

Research Article

An emerging weed: rapid spread of *Solanum carolinense* in AustriaSwen Follak^{1,*}, Daniel Chapman², Michael Schwarz³ and Franz Essl⁴¹Institute for Sustainable Plant Production, Austrian Agency for Health and Food Safety, Vienna, Austria²Biological and Environmental Sciences, Faculty of Natural Science, University of Stirling, Stirling FK9 4LA, United Kingdom³Data, Statistics and Risk Assessment, Austrian Agency for Health and Food Safety, Vienna, Austria⁴Division of BioInvasions, Global Change & Macroecology, Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria

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Abstract

Solanum carolinense is a perennial herb native to North America and regarded to be a major agricultural problem in crops and pastures in several parts of the world. In south-eastern Austria, *S. carolinense* is in a phase of range filling and ongoing spread. Floristic relevés demonstrated that the species infests different crop types, such as soybean, maize and oil pumpkin, and grassland, but also non-agricultural habitats are already invaded. Widespread invasion clusters were found in almost one fifth of the crop fields surveyed, indicating locally severe infestations. A species distribution model shows that only a relatively small part of Austria is currently climatically suitable, but most of it is used for agriculture. The study highlights the need to take effective measures to halt the further spread of the species and to avoid significant yield losses.

Key words: agriculture, distribution, habitat, impact, invasive alien plants, management**Introduction**

Solanum carolinense L. (Solanaceae) is a perennial herb native to North America (Wahlert et al. 2015). The species was accidentally introduced into Europe most likely in the middle of the 20th century. In its native range, it is regarded to cause major agricultural problems in crops and pastures, as it has several weedy attributes, namely it reproduces vegetatively, grows rapidly, thrives in a variety of biotic and abiotic conditions, is toxic to livestock, and is a host of several pests and diseases (Bassett and Munro 1986; Wahlert et al. 2015). *Solanum carolinense* has already been found infesting crop fields in several European countries, such as Austria, Italy and Germany (EPPO 2022a). In 2022, *S. carolinense* has been included in the EPPO A2 List of pests recommended for regulation as quarantine pests (EPPO 2022b).

In Austria, the species has been known since the end of the 1990s. Few studies have already shown that *S. carolinense* spreads locally (Follak 2020)

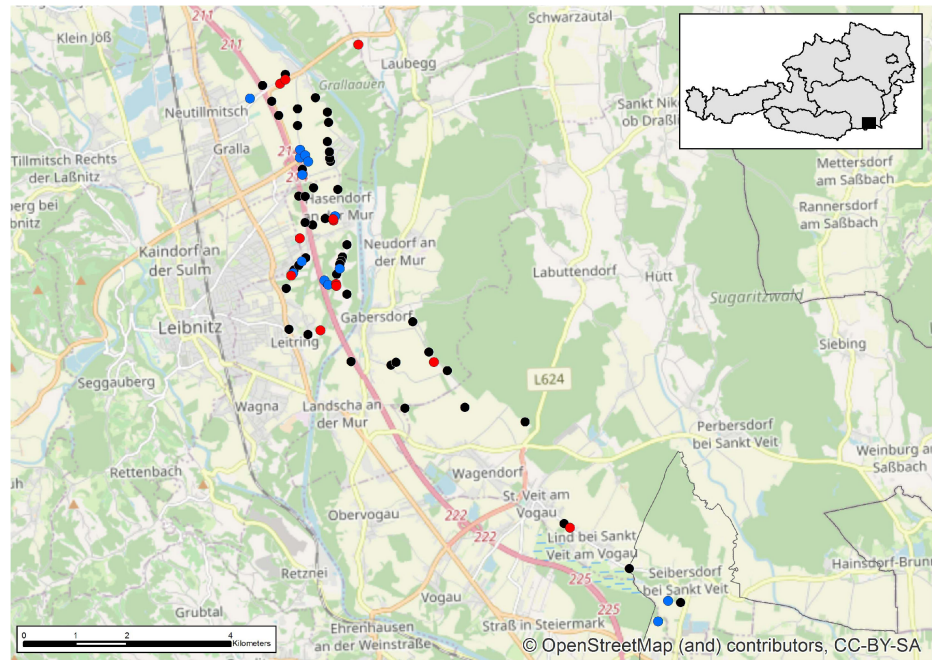


Figure 1. Map of the study area showing the distribution of *Solanum carolinense* with observations from 2019 to 2022 (dots). Different colors are according to population classification: black = 1 (single, isolated individuals), blue = 2 (clustered groups ± dispersed individuals throughout the field), red = 3 (widespread clusters, indicative of a substantial infestation). Distribution data is based on Follak (2020) and was updated with new records for this study.

and that there is a high risk of invasion for the Austrian territory using climate matching (Follak and Strauss 2010). Here, we expand the knowledge of the ongoing spread of *S. carolinense* in Austria and assess its spread dynamics based on new data and modelling. Specifically, the aims of the study were to determine (1) the local distribution, frequency and level of infestation of *S. carolinense* based on an on-site survey, (2) its presence in crops and other habitats based on floristic relevés, and (3) its potential distribution under current climate in Austria using species distribution modelling.

Materials and methods

Local distribution and infestation levels

Infestations of *Solanum carolinense* were surveyed in detail in the invasion hotspot of the species in southern Austria in order to better characterize the spread pattern and extent of weedy distribution in fields. The study area (approximately 30 km²) involved parts of the district Leibnitz in southern Austria (federal state of Styria, Figure 1). The survey is based on eight field trips conducted from 2019 (Follak 2020) to 2022. Populations of *S. carolinense* were recorded and each location was georeferenced. Information on the habitat (i.e. infested crop) was noted. Maps showing the spatial distribution of *S. carolinense* were created based on the coordinates obtained using ArcMap 10.2.2 (ESRI). A nominal rating scale of 1 to 3 was used to classify *S. carolinense* population sizes, based on visual estimates from the field

edge. Rating levels were: 1 = single, isolated individuals at the field margin, 2 = clustered groups along the field margin \pm dispersed individuals throughout the field, 3 = widespread clusters, indicative of a substantial infestation.

Floristic characterization and cover values

In 2022, relevés (n = 10) from different crop types, grassland and ruderal grassland infested by *S. carolinense* were recorded to characterize the floristic composition of the invaded vegetation types, and to provide information on its abundance (i.e. cover values). Relevés were established randomly and plot size was kept at 30 m². In addition, in maize, recordings were made along a transect (I = field margin, II = 10 m, III = 30 m away from the edge, each transect plot 10 m² in size) to document the performance of *S. carolinense* also inside the field under shaded conditions. Percentage ground cover (0 to 100%) of each plant species in the plots was visually estimated (Andújar et al. 2010). Botanical nomenclature and syntaxonomic classification follow Fischer et al. (2008) and Mucina et al. (2016), respectively.

Species Distribution Modelling

A global-scale species distribution model (SDM) was used to identify the area of Austria that is most at risk of invasion by *S. carolinense* under current climatic conditions. The modelling followed a recent modification of standard presence-background (presence-only) ensemble distribution modelling for emerging invasive non-native species (Chapman et al. 2019). The model was adopted from EPPO (2022a) and adapted for this study. Full details on the SDM can be found in EPPO (2022a). In overview, *S. carolinense* occurrence records were obtained from the native and introduced range from Gbif (<https://www.gbif.org/>), iDigBio Portal (<https://www.idigbio.org/portal>) and USGS Biodiversity Information Serving Our Nation (BISON) (formerly <https://bison.usgs.gov>, now <https://www.gbif.us>). The data was amended by records from the Expert Working Group performing the Pest Risk Assessment on *S. carolinense*. Records were modelled against pseudo-absences sampled from a background region combining areas deemed either accessible to the species or physiologically unsuitable for it (i.e. aiming to exclude suitable but inaccessible areas). An ensemble modelling strategy involving seven model algorithms was employed using the BIOMOD2 R package v3.4.6 (Thuiller et al. 2009, 2016). Predictor variables were selected based on the life history and habitat requirements of *S. carolinense* and likely limiting factors for establishment in Europe. Predictors included climate (growing degree-days, mean minimum temperature of the coldest month, annual precipitation and precipitation seasonality) and land cover (urban areas, cropland and grassland) from the CHELSA database V2.1 (Karger et al. 2017) and the Global Land Cover SHARE database (Latham et al. 2014), respectively. From the global model, the predicted suitability in



Figure 2. Representative images of *Solanum carolinense* occurrences in the study area: (a) in cereals, (b) in soybean, (c) typical small cluster in maize, (d) heavy infestation in maize, (e) in oil pumpkin and (f) in grassland (©S. Follak).

Austria was examined to estimate the suitable area and the overlap of the species with agricultural areas, as represented in the Global Land Cover SHARE database.

Results

Local distribution and infestation levels

In total, 72 populations of *S. carolinense* have been documented from 2019 to 2022 (Figure 1). Based on the survey data, the distribution of *S. carolinense* extends along a narrow band east and west of the A2-motorway (red color) at a length of approximately 10 km and a width of a few km with the highest density of records east of Gralla and Leibnitz. The species was found in all major crop types cultivated in this area. The majority of infested crops were maize (60%), followed by oil pumpkin (24%), soybean (10%), and others (cereals, grassland) (Figure 2). The number of infested fields assigned a population size rating of 1 was highest at 64%, while fields assigned a rating of 2 and 3 were at 19% and 17%, respectively. Most of the surveyed fields were infested at the field edge and small clusters of *S. carolinense* were observed in the field. Few fields were heavily infested including maize (Figure 2d) and oil pumpkin (i.e. with a rating level of 3).

The majority of the more heavily infested fields tend to be in the upper part of the study area.

Floristic characterization and cover values

The relevés and detailed information on locality and site characteristics are provided in Table 1 and Supplementary material Table S1, respectively. The data shows that *S. carolinense* invades thermophilous weed communities rich in C_4 species. The weed communities belong to the class *Digitario sanguinalis-Eragrostietea minoris* Mucina, Lososová et Šilc in Mucina et al. 2016 (Mucina et al. 2016), which is widespread in the lowlands of temperate Central Europe (FloraVeg.EU 2023). The most frequent species were panicoid grasses, such as *Echinochloa crus-galli* (L.) P. Beauv., *Setaria* spp., *Panicum dichotomiflorum* Michx., *Digitaria sanguinalis* (L.) Scop. and *Sorghum halepense* (L.) Pers. together with *Calystegia sepium* L. and *Convolvulus arvensis* L. In the study area, the sites of the relevés are mainly characterized by moderately dry loamy soils (<https://bodenkarte.at>); however, a few sites in valley bottoms are influenced by high groundwater levels (e.g., relevé 7, Table 1). Thus, *S. carolinense* also occurs together with hydrophilic species such as *Rorippa palustris* (L.) Besser and *Gnaphalium uliginosum* L. In maize, *S. carolinense* cover values at the field margin were sometimes high (up to 70%), and even within the field cover values reached up to 20%. In oil pumpkin and soybean, cover values of up to 15% were recorded.

Solanum carolinense also infests and persists in (fallow) ruderal fertilized grassland that mainly comprised perennial grasses like *Dactylis glomerata* L., *Phleum pratense* L., *Elymus repens* (L.) Gould, and *Festuca pratensis* Huds. (Figure 2f). In these plots, perennial herbs such as *Taraxacum officinale* agg., *Triflourm repens* L. and *Potentilla anserina* L. were abundant. Panicoid grasses also occurred at these sites indicating their former use as cropland (Table 1). The cover values of *S. carolinense* were between 5 and 10%.

Potential distribution in Austria

The SDM identifies suitable areas in the lowlands of Austria, namely in the south and north of the country (Figure 3). The suitable area accounts for approximately 8% of the Austrian territory (based on proportion of model grid cells with projected suitability above the suitability threshold of 0.34) and 62% of this area is used for agriculture (based on the mean cover of croplands in these grid cells). The study area is projected as suitable (Figure 3). The model also projects a climatically suitable region in the north of Austria (parts of the Danube valley), which is largely used for agriculture but is currently uninvaded. The model suggests that the main limiting factor in Austria is low summer temperature, with low precipitation limiting towards the eastern border of the country. Thus, cool mountainous areas in the Alps and the Alpine foothills and parts of eastern Austria with its dry Pannonian climate are currently not suitable for the species.

Table 1. Floristic composition of relevés with occurrences of *Solanum carolinense* in Austria. Relevés 1 to 7 were from crop fields (maize: 1 to 4, soybean: 5 and 6, oil pumpkin: 7), 8 from a grassland and 9 and 10 from ruderal grasslands. In relevés 1 to 4, recordings were made along a transect (I = field margin, II = 10 m, III = 30 m away from the field edge). Percentage ground cover (0 to 100%) of each species was visually estimated. For information on locality and site characteristics, see Table S1.

Relevés no.	1			2			3			4			5	6	7	8	9	10
Transect_plot ID	I	II	III	I	II	III	I	II	III	I	II	III						
<i>Solanum carolinense</i> L.	18	.	.	70	20	10	30	.	.	15	.	5	3	15	8	5	10	7
<i>Achillea millefolium</i> L.	0.3	15
<i>Agrostis stolonifera</i> L.	1	.	.	.
<i>Amaranthus retroflexus</i> L.	5	.	.	.
<i>Ambrosia artemisiifolia</i> L.	2	5
<i>Artemisia vulgaris</i> L.	0.5
<i>Calystegia sepium</i> L.	10	20	5	0.2	.	0.5	0.5	.	.	15	2	3	0.7	.	0.2	0.2	.	0.5
<i>Capsella bursa-pastoris</i> (L.) Medik.	.	.	0.1	0.1	0.1	.	.	0.2	0.1	.	.
<i>Cardamine hirsuta</i> L.	0.1	0.2
<i>Carex hirta</i> L.	0.2
<i>Chenopodium album</i> L.	0.2	0.2	0.2	.	.	0.1	0.1	.	.
<i>Chenopodium polyspermum</i> L.	.	.	0.1	0.2	.	.	.
<i>Cirsium arvense</i> (L.) Scop.	5	0.1	3	1	.
<i>Convolvulus arvensis</i> L.	.	.	.	5	20	20	0.5	.	.	0.5	.	.	0.5	0.2	.	0.2	0.2	0.2
<i>Conyza canadensis</i> (L.) Cronquist	0.2	.	0.2	0.2
<i>Crepis biennis</i> L.	0.2	.
<i>Crepis capillaris</i> (L.) Wallr.	0.7	0.2
<i>Cucurbita pepo</i> L.	50	.	.	.
<i>Cynodon dactylon</i> (L.) Pers.	5	1	.	.	2	0.3
<i>Cyperus esculentus</i> L.	40
<i>Dactylis glomerata</i> L.	60	20	3
<i>Daucus carota</i> L.	0.1
<i>Digitaria sanguinalis</i> (L.) Scop.	3	.	0.2	1	2	3	0.2	.	5	1	3	5
<i>Echinochloa crus-galli</i> (L.) P. Beauv.	0.2	.	.	3	1	1	2	20	2	.	.	0.2
<i>Elymus repens</i> (L.) Gould	2	0.5	.	.	3	.	.	0.5	.	.	.	20	15
<i>Epilobium tetragonum</i> L.	0.1	.	.	.
<i>Equisetum arvense</i> L.	.	.	.	1	0.5	.	2
<i>Erigeron annuus</i> (L.) Desf.	0.5	.	1	1
<i>Euphorbia esula</i> L.	0.1	0.2
<i>Fallopia bohemica</i> (Chrtk & Chrtková) J.P. Bailey	0.5
<i>Fallopia convolvulus</i> (L.) Á.Löve	0.1	0.5
<i>Festuca arundinacea</i> Schreb.	0.5	0.2
<i>Festuca pratensis</i> Huds.	15	.	0.5
<i>Festuca rubra</i> L.	7	.
<i>Galinsoga ciliata</i> (Raf.) Blake	10	3	3	2	.	0.5	.	.	.
<i>Galinsoga parviflora</i> Cav.	10	3	3	5	.	.	.
<i>Galium album</i> Mill.	5	0.2
<i>Galium aparine</i> L.	0.3
<i>Geranium pusillum</i> L.	0.1
<i>Glechoma hederacea</i> L.	2	.
<i>Glycine max</i> (L.) Merr.	70	25
<i>Gnaphalium uliginosum</i> L.	0.1	.	.	.
<i>Holcus lanatus</i> L.	5	.
<i>Hordeum distichon</i> L.	0.5	2	5
<i>Hypericum perforatum</i> L.	3	.
<i>Hypochaeris radicata</i> L.	0.1	0.2	.	.	.
<i>Knautia arvensis</i> (L.) Coult.	0.1	.
<i>Lactuca serriola</i> L.	0.5	.
<i>Lamium purpureum</i> L.	0.2	0.2	.	0.3	.	0.2	0.2	0.1	.	.	0.2	0.2
<i>Linaria vulgaris</i> Mill.	3	.
<i>Lolium perenne</i> L.	0.2	10	0.5	1
<i>Lotus corniculatus</i> L.	0.2	.
<i>Lysimachia vulgaris</i> L.	0.2	.	.	.
<i>Mentha arvensis</i> L.	.	0.5	.	.	5	10	5	0.3

Table 1.(continued).

Relevés no.	1			2			3			4			5	6	7	8	9	10
	I	II	III	I	II	III	I	II	III	I	II	III						
<i>Oenothera biennis</i> agg.	0.2
<i>Oxalis stricta</i> L.	0.2
<i>Panicum dichotomiflorum</i> Michx.	2	.	0.2	1	50	5	.	0.7
<i>Parthenocissus inserta</i> (Knerr) Hitchc.	20
<i>Persicaria bistorta</i> Delarbre	2
<i>Persicaria hydropiper</i> (L.) Delarbre	.	.	0.1
<i>Phleum pratense</i> L.	10	.	.
<i>Phytolacca americana</i> L.	2
<i>Plantago lanceolata</i> L.	3	2
<i>Plantago major</i> L.	2	.	0.1	5
<i>Poa pratensis</i> L.	3	.	5
<i>Polygonum aviculare</i> agg.	0.2	.	0.2	.	.
<i>Populus alba</i> L.	0.1	.	.	.
<i>Populus nigra</i> L.	0.3	.	.	.
<i>Portulacca oleracea</i> L.	1	0.1	.	.
<i>Potentilla anserina</i> L.	10	.
<i>Potentilla argentea</i> L.	0.5	.
<i>Potentilla reptans</i> L.	0.1
<i>Ranunculus repens</i> L.	0.2	.
<i>Robinia pseudoacacia</i> L.	0.1
<i>Rorippa palustris</i> (L.) Besser	8	.	.	.
<i>Rubus caesius</i> L.	1	.	.	0.3	.	.	0.2	5
<i>Rumex obtusifolius</i> L.	0.1	2
<i>Rumex thyrsiflorus</i> Fingerh.	0.2	.
<i>Salix alba</i> L.	1	.	.	.
<i>Setaria faberi</i> R.A.W. Herrm.	0.5
<i>Setaria pumila</i> (Poir.) Roem. & Schult.	0.5	.	.	1	1	1	0.5	.	.	1	.	.	1	15	.	5	5	3
<i>Setaria viridis</i> (L.) P.Beauv.	0.5
<i>Silene alba</i> Poir.	0.2
<i>Solanum nigrum</i> L.	0.7	.	.	.
<i>Sonchus oleraceus</i> L.	0.2	0.7	.	.	.
<i>Sorghum halepense</i> (L.) Pers.	1	2	0.3	5	.	10	.
<i>Stachys palustris</i> L.	.	.	.	1
<i>Stellaria media</i> (L.) Vill.	0.2	0.2	1	0.2	1	1	0.2	1	1	.	2	1	.	.	.	0.1	.	.
<i>Taraxacum officinale</i> agg.	.	.	0.1	0.1	.	.	0.1	.	1	.	0.3	0.1	0.5	15
<i>Trifolium hybridum</i> L.	0.2	.	.
<i>Trifolium pratense</i> L.	0.1	0.2	0.5
<i>Trifolium repens</i> L.	0.2	15
<i>Tripleurospermum inodorum</i> (L.) Sch. Bip.	0.1
<i>Ulmus laevis</i> Pall.	.	0.2	0.2	0.3	.	.	.
<i>Urtica dioica</i> L.	.	.	0.1	2
<i>Verbascum nigrum</i> L.	2	.
<i>Veronica chamaedrys</i> L.	0.2	.
<i>Veronica persica</i> Poir.	0.1	0.2
<i>Vicia cracca</i> L.	.	.	.	0.3
<i>Zea mais</i> L.	80	95	95	70	90	90	70	90	90	80	95	95

Discussion

Local distribution and further spread

The map of populations recorded from 2019 to 2022 shows the currently known distribution of the species in the study area. No populations could be observed by the authors further north (i.e. above the national road [orange] crossing the river Mur). The main boundaries are the urban settlements

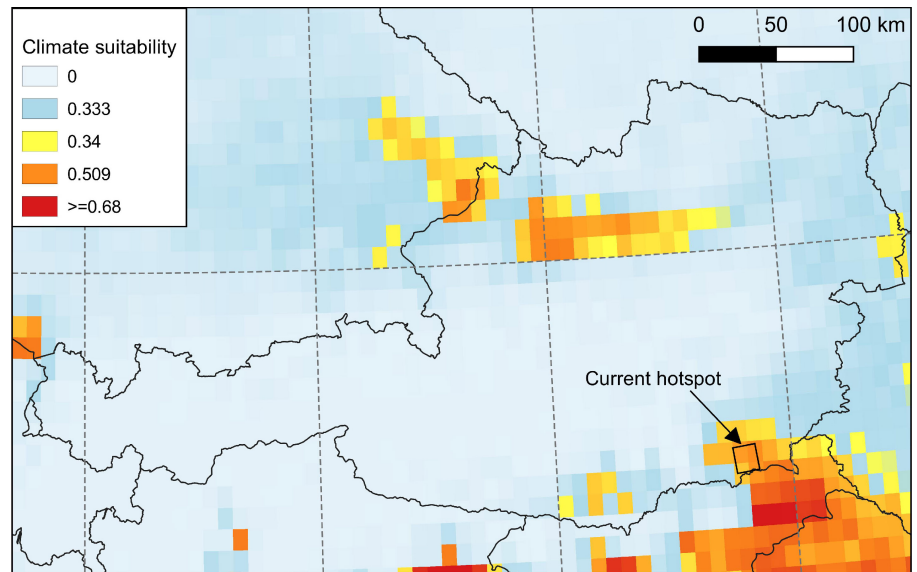


Figure 3. Projected suitability of *Solanum carolinense* establishment under current climate (1981–2010) in Austria. Yellow to red shading indicates suitability according to the selected threshold (≥ 0.34) (EPPO 2022a, adapted). The study area (Figure 1) is located in the marked grid cell.

(Gralla, Leibnitz) in the west and the forest area in the east (Figure 1). Further south, in the settlements of Landscha/Mur and Obervogau no populations were detected either, while east of the motorway, occurrences are much more scattered.

The results demonstrate that *S. carolinense* is in a phase of rapid local spread. The species has successfully established and become a significant weed in the last years in the study area. The region is intensively used for agriculture and thus, further expansion is likely due to the connectivity of this habitat. The spread within fields and from field to field is largely driven by agricultural machinery (Wehtje et al. 1987; Follak 2020). In addition, other non-agricultural habitats (including roadsides, ruderal grassland) are already invaded by *S. carolinense*, which could facilitate its spread further, as they may function as “stepping stones” for the infestation of surrounding crop fields. *Solanum carolinense* grows in a broad range of environmental conditions from semi shade to full sun and well drained to (seasonally) wet soils as shown by the relevés, allowing it to infest a variety of cropping systems and ruderal habitats in the study area. According to the SDM, the areas around the invasion hotspot are climatically suitable, so there is potential for further expansion in south-eastern Austria. A previous CLIMEX model, however, predicted more potential for establishment under current climate in Austria (Follak and Strauss 2010). In this respect, the prediction of the SDM for 2041 to 2070 under a moderate SSP1-2.6 climate change scenario, suggests an increase of the suitable area up to 33% of the territory of Austria (EPPO 2022a).

Infestation levels and agricultural impact

Although quantitative data on yield losses under Central European conditions is not available, the study indicated that individual fields were

very heavily infested and that significant yield losses were to be expected due to *S. carolinense*. This is especially the case for low-growing crops such as soybean and oil pumpkin (Figure 2). Studies from North America revealed that *S. carolinense* was not a strong competitor in maize (e.g. Whaley and Vangessel 2002). However, in the present study, our findings were different: high degrees of cover with presumed corresponding competitive effects could be observed (Figure 2d, Table 1). In North America, the species is particularly a common and troublesome weed in pastures and rangeland (Van Wyche 2020). Some infestations of grassland grown for fodder production were also detected in the study area. This is considered to be critical, as all parts of the plant are poisonous (Wahlert et al. 2015).

Implications for further monitoring and management

Regular surveys are necessary to determine the occurrence and spread of the species and a basis for this was established in this study. Monitoring should include areas close to known occurrences, which are most at risk of being invaded (Figure 3). Farmers should be made aware of the species so that they can take early action. That is of particular importance with *S. carolinense*, as established populations are considered difficult to control, because of its extensive root system and high regeneration capacity. According to data from North America, *S. carolinense* is only moderately susceptible to several herbicides and multiple applications and/or tank mixtures are required for adequate control in crops and pastures (e.g., Whaley and Vangessel 2002; Philips et al. 2016). Information on the mechanical and chemical control of *S. carolinense* is hardly available under the conditions in Austria and all over Central Europe (Klingenhagen et al. 2012).

The study shows that *S. carolinense* is locally naturalized in Austria and has already established numerous populations in the infested region. Thus, effective measures to stop the further spread of this emerging weed are needed to avoid future yield losses.

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Authors’ contribution

SF: conceptualization, data collection, wrote the manuscript, DC: species distribution modelling, designed map and reviewed the manuscript, MS: designed map and reviewed the manuscript, FE: data collection and reviewed the manuscript.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Floristic relevés: Recording date, habitat, plot size, habitat, exposition, altitude, coordinates and locality.

This material is available as part of online article from:

http://www.reabic.net/journals/bir/2023/Supplements/BIR_2023_Follak_et_al_SupplementaryMaterial.xlsx