M. & Lauerer M. (2022) Spreading of the cup plant (*Silphium perfoliatum*) in northern Bavaria (Germany) from bioenergy crops. NeoBiota 79: 87-105. doi: 10.3897/neobiota.79.94283.

Ende L.M., Schwarzer S.-J., Ebner A., Lauerer M. (2023) Competitiveness of the exotic *Silphium perfoliatum* against the native *Urtica dioica*: A field experiment. International Journal of Ecology 2023: 1-12. doi: 10.1155/2023/5512148

Ende L.M., Hummel L., Lauerer M. (2024) Dispersal and persistence of cup plant seeds (*Silphium perfoliatum*): do they contribute to potential invasiveness? Plant Ecology and Evolution 157 (1): 75-87. doi: 10.5091/plecevo.104640

Weitere Publikation zum Thema der Dissertation:

Ende L.M. & Lauerer M. (2020) Spontanvorkommen der Silphie im Bayreuther Raum: birgt diese neue Bioenergiepflanze ein Invasionspotenzial? Natur und Landschaft 95 (7): 310-315. doi: 10.17433/7.2020.50153819.310-315.

Weitere Publikation zu einem anderen Thema:

Hüllbusch E., Brandt L.M., Ende P. & Dengler J. (2016) Little vegetation change during two decades in a dry grassland complex in the Biosphere Reserve Schorfheide-Chorin (NE Germany). Tuexenia 36: 395–412. doi: 10.14471/2016.36.019

(Eidesstattliche) Versicherungen und Erklärungen

(§ 8 Satz 2 Nr. 3 PromO Fakultät)

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