Epilobium brachycarpum: a fast-spreading neophyte in Germany

Die schnelle Ausbreitung des Neophyten *Epilobium brachycarpum* in Deutschland

Thomas Gregor[1,2*], Dirk Bönsel[2], Indra Starke-Ottich[2],
Oliver Tackenberg[3], Rüdiger Wittig[3] & Georg Zizka[1,2,3]

[1]*Senckenberg Research Institute, Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, D-60325 Frankfurt/Main, Germany*
[2]*Senckenberg Research Institute, Department Botany and Molecular Evolution, Senckenberganlage 25, D-60325 Frankfurt/Main, Germany*
[3]*J.W. Goethe University, Department of Ecology and Geobotany, Institute for Ecology, Evolution and Diversity, Senckenberganlage 31–33, D-60054 Frankfurt am Main, Germany*
**Corresponding author, e-mail: thomas.gregor@senckenberg.de*

Abstract

Only a small proportion of introduced plant species become invasive and may eventually create ecological or economic problems. In many species it is still not clear which traits cause biological invasions. As a case study we focussed on the fast-spreading *Epilobium brachycarpum* in Central Europe to investigate the potential of this species to become a transformer or agricultural weed. We (1) documented the spread of the species in Central Europe, (2) modelled its range and (3) seed dispersal, (4) described its phytosociological alignment, (5) analysed the traits of invaded vegetation types, (6) described seed production, population densities and life cycle, (7) did competition and germination tests, and (8) drafted a risk assessment. Relevant traits and characteristics of *E. brachycarpum* are (i) formation of dense stands under ruderal conditions, (ii) high seed production, (iii) effective seed dispersal, (iv) high competitiveness on bare soils against other ruderal plants, and (v) ecological niche shift compared to its native range. We expect *E. brachycarpum* to settle in the Mediterranean, sub-Mediterranean and many parts of temperate Europe within the next decades in habitats strongly altered by human activities, especially open stands of the alliance *Sisymbrion*. We predict that *E. brachycarpum* will become a noxious weed in vineyards, and that it will also colonise vegetation of the alliances *Bidention* and *Carici-Epilobion*.

Keywords: invasive species, neophyte, *Sisymbrion*, transformer, weed

Erweiterte deutsche Zusammenfassung am Ende des Textes

1. Introduction

Epilobium brachycarpum is the sole member of *Epilobium* sect. *Xerolobium* (WAGNER et al. 2007) and is easily recognised by its short (15–30 mm) fruits and its annual lifecycle. Further features separating it from all other *Epilobium* species occurring in Central Europe are the peeling epidermis of the stem, the early shedding leaves and the seeds, which are constricted near the base and have a deciduous coma. The plants from this region present a small-flowered, self-pollinating form, though large-flowered outcrossing genotypes are known from the original range where the species is highly variable and several taxa have been named. *Epilobium brachycarpum* has a somatic chromosome number of 2n = 24, differing from the usual *Epilobium* number of 2n = 36; indeed, hybrids with other *Epilobium* species are not known. The species originates from Western North America, and its distribution extends from British Columbia in the northwest to California and Baja California in the southwest, from Saskatchewan and the Dakotas in the northeast to New Mexico in the southeast. It is a common plant and grows from sea level to altitudes of up to 3 000 m on dry soils in open or disturbed woodland, grassland, scree and along roadsides (HITCHCOCK et al. 1961, BALDWIN et al. 2012). The plant shows a ruderal strategy (after GRIME 1974), and is known as a weed in vineyards, olive groves and grapefruit plantations. *Epilobium brachycarpum* has been introduced to South America where it has been described since 1974 from Argentina (SOLOMON 1982) and is now widespread in the provinces of Chubut, Neuquén, Río Negro (ZULOAGA & MORRONE 1999) and Cordoba (herbarium voucher J.G. Seijo 2042 in MO), even extending to Chile (MACAYA & FAÚNDEZ 1998). Recently, *E. brachycarpum* has also reached New Zealand where it was recorded in the *Nothofagus* forest in the Canterbury region of the Ruataniwha Conservation Park (CHANDLER 2009).

Invasions by alien species can lead to environmental change, resulting in economic and biodiversity losses (WILLIAMSON 1996, MCNEELY et al. 2001). However, not every introduction develops into a threat to biodiversity, and it is still difficult to predict the invasive success of a species (MAILLET & LOPEZ-GARCIA 2000, but see RICHARDSON & REJMANEK 2004 for Pinopsida). The DAISIE project (LAMBDON et al. 2008) identified nearly 6 000 alien vascular plant species in Europe, including *E. brachycarpum* naturalised in France and Germany. In Central Europe, the great majority of the species listed in the DAISIE data base fit rather well into the existing ecosystems without altering them substantially or causing a serious decline in other taxa (for Poaceae see SCHOLZ 2011). Furthermore, many neophytes (post-1500 aliens) settle only in habitats not present in pristine landscapes, such as the saline verges of highways (e.g. REZNICEK & CATLING 1987 for *Carex praegracilis* in western North America; SCHNEDLER & BÖNSEL 1989 for *Atriplex micrantha* in Hesse/Germany).

The spread of *E. brachycarpum* in Europe offers the possibility to document an introduction from its earliest stages. Botanists became aware of the unfamiliar species while it was still very rare, and it has been arduously monitored since. However, these data are not based on systematic sampling (DELISLE et al. 2003). Only 20 years after its discovery in Central Europe, *E. brachycarpum* forms huge populations in wastelands in Germany (Fig. 1, Fig. 2). To evaluate the questions if *E. brachycarpum* has the potential to become a transformer, i.e. a plant that changes “the character, condition, form or nature of an ecosystem over a substantial area” (PYŠEK et al. 2004), in Central Europe or if there is a risk that it may become an agricultural weed, we focus on its invasion potential from different perspectives: (1) Reporting spread and current distribution in Central Europe; (2) modelling native and invaded range; (3) modelling seed dispersal; (4) documenting vegetation association in Central Europe; (5) estimating potentially suitable vegetation by comparison of traits of the alliances within the Central European vegetation system; (6) measuring seed production, population densities and life cycle; (7) testing germination and competition, and (8) drafting a risk assessment.

Fig. 1. Dense stand of dead *Epilobium brachycarpum* at a former main freight yard Frankfurt/Main, together with flowering *Senecio inaequidens* (October 2009).

Abb. 1. Dichter Bestand von abgestorbenem *Epilobium brachycarpum* auf dem ehemaligen Hauptgüterbahnhof in Frankfurt am Main zusammen mit blühendem *Senecio inaequidens* (Oktober 2009).

Fig. 2. Seedlings of *Epilobium brachycarpum* at the beginning of the 2-leaf-stage. Former main freight yard Frankfurt/Main (March 2010).

Abb. 2. Jungpflanzen von *Epilobium brachycarpum* am Beginn des 2-Blattstadiums. Hauptgüterbahnhof in Frankfurt am Main (März 2010).

2. Methods

2.1 Distribution in Central Europe

Data of the occurrence of *Epilobium brachycarpum* in Europe have been derived from several literature and internet sources as well as from personal communications. A detailed list of all of the included records is available from the corresponding author. The maps used in this study were produced using ArcGIS version 10.

2.2 Range modelling and modelling of seed dispersal

To establish the occurrence of *E. brachycarpum* in North America, records are derived from a variety of sources. Many of the occurrence data have been accessed through the Global Biodiversity Information Facility database (GBIF Data Portal, www.data.gbif.org). Furthermore, North American herbaria were screened, including ASU, COLO, CSU, NY, OSC, UBC and WTU (acronyms according to THIERS 2012). Altogether 1 330 records have been used for the Ecological Niche Modelling (ENM) of the North American range.

We computed the habitat suitability in order to analyse the current range of *E. brachycarpum* – that native to North America and the invaded range in Europe – using the programme MAXENT (PHILLIPS & DUDÍK 2008). As environmental variables we used altitude and a set of bioclimatic variables that characterise the current climate (1950–2000) and are frequently used in range modelling. These data were derived from the WorldClim global climate database (www.worldclim.org, HIJMANS et al. 2005). Using the 19 presented bioclimatic variables, we selected a subset of seven less-correlated variables (ELITH et al. 2006) which are related to species ranges in many studies: Annual Mean Temperature, Mean Diurnal Range, Temperature Seasonality, Mean Temperature of Warmest Quarter, Precipitation Seasonality, Precipitation of Wettest Quarter and Precipitation of Driest Quarter (for a similar approach see CUNZE et al. 2013). We also considered proportional estimates for the vegetation cover, namely herbaceous vegetation and bare ground (HANSEN et al. 2003a, b, c). We computed the ecological niche from the North American dataset, i.e. the ecological niche in the native range. Subsequently, we projected this niche to Europe – i.e. the adventive range – and compared this with the current occurrences. In MAXENT 30% of the species occurrence data was used as the test dataset, and the maximal number of background points was set to 10 000. We used only the linear features, product features and quadratic features for the development of the model.

The dispersal kernels were computed using the process based on the seed dispersal model PAPPUS (TACKENBERG 2003) and we followed the approach presented by TACKENBERG & STOECKLIN (2008): For each hour of one week with good weather conditions for long-distance wind we simulated 2 000 individual trajectories of diaspores. From these trajectories, we calculated a dispersal kernel, i.e. a frequency distribution of dispersal distances. *Epilobium brachycarpum* is characterized in the model by a release height of 0.4 m and a terminal velocity of the diaspores 0.14 m s^{-1}. Terminal velocity was measured on ten intact diaspores according to the LEDA-protocol (KNEVEL et al. 2005).

2.3 Phytosociological alignment and traits of alliances

We document the phytosociological alignment of *E. brachycarpum* by relevées from the Rhine-Main area and northern Bavaria made between 2004 and 2009 applying the Braun-Blanquet method (DIERSCHKE 1994). The size of the relevées varied between 4 and 25 m². The permanent plots were marked with metal bars. The nomenclature of the vascular plants follows BUTTLER & HAND (2008).

To identify alliances suitable for *E. brachycarpum,* we rated Central European alliances according to a rank scale of five (low to high) for the following factors: (1) water content of soil, (2) Ca^{+2} and Mg^{+2} content of soil or water, (3) nutrient content of soil or water, (4) environmental dynamics, (5) degree of hemeroby, (6) frequency of stress-tolerant species, (7) salt tolerance, (8) altitude, (9) height of vegetation, and (10) frequency of annual taxa. The information for the ratings was derived from synopses of the Central European vegetation (Austria: MUCINA et al. 1993a, b, GRABHERR & MUCINA 1993;

Czech Republic: CHYTRÝ 2007, 2009, CHYTRÝ et al. 2001; Germany: OBERDORFER 1977, 1978, 1983, 1992; The Netherlands: SCHAMINÉE et al. 1995, 1996, 1998, STORTELDER et al. 1999) and personal experience.

2.4 Seed production, population densities and life cycle

Seed production of 17 average sized plants was measured in September 2009 at three plots in Frankfurt/Main: i) a construction site at the Rebstock area (50.113969° N / 8.619522° E); ii) a former main freight yard (50.108432° N / 8.631333° E); and iii) a ruderal area near Leuna street east of the Industriepark Hoechst (50.086644° N / 8.552975° E). Per plant seed production of 20 well-developed fruits were measured. Abundance and proportion of plants browsed by European Rabbit (*Oryctolagus cuniculus*) were recorded in randomly chosen plots at the former main freight yard (4 m², September 2009, n = 11) and the Rebstock area (1 m², October 2009, n = 11). For eleven unbrowsed and six browsed plants we measured height and seed production. From October 2009 to September 2010, we observed the life cycle at the former main freight yard at marked plots of 1 m². Plots 1–3 were monitored from October 2009 to January 2010, when they were destroyed by building activity. Plot 4 was investigated from January to September 2010. Each month, we estimated vegetation cover of each species for the 1 m² plot. We also counted all plants and noted their individual phenological state in four marked subplots of 10 × 10 cm at each of the four plots.

2.5 Competition and germination tests

Germination was qualitatively tested in a common garden experiment using two types of soil: (i) garden soil (German: *Einheitserde*), and (ii) a mixture of 90% of pure sand with 10% garden soil. On 2 November 2010, 1 g of seeds of *E. brachycarpum* and of *Epilobium lamyi*, *Erigeron canadensis* and *Senecio inaequidens* (species often growing together with *E. brachycarpum*) was sown on two 40 × 40 cm^2 plots of both soil types to test the germination ability of these species. On plots of the same size and the same soils, mixtures of 1 g of *E. brachycarpum* and 1 g of one of the other species were sown to test for competition (two plots each). The seeds of each species represented a mixture of diaspores collected in October 2010 at three sites in and around Frankfurt.

For a competition test under greenhouse conditions from 2 February until 7 August 2010, we used the same soil types and seed mixtures as mentioned above. The cotyledon phase of one individual of *E. brachycarpum* and one of the other species (*E. lamyi*, *Senecio inaequidens*), respectively, were planted in pots of 4 × 4 cm^2 surface, with 20 pots of each combination.

To test the germination ability of submerged seeds in the greenhouse, in February 2010, we densely (1g/pot) sowed *E. brachycarpum* into two pots (surface 10 × 30 cm^2) with garden soil and flooded one pot with 2 cm and the other pot with 6 cm of water. To test the survival of the periodically flooded seedlings, we flooded two identical pots densely covered with seedling (cotyledon phase, plant height less than 1 cm) with 2 or 6 cm of water. In all cases, we gradually removed the water after 4 weeks so that, after one more week, the soil was approximately as humid as the soil of the above-mentioned pot experiments. In another experiment, 25 seeds collected in September of 2010 in Frankfurt/Main were continuously covered with 5 cm of water from 22 December 2011 until March 2012.

2.6 Risk assessment

Factors for the prediction of the invasiveness of aliens in agricultural ecosystems have been derived from MAILLET & LOPEZ-GARCIA (2000). They identified the weed status in the native distribution area as the best predictor. Further important characteristics are an occurrence in ruderal habitats, annual life form and C_4 photosynthetic pathway. Other criteria positively linked to invasiveness and often found for agricultural weeds are belonging to a "weedy family", such as Poaceae or Asteraceae, a high seed production and wind dispersal of the seeds.

3. Results

3.1 Spread and current distribution in Central Europe

In Germany, the first records originated from Rhineland-Palatinate in Southwest Germany: in 1994, the species was found at a rhyolite pit near an area of the US army near Kirchheimbolanden (LANG & WOLF 2000) and in sandy fields near Ingelheim in 1995 (DECHENT & BAUM 2003). No further records were detected until 1999, when the species was found in the neighbouring state of Hesse near Wiesbaden and spread continuously from this location (BÖNSEL & OTTICH 2005). In 2002, a second centre of invasion was found in northern Bavaria (HÖCKER & HETZEL 2007). The spread continuously increased until 2008 but appears to have slowed down since (Fig. 3). According to our literature survey, the early records in Germany came from various habitats (i.e. stone or sand pit, ruderal site in city, soil deposit, commercial area, agricultural field, harbour, garden, xerophytic grassland, forest and military area). Later, railway areas became an important habitat (Fig. 4). Agricultural fields or xerophytic grassland, sites where the species might become problematic, are only rarely colonised thus far. In Central Europe, rather isolated distribution centres exist in Germany, France and northern Spain (Fig. 5). In the range centred in the Rhine-Main area the distance from the range centre to its present limits is approximately 150 km in 2011 (Fig. 6). The extension of the distribution in the Rhine-Main area is calculated to be approx. 8 km yr^{-1}.

3.2 Range modelling and seed dispersal

In the Ecological Niche Modelling (ENM) for the native area (Fig. 7a) temperature seasonality, annual mean temperature, annual precipitation and precipitation of the driest quarter were the most important variables affecting the distribution of *Epilobium brachycarpum*. When using the niche derived from the North American data for predicting habitat suitability in Europe, the Mediterranean region revealed the highest values, whereas the habitat suitability in North-Western and Central Europe was predicted to be rather low (Fig 7b).

Epilobium brachycarpum seeds are effectively adapted to wind dispersal. Their low fall velocity of 0.14 m s^{-1} allows effective wind dispersal, even over long distances. In our simulations, 12% of the seeds were dispersed over more than 100 m, and 10% even had the potential to be dispersed over several kilometres (Fig. 8).

3.3 Phytosociological alignment

The analysis of 69 vegetation relevées (Table 1 in the supplement) from northern Bavaria (HÖCKER & HETZEL 2007) and the Frankfurt/Main area in Hesse (2004, 2007 and 2008) reveals a pronounced preference of *E. brachycarpum* for short-lived ruderal communities. In Germany the species is a pioneer species of disturbed soils. The taxa most often associated with *E. brachycarpum* (co-occurrence rates > 35%) were *Erigeron canadensis*, *Lactuca serriola*, *Tripleurospermum perforatum*, *Daucus carota*, *Taraxacum* sect. *Ruderalia* and *Apera spica-venti*. The habitats are typically open, poor in fine earth, rather dry and warm, nutritious and base poor. These are young ruderal habitats, which are found on fallow land, pits, landfills, soil deposits and railroad areas. In 71% of the relevées, the vegetation can be assig-ned to the *Sisymbrietalia* J. Tx. in Lohmeyer et al. 1962 and the *Sisymbrion* Tx. et al. in Tx. 1950, mostly to the *Erigeronto-Lactucetum serriolae* Lohmeyer in Oberd. 1957. One relevée from Bavaria can be attributed to the association *Bromo-Corispermetum leptopteri* Sissingh 1950*.* Some 6% of the relevées belong within the *Dauco-Melilotion* Görs ex Gutte

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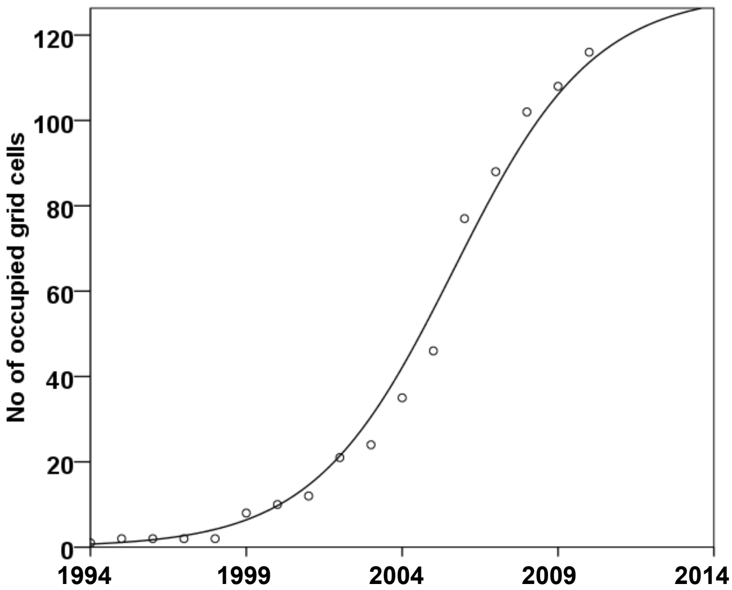

Fig. 3. The cumulative number of grid records (approx. 12 × 11 km) for *Epilobium brachycarpum* in Germany during 1994–2010 (dots) can be described by a logistic growth function (R^2 = 0.98).

Abb. 3. Kumulierte Zahl der Nachweise in TK25-Karten (ca. 12 × 11 km) von *Epilobium brachycarpum* in Deutschland 1994–2010 (Punkte) beschrieben als logistische Wachstumsfunktion (R^2 = 0.98).

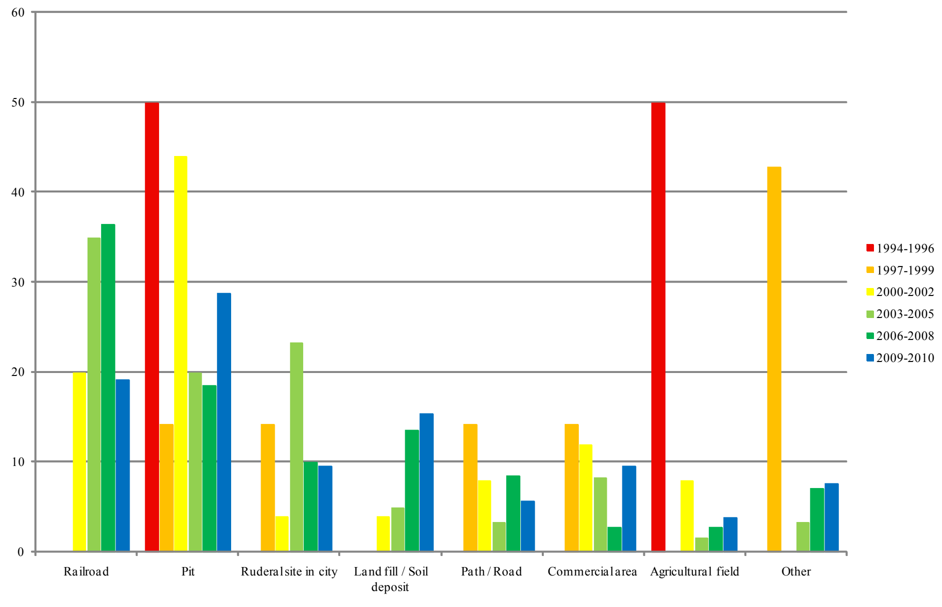

Fig. 4. Percentages of the records of *Epilobium brachycarpum* from Germany for the different colonised habitats.

Abb. 4. Anteile der Nachweise von *Epilobium brachycarpum* in Deutschland in den besiedelten Habitaten.

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1972 to the *Berteroetum incanae* Sissingh et Tideman in Sissingh 1950 or *Tanaceto-Artemisietum vulgaris* Br.-Bl. 1931 corr. 1949. *Epilobium brachycarpum* often reaches a high coverage: in 19% of the relevées, the dominance of *E. brachycarpum* is documented, with the stands nearly lacking any other species.

In the course of succession, vegetation types dominated by *E. brachycarpum* transform to more or less dense vegetation (Table 1, relevées 54–56), including woody plants, and the annual *E. brachycarpum* begins to disappear. This was observed, e.g. in the Messel pit fossil site south of Frankfurt/Main. At this site, the vegetation of the *Sisymbrion* rich in *E. brachycarpum* was replaced by vegetation dominated by *Arrhenatherum elatius*; *E. brachycarpum* is found there only occasionally and with reduced vitality. Table 2 shows the alliances whose traits have a similarity of at least 50% with the traits of the *Sisymbrion*.

3.4 Seed production, population densities and life cycle

The seed production per fruit was rather stable and varied between 14 and 30 seeds, with a mean of 24.1 (± 3.1 SD). The number of fruits per plants was more variable, ranging from 206 to 1 034, with a mean of 579 (± 325 SD). Thus, the seed production per plant varied from 3 316–27 246, with a mean of 14 522 (± 8 884 SD). The abundance of fruiting plants varied in 22 plots between ten and 126 plants per 1 m², with an average of 45.8 (± 27.5 SD) plants per m². Seed production per m² is therefore about 665 000. For the 48 ha of the former main freight yard, this would mean the enormous seed production of approximately 31.9×10^{10} seeds for 2009.

21% of the plants at the former main freight yard were browsed by European Rabbit, whereas the proportion was 33% in the Rebstock area. Browsing did not reduce seed production. Browsed plants (n = 6), which generally developed higher numbers of branches, even had a higher seed production than unbrowsed plants (n = 11) with means of 17 963 (± 9 443 SD) versus 12 646 (± 8 409 SD) seeds per plant. Herbivory by insects was not obvious.

Vegetation cover for the plots 1-3 and 4, monitored between October 2009 to September 2010 and between January to September 2010, is given in Tables 3 and 4. The inundation of plot 1 during November and December 2009 did not markedly influence the coverage of *E. brachycarpum.* Percentages of development stages of *E. brachycarpum* gained from the subplots are shown in Table 5. The germination begins in September and continues until December, with the latest observations in March. In subplots of plot 4, we observed an increase in seedling number per 100 cm² from 220 to 400 and 100 to 230 between February and March. The number of seedlings and young plants can be very high, and the *E. brachycarpum* seedlings can cover the ground in more than one layer with 100% coverage. On 1 January 2010, we counted in the twelve permanent subplots of 10×10 cm^2 size an average of 299 (± 266 SD; min. 80, max. 1 000) seedlings, amounting to approximately 7 475 seedlings per m². But numbers can be even higher near mother plants and the distribution of the seedlings is extremely patchy. A pronounced heat period occurred during July and August 2010, killing nearly all of the plants (Fig. 9).

3.5 Germination tests and competition tests

In the common garden experiment, *E. brachycarpum* was the only species that germinated on garden soil and a mixture of sand and garden soil by November 2010. The flooding of the seeds or seedlings did not harm the plants. The seedling cover was as dense as in the

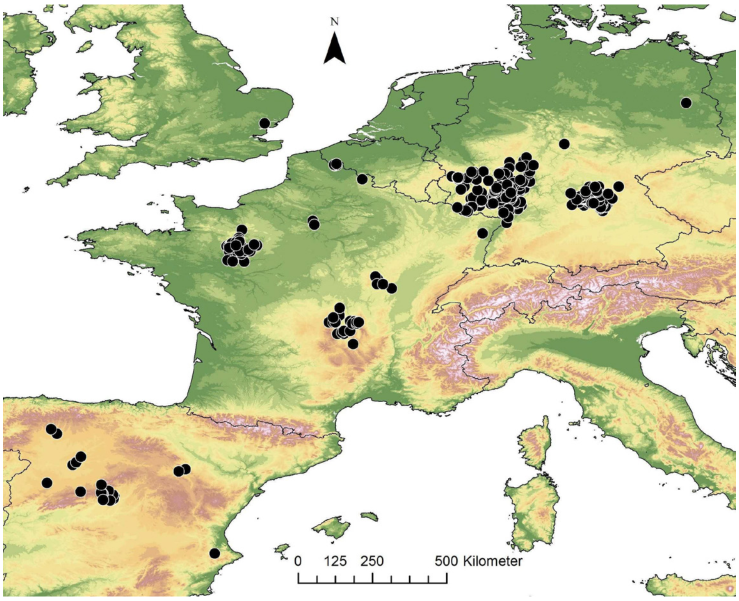

Fig. 5. Records of *Epilobium brachycarpum* in Europe during 1978–2011.

Abb. 5. Nachweise von *Epilobium brachycarpum* in Europe 1978–2011.

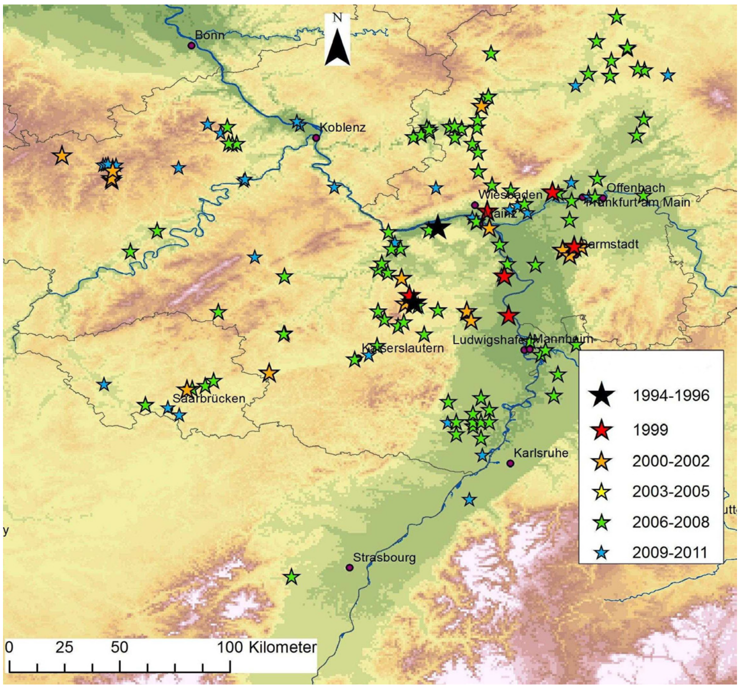

Fig. 6. Records of *Epilobium brachycarpum* centred in the Rhine-Main area during 1994–2011 and divided into classes according to the time of recording.

Abb. 6. Nachweise *von Epilobium brachycarpum* in Zeitklassen zwischen 1994–2011, die mutmaßlich zum Verbreitungszentrum Rhein-Main-Gebiet gehören.

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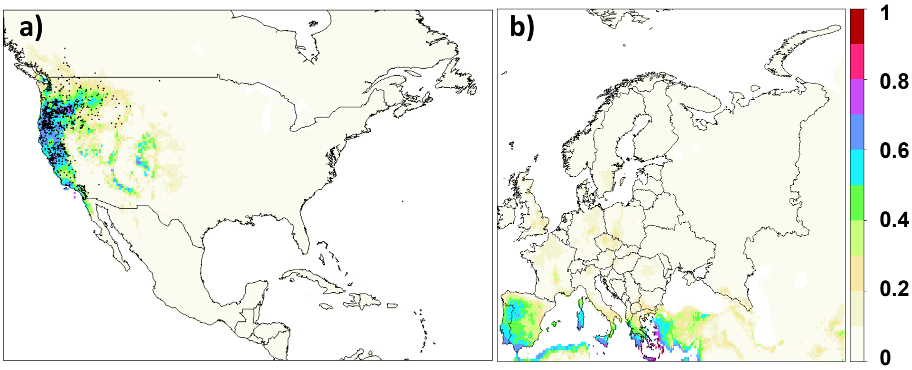

Fig. 7. Habitat-Suitability for *Epilobium brachycarpum* in North America (a) and Europe (b) derived from Ecological Niche Modelling. The habitat suitability map for Europe is derived from the niche postulated from the North-American data. Black dots: occurrences for the model based on AUC = 0.94.

Abb. 7. Habitateignung von *Epilobium brachycarpum* in Nordamerika (a) und Europe (b) nach Ecological Niche Modeling. Die Habitateignung für Europa wurde nach der aus den nordamerikanischen Daten postulierten Nische errechnet. Die schwarzen Punkte geben die Funde an, auf denen die Modelbildung beruht (AUC = 0.94).

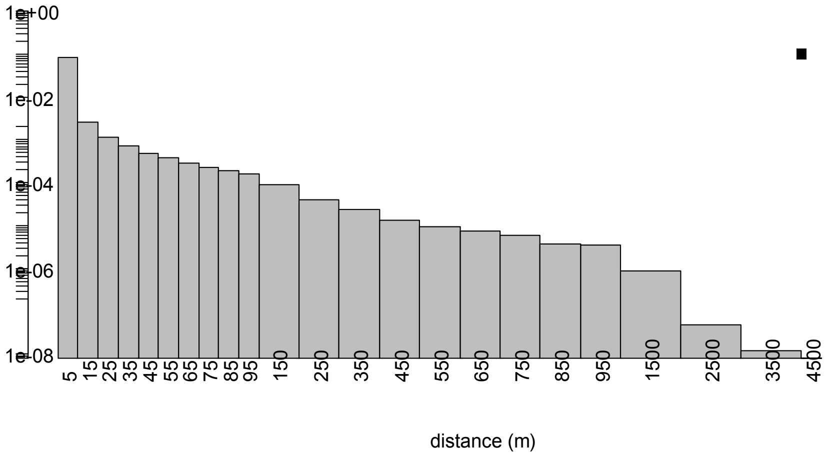

Fig. 8. Dispersal kernels showing the proportion of seeds landing in distinct distance intervals. An additional 10% of the diaspores may be dispersed over several kilometres (cf. black dot).

Abb. 8. Anteile der Samenausbreitung in Entfernungsintervallen. 10% der Samen können zusätzlich über mehrere Kilometer verbreitet werden (schwarzer Punkt).

unflooded garden experiments. After 2–3 days (water level 2 cm) or 6–8 days (water level the submerged young plants emerged, and all of the submerged plants survived and flowered in July. Twenty three of 25 seeds covered with 5 cm of water from 22 December 2011 until 3 January 2012 germinated, and the young plants with epicotyls of 2–3 cm floated on the water. Eleven floating plants survived until 27 January 2012 and seven plants until 10 February 2012. All of the plants had died by 12 March 2012.

Table 2. Alliances of the Central European phytosociological system which correspond in the traits W (water availability), C/M (availability of calcium and magnesium), N (availability of nutrients), D (environmental dynamics), Hem (hemeroby), St (stress resistance), Salt (availability of sodium or potassium salts), Al (altitude), Hei (plant height) and An (occurrence of annuals) at least with a similarity of 50% with the *Sisymbrion*. ART = *Artemisietea*, BID = *Bidentetea*, IS-NA = *Isoëto-Nanojuncetea*, MO-AR = *Molinio-Arrhenatheretea*, PO-PO = *Polygono-Poëtea,* STE = *Stellarietea*. × = trait value identical to *Sisymbrion*.

Tabelle 2. Verbände des mitteleuropäischen pflanzensoziologischen Systems die in den Zeigerwerten für W (Wasserverfügbarkeit), C/M (Verfügbarkeit von Calcium und Magnesium), N (Verfügbarkeit von Nährstoffen), D (Umweltdynamik), Hem (Hemerobie), St (Stress Resistenz), Salt (Verfügbarkeit von Natrium- oder Kalium-Salzen), Al (Meereshöhe), Hei (Pflanzen-Höhe) und An (Häufigkeit von einjährigen Arten) mindestens eine Ähnlichkeit von 50 % mit dem *Sisymbrion* aufweisen. ART = *Artemisietea*, BID = *Bidentetea*, IS-NA = *Isoëto-Nanojuncetea*, MO-AR = *Molinio-Arrhenatheretea*, PO-PO = *Polygono-Poëtea,* STE = *Stellarietea*. × = Zeigerwert identisch mit *Sisymbrion*.

Alliance (Class)	W	C/M	N	D	Hem	St	Salt	Al	Hei	An	Similarity with *Sisymbrion*
Sisymbrion (STE)	2	3	4	5	5	1	2	3	2	5	
Digitario-Setarion (STE)	×	2	×	×	×	×	1	2	×	×	70%
Caucalidion platycarpi (STE)	×	5	3	×	×	×	1	×	×	×	70%
Salsolion ruthenicae (STE)	×	×	3	×	×	×	4	2	×	×	70%
Dauco-Melilotion (ART)	×	×	5	4	×	×	1	×	×	4	60%
Fumario-Euphorbion (STE)	3	4	5	×	×	×	1	×	×	×	60%
Lolio-Plantaginion (MO-AR)	3	×	×	×	×	4	×	×	1	3	60%
Chenopodion rubri (BID)	4	×	5	×	1	×	×	2	×	×	60%
Bidention tripartitae (BID)	4	×	5	×	1	×	1	×	×	×	60%
Aperion spicae-venti (STE)	3	2	3	×	×	×	1	2	×	×	50%
Polygono-Chenopodion polyspermi (STE)	3	2	5	×	×	×	1	2	×	×	50%
Arction lappae (ART)	3	×	5	4	×	×	1	×	×	4	50%
Saginion procumbentis (PO-PO)	3	×	×	×	×	3	3	×	1	3	50%
Convolvulo-Agropyrion repentis (ART)	3	×	×	4	×	2	3	×	×	3	50%
Nanocyperion flavescentis (IS-NA)	4	×	×	×	1	×	1	2	1	×	50%
Galio-Alliarion (ART)	4	×	×	3	3	×	1	×	×	3	50%
Digitario-Setarion (STE)	×	2	×	×	×	×	1	2	×	×	50%

The winter of 2010/2011 was unusually cold and characterised by long-lasting snow cover (end December until early February). Nevertheless, *E. brachycarpum* survived these conditions. On the plots without competition, the three other species did not germinate earlier than the beginning of April. On the competition plots, only a few individuals of the other species sown together with *E. brachycarpum* germinated in April at the margins of the plots. Within the dense stands of *E. brachycarpum* already present since November 2011, no germination of the other species was observed. In the competition tests, *E. brachycarpum* grew significantly higher than *Senecio inaequidens* and *Epilobium lamyi* on both the garden soil and sand (Fig. 10). Moreover, on garden soil, 90% of the individuals of *E. brachycarpum* flowered at the end of the experiment; contrastingly, of the competing species only 35% (*Senecio inaequidens*) and 15% (*E. lamyi*) of the individuals developed flowers. On sand, only individuals of *E. brachycarpum* (45%) came into flower.

3.6. Risk assessment

Epilobium brachycarpum has the following traits which give a positive prediction of invasiveness in agricultural ecosystems: (1) weed status in the native distribution area, (2) occurrence in ruderal habitats, (3) annual life form, (4) high seed production, (5) buoyancy of seeds, (6) high migration capacity by wind dispersal, (7) expansive spread, and probably (8) benefit from climate change. *Epilobium brachycarpum* does not belong to a problematic family with many invasive taxa and does not use the C_4 photosynthetic pathway.

4. Discussion

4.1 Spread and current distribution in Central Europe

As far as we can reconstruct, a phase of rare introductions (see ESSL et al. 2009, RICHARDSON et al. 2000) did not occur for *Epilobium brachycarpum.* Furthermore, we have no information about the pathway of introduction into Central Europe according to the categories applied by HULME et al. (2008). Most likely, it was not a release or an escape of a commodity, but it might have been a contaminant of a commodity or a stowaway.

In Germany, the phase of local establishment occurred circa 1994–1998; 1999–2001 were years of regional naturalisation. Since about 2002, the species became invasive according to the definition of PYŠEK et al. (2004). However, the expansion seems to have slowed down since 2008 (Fig. 1). Considering the dispersal capacity of the species, we believe that new centres of occurrences outside the present distribution range will appear soon and then serve as starting points for the rapid colonisation of adjacent areas. The lag phase that is observed in many invaders (KOWARIK 2010) is not apparent in that species, but short-term introduction may have passed unnoticed.

The spreading rate of about 8 km yr^{-1} corresponds to the 9.1 km yr^{-1} observed for *Epilobium ciliatum* in England (WILLIAMSON et al. 2003). Provided with a persistent spreading rate, *E. brachycarpum* should reach the Swiss border in the Rhine Valley about 2030 and the north-eastern border of Germany in 2080. Nevertheless, the recently isolated records from Alsace, Northern Hesse and Brandenburg suggest a much more rapid spread from the newly established foci (see above). In Eastern Europe, with its more continental climate, the conditions for this autumn-germinating plant are less favourable, possibly limiting the expansion of *E. brachycarpum* toward the east.

The vicinity of the early records of *E. brachycarpum* in Rhineland-Palatinate and Hesse to the installations of the US army suggested a connection with transatlantic military transports. An introduction by mining machinery from Canada seemed probable for the first record in France from a stone pit near Vouré (dép. Mayenne) (MAGNANON 1995). Based on the studies of the expansion in Central Europe, at least two ways of long-distance dispersal currently seem feasible: (i) transports between pits by lorries serving several adjacent pits, and (ii) distribution by rail. The banded records along railway lines (Fig. 4) are a strong indicator for the second presumption.

Table 3. Vegetation of permanent plots 1–3 (all 1 m²) at the former main freight yard in Frankfurt/Main (1- 50.108795° N / 8.634731° E, grus; 2- 50.108697° N/ 8.635067° E, sand and grus; 3- 50.108356° N, / 8.635279° E, gravel).

Tabelle 3. Vegetation der Dauerflächen 1–3 (jeweils 1 m²) auf dem ehemaligen Hauptgüterbahnhof in Frankfurt am Main (1: 50,108795° N / 8,634731° E, Grus; 2: 50,108697° N/ 8,635067° E, Sand und Grus; 3: 50,108356° N, / 8,635279° E, Schotter).

	plot 1			plot 2			plot 3		
Date	13.10. 2009	25.11. 2009	01.01. 2010	13.10. 2009	25.11. 2009	01.01. 2010	13.10. 2009	25.11. 2009	01.01. 2010
Height (cm)	30	30	30	70	70	70	130	130	130
Cover higher plants (%)	25	10	7	5	2	2	15	15	10–15
Cover mosses (%)	10	10	10	0	0	0	0	0	0
Epilobium brachycarpum	2a	2a	2a	1	+	1	2a	2a	2a
Senecio inaequidens	2a	2a	+	+	+	+	2a	2a	1
Digitaria sanguinalis subsp. *sanguinalis*	2a		+	+					
Erigeron canadensis	+	+	r	+					
Dittrichia graveolens	1		+						
Epilobium spec.	r								
Convolvulus arvensis	r								
Populus spec.	r								
Taraxacum sect. *Ruderalia*	r								
Salsola tragus				+			+		
Lepidium densiflorum				r					
Senecio viscosus							+		
Anchusa officinalis							r		
Bromus tectorum							r	r	+
Bryum bicolor	2a	2a	2a						

Considering the original distribution area in America and assuming niche conservatism, one might expect a more rapid spread in the Mediterranean region (see Fig. 5); however there is no support for this hypothesis to date. Following its first recorded appearance in 1978 in Madrid (Izco 1983), *E. brachycarpum* is now widespread in the Madrid area and has started to expand to the adjacent Ávila province (Muñoz 2009). However, *E. brachycarpum* is still a rare plant in the Iberian Peninsula and has not yet been found in Portugal; neither is it known from Morocco.

From the Madrid area, Rivas-Martínez et al. (2002) described the association *Epilobio brachycarpi-Chenopodietum opulifolii* Rivas-Martínez & Izco 2002 with *E. brachycarpum* as the characteristic species. This association is rich in annual species and grows on dry ruderal sites on urban waste and altered siliceous sandy soils. The *Epilobio brachycarpi-Chenopodietum opulifolii* is classified as a member of the *Chenopodion muralis* Br.-Bl. 1936. This Mediterranean alliance is close to the *Sisymbrion*. Therefore, it seems that, also in Spain, *E. brachycarpum* has not yet colonised farmland or (semi)natural vegetation.

Table 4. Vegetation of permanent plot 4 (1 m²) at the former main freight yard in Frankfurt/Main (50.106906° N / 8.634465° E, grus and gravel).

Tabelle 4. Vegetation der Dauerfläche 4 (1 m²) auf dem ehemaligen Hauptgüterbahnhof in Frankfurt am Main (50,106906° N / 8,634465° E, Grus und Schotter).

	24.02. 2010	31.03. 2010	27.04. 2010	27.05. 2010	30.06. 2010	29.07. 2010	01.08. 2010	30.08. 2010
Species (n)	13	14	16	10	11	7	7	8
Cover higher plants (%)	20	20	25	25	30	30	60	65
Cover mosses (%)	15	10	5	10	5	10	20	25
Epilobium brachycarpum	2b	2b	2b	2b	2a	2a	2b	1
Medicago lupulina	+	+	+	1	2a	2a	3	4
Erigeron canadensis	+	+	+	+	+	1	1	1
Senecio inaequidens	1	+	+	+	+	+	+	1
Arenaria serpyllifolia	+	+	+	2m	2m			
Poa annua	+	+	+	+	+			
Epilobium spec.	+	+	+		+			
Draba verna	+	+	+					
Geranium spec.	+	+						
Poaceae indet.	+	+						
seedling indet.	+							+
Dittrichia graveolens	+							
Setaria viridis	+							
Sagina micropetala		+	+					
Saxifraga tridactylitis		+	+					
Festuca spec.		+	+					
cf. *Melilotus*		+						
Cerastium spec.			+					
Acer spec.			r	r				
Populus spec.			r	r	r			
Plantago arenaria			+	+	+	+	+	+
Vulpia myuros			+	+	+			
Tortula spec.	x							
Bryum argenteum	x	x						
Bryum bicolor	x	x						
Barbula unguiculata	x	x						
Bryum caespiticium	x	x						
Ceratodon purpurens	x	x						
Funaria hygrometrica		x						

4.2 Range modelling and seed dispersal

The potential distribution area projected by ENM corresponds quite well with the realised range in the native area of the species. Looking at Europe, we see a different picture: the ENM based on the distribution and environmental data from North America identifies Mediterranean Europe as most suitable for the species. Surprisingly, most parts of Northwestern and Central Europe are characterised by very low habitat suitability (Fig. 5). One possible explanation for this mismatch is that the ecological niche has changed, which has been

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proven several times for invasive species (BROENNIMANN et al. 2007). However, we can only speculate if a new infraspecific taxon has evolved in Europe. This interesting question deserves further detailed molecular studies and reciprocal transplantation experiments.

Niche expansion or shift during the invasion process has been observed for such aggressive neophytes as *Ambrosia artemisiifolia* (ESSL et al. 2009, but see also CUNZE et al., in print), and a shift of the habitat preference is already apparent in *E. brachycarpum*. Although *E. brachycarpum* in Central Europe was not initially observed in railway areas (Fig. 2), this changed dramatically from 2001 and thereafter: railway areas became the most observed habitat, offering excellent opportunities for dispersal. This observed difference is not necessarily the result of niche expansion but might be due simply to the delayed colonisation of suitable habitats, which are well linked by transport opportunities. The projection of further development and dispersal is hardly possible and makes risk analyses of biological invasions so difficult (RUIZ & CARLTON 2003).

If we take into account that the climatic niche, which the neophyte *E. brachycarpum* has realised in Central Europe, is near the (low) temperature limits of the niche realised in North America, we can assume that the species will benefit in Central Europe from the expected climate change. Most important for the expansion and persistence of *E. brachycarpum* in Europe will be the continuous human impact that regularly provides suitable habitats.

Epilobium brachycarpum seeds are effectively adapted to wind dispersal, even over distances of several kilometres. Huge populations as they form e.g. in abandoned railway areas probably function as source population for several square kilometres. In 2009/2010, odd *E. brachycarpum* plants in paving slabs could be regularly found 1–2 km away from the former main freight yard in the densely populated Frankfurt/Main-Bockenheim.

4.3 Phytosociological alignment

The similarities in the ecological classification of the *Sisymbrion* and other Central European alliances provide some probability that *E. brachycarpum* will be able to invade various types of farmland appropriate for its annual life form. Vineyards, where societies of the *Veronico-Euphorbion* Sissingh ex Passarge 1964 are common, seem to be suitable like several types of ruderal vegetation of the *Artemisietea vulgaris* Lohmeyer et al. ex von Rochow 1951 and the *Stellarietea mediae* Tx. et al. ex von Rochow 1951.

Habitats which also might be suitable for *E. brachycarpum* are societies of the *Carici piluliferae-Epilobion angustifoliae* Tx. 1950. *Epilobium brachycarpum* is common in early succession of clear-cuts in *Pseudotsuga menziesii*-forests in the western Cascades (GEYER 1995, HALPERN 1989, HALPERN et al. 1997). Like in its ruderal habitats in Central Europe, it co-occurs here with *Erigeron canadensis*.

Ruderal stands of the *Sisymbrion* change after invasion of *E. brachycarpum* from rather open habitats with sparse plant cover due to mass occurrence of *E. brachycarpum* to rather dense habitats. Shortly after invasion such habitats became unsuitable as nesting sites for the Little Ringed Plover (*Charadrius dubius*) caused by the density of the *E. brachycarpum* stands (personal observations in Frankfurt/Main). Nevertheless, according to the data, the transformation of the habitats – typically of the pioneer type – by *E. brachycarpum* occurs only for a limited number of years. Thereafter, *E. brachycarpum* is outcompeted by the typical (perennial and taller) elements of succession in these habitats, e.g. *Arrhenatherum elatius*, *Calamagrostis epigejos* or *Tanacetum vulgare* (Table 1). As the species is able to grow in wetlands in its native distribution area (RIEFNER & BOYD 2007), we conclude that

Table 5. Individual development of *Epilobium brachycarpum* at plot 4; mean of four subplots of 10 cm × 10 cm. The standard deviation is shown in brackets, the proportion of classes as a percentage.

Tabelle 5. Entwicklung von *Epilobium brachycarpum* auf Dauerfläche 4; Durchschnitt von vier Teilflächen von jeweils 10 cm × 10 cm. Standardabweichung in Klammern; Klassenanteile in Prozent.

	Seedling	2 leaf pairs	3–4 leaf pairs	< than 5 cm	5–10 cm	10–20 cm	20–40 cm	Dead	Total plants
13.10.2009	1								102 (± 137 SD)
25.112009	1								115 (± 78 SD)
01.01.2010	1								299 (± 256 SD)
24.02.2010	1								280 (± 153 SD)
31.03.2010	1								273 (± 87 SD)
27.04.2010	0.33	0.33	0.33						190 (± 71 SD)
27.05.2010	0.16	0.53	0.33						128 (± 31 SD)
30.06.2010				0.25	0.65	0.1			93 (± 33 SD)
29.07.2010				0.43	0.44	0.13			35 (± 33 SD)
01.08.2010						0.32	0.07	0.61	12 (± 11 SD)
30.09.2010	0.3					0.39		0.31	14 (± 18 SD)

temporarily wet habitats, which are the typical habitats of many other *Epilobium* species, will be colonised in Europe. The long survival of the seedlings under flooding conditions shown by our experiments supports this hypothesis.

4.4 Seed production, population densities and life cycle

As in the western Cascades in Oregon (GEYER 1995, HALPERN 1989), *E. brachycarpum* produces large amounts of windborne seeds between July and September. Germination occurs predominantly during fall, plants overwinter as seedlings, and early fall. *Epilobium brachycarpum* probably does not form a seed bank. The seedlings show a remarkable resilience against flooding, which they tolerate for several weeks. Disturbance seems to increase reproduction generally, in Frankfurt by browsing of rabbits in Oregon by artificial soil disturbance.

Densities in Central Europe of up to 126 fruiting plants per m² are in the lower part of the range known from clear cuts in the Western Cascades (GEYER 1995) where *E. brachycarpum* can reach densities of up to 367 fruiting plants per m² and even 575 plants per m² in plots with removal of competitors, but seed production per plant is drastically higher in Frankfurt compared to Oregon. We measured a mean of 14 522 (± 8 884 SD) per

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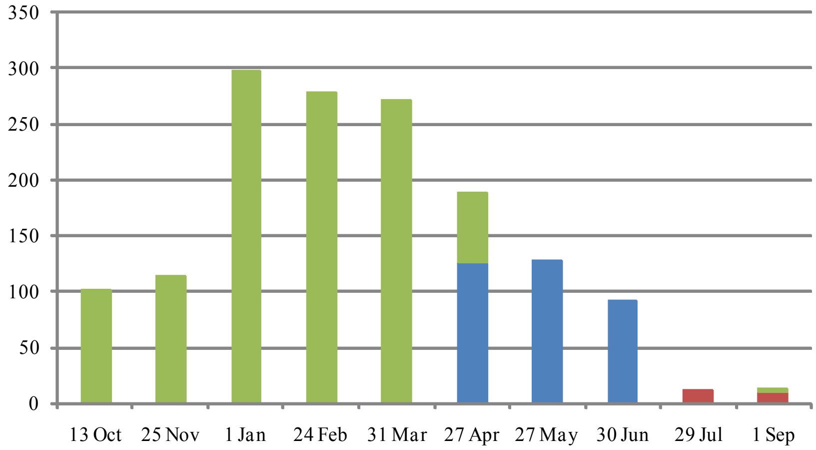

Fig. 9. Mean number of *Epilobium brachycarpum* plants at different developmental stages in subplots of 10 × 10 cm at the former main freight yard in Frankfurt/Main. Data from October 2009 to January 2010 from plots 1–3, those for the other months from plot 4. Green = seedlings, blue = sterile plants, red = flowering or fruiting plants.

Abb. 9. Durchschnittliche Anzahl von *Epilobium-brachycarpum*-Pflanzen verschiedener Entwicklungsstadien auf Teilflächen von 10 × 10 cm auf dem Hauptgüterbahnhof in Frankfurt am Main. Daten wurden zwischen Oktober 2009 und Januar 2010 auf den Dauerflächen 1–3 und für die anderen Monate auf der Dauerfläche 4 erhoben. Grün = Keimlinge, blau = sterile Pflanzen, rot = blühende oder fruchtende Pflanzen.

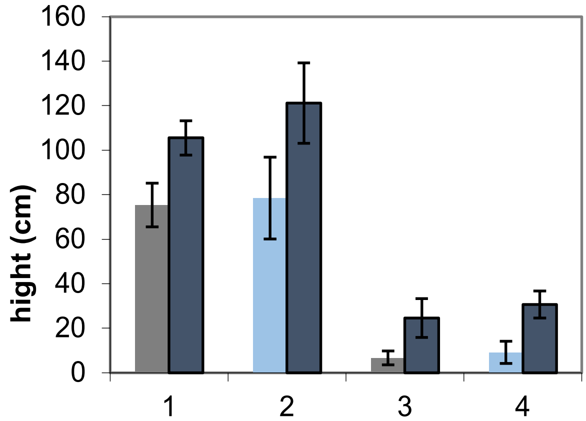

Fig. 10. Competition tests under greenhouse conditions, 2 February to 7 August 2010. 1: *Senecio inaequidens* (grey) and *Epilobium brachycarpum* (dark blue) in garden soil. 2: *Epilobium lamyi* (middle blue) and *Epilobium brachycarpum* (dark blue) in garden soil. 3: *Senecio inaequidens* (grey) and *Epilobium brachycarpum* (dark blue) in sand. 4: *Epilobium lamyi* (middle blue) and *Epilobium brachycarpum* (dark blue) in sand.

Abb. 10. Konkurrenztests unter Gewächshausbedingungen vom 2. Februar bis zum 7. August 2010. 1: *Senecio inaequidens* (grau) und *Epilobium brachycarpum* (dunkelblau), auf Gartenerde. 2: *Epilobium lamyi* (mittelblau) und *Epilobium brachycarpum* (dunkelblau) auf Gartenerde. 3: *Senecio inaequidens* (grau) und *Epilobium brachycarpum* (dunkelblau) auf Sand. 4: *Epilobium lamyi* (mittelblau) *und Epilobium brachycarpum* (dunkelblau) auf Sand.

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plant, GEYER (1995) gives figures of just 31–109 seeds per plant in clear cuts and of a maximum of 4 034 seeds per plant for a greenhouse experiment with one plant per pot. We also found higher numbers of seeds per fruit (24.1 ± 3.1 SD) compared to Oregon (8–10 in clear cut, 14–15 in greenhouse) and of fruits per plant: 579 (± 325 SD) compared to 8–21 in clear cuts and 198–278 in greenhouse. Increased sexual reproduction is a common feature among invasive plants (e.g. BECKMANN et al. 2009).

Epilobium brachycarpum is well adapted to ruderal habitats by the very high numbers of seeds that germinate between September and March. The plant can withstand adverse conditions, including inundation, for several weeks (own observations and pers. comm. A. Malten). Very dry summer conditions in Central Europe cause a severe dieback and retard growth, and the dwarfed surviving plants produced only a few seeds.

4.5 Germination tests and competition tests

According to our competition experiments, *E. brachycarpum* displayed more vigorous growth than *Senecio inaequidens*, one of the most successful invaders of the last decades in Germany. The growth was also superior to the native *Epilobium lamyi*, which often colonises the same habitats as *E. brachycarpum.*

4.6 Risk assessment

A weed risk assessment for Australia (PHELOUNG et al. 1999) was not able to classify *E. brachycarpum* decisively. The plant belongs to those taxa, albeit with the highest possible score (score 6, class span 1–6), which must be evaluated for their potential to damage the productive capacity or environment. Performing a risk assessment according to GABLIS (German-Austrian Black List Information System, ESSL et al. 2011) yields a similar result. *Epilobium brachycarpum* is rated as a member of the “Grey List-Watch List”. In our opinion, this classification does not take the already-observed niche expansion into account and, therefore, underestimates the potential of *E. brachycarpum* as an invasive plant.

Epilobium brachycarpum is a noxious weed in Californian vineyards (SANGUANKEO et al. 2009). There is concern about glyphosate resistance, albeit the species is not listed among the 21 species currently known to have evolved this type of resistance (HEAP 2012). The invasion of vineyards and farmland in Central Europe, thus, would not require a major niche shift. We regard it as probable that the plant will become a weed in the vineyards of Europe as well, although we know of only a single occurrence in 2010 in such a habitat in the Mosel Valley (Germany/Rhineland-Palatinate, pers. comm. D. Korneck).

Erweiterte deutsche Zusammenfassung

Einleitung – *Epilobium brachycarpum* ist im westlichen Nordamerika heimisch. Dort kommt die Art natürlicherweise vor allem in offenen Waldgesellschaften vor und tritt auch als Unkraut in Weinbergen und anderen Dauerkulturen auf. Die Art ist von anderen in Deutschland vorkommenden Weidenröschen-Arten durch die kurzen, nur 15–30 mm langen Früchte, die überwiegend winterannuelle Lebensform, die linealischen bis schwach lanzettlichen, früh abfallenden Blätter und die sich ablösende Epidermis deutlich unterschieden. Dies führte dazu, dass Vorkommen der Pflanze überdurchschnittlich gut erfasst wurden. Das Herkunftsgebiet liegt im westlichen Nordamerika. Dort ist die Art als Unkraut in Weinbergen und anderen Dauerkulturen bekannt.

Nur wenige sich einbürgernde Arten stellen eine wirtschaftliche Bedrohung dar oder haben das Potential, Lebensräume nachhaltig zu verändern (Transformer im Sinne von PYŠEK et al. 2004). Welche Eigenschaften derartige biologische Invasionen begünstigen, ist bei vielen Arten noch unklar. Die schnelle Ausbreitung von *E. brachycarpum* in Mitteleuropa lässt es geraten erscheinen, das Potenzial dieser Art als aggressiver Neophyt, als Transformer, abzuschätzen.

Material und Methoden – Wir verwendeten folgende Ansätze: (1) Darstellung der Besiedlungsgeschichte und der aktuellen Verbreitung in Europa, (2) Modellierung des Heimatareals in Nordamerika und des neophytischen Areals in Europa, (3) Modellierung der Samenausbreitung, (4) Dokumentation des pflanzensoziologischen Gesellschaftsanschlusses in Mitteleuropa, (5) Identifikation der potentiell besiedelbaren Vegetationstypen auf der Grundlage der Ähnlichkeiten von ökologischen Zeigerwerten von Verbänden des mitteleuropäischen Vegetationssystems, (6) Messungen der Samenproduktion, Populationsdichte und des Lebenszyklus auf Ruderalstandorten in Frankfurt am Main, (7) Keimungs- und Konkurrenztests unter Freiland- und Gewächshausbedingungen, (8) Risikoabschätzungen nach etablierten Tests.

Ergebnisse – (1) In Deutschland wurde *E. brachycarpum* erstmals 1994 in Rheinland-Pfalz festgestellt (LANG & WOLF 2000). 1999 wurde die Pflanze in Hessen (Rhein-Main-Gebiet) nachgewiesen, wo sie sich seither kontinuierlich ausbreitet (BÖNSEL & OTTICH 2005). 2002 wurde ein weiteres Ausbreitungszentrum in Nordbayern bekannt (HÖCKER & HETZEL 2007). Die kontinuierliche Ausbreitung bestand bis etwa 2008; seitdem verläuft der Zuwachs der Neunachweise in Messtischblättern etwas langsamer (Abb. 3). Die Ausbreitungsgeschwindigkeit für das im Rhein-Main-Gebiet zentrierte Areal beträgt etwa 8 km pro Jahr. Besiedelte Habitate sind u. a. Abbaugruben, Ruderalflächen in Städten und Bahngelände. In Europa bestehen weiterhin Verbreitungsinseln in Frankreich, Spanien und England (Abb. 5).

(2) Die Modellierung des potentiellen Verbreitungsgebietes von *E. brachycarpum* mithilfe von ökologischer Nischenmodellirung (ENM) basierend auf den Daten der Verbreitung in Nordamerika zeigt eine hohe Habitateignung für die Mittelmeerregion. Die Habitateignung in Nordwest- und Mitteleuropa ist dagegen vergleichsweise gering (Abb. 7b). (3) Diasporen von *E. brachycarpum* werden sehr effektiv und potentiell über mehrere Kilometer durch Wind ausgebreitet (Abb. 8).

(4) Die Analyse von Vegetationsaufnahmen (Tabelle 1 in der Beilage) zeigt eine deutliche Bindung an kurzlebige Ruderalvegetation (*Sisymbrion*). In Gesellschaften des *Dauco-Melilotion* kommt *E. brachycarpum* nur ausnahmsweise vor. (5) In Tabelle 1 sind die Verbände aufgeführt, die in ihren Zeigerwerten mindestens eine Übereinstimmung von 50 % mit dem *Sisymbrion* aufweisen.

(6) Die Samenproduktion pro Frucht wurde mit 24,1 (± 3,1) bestimmt. Früchte pro Pflanze wurden 579 (± 325) gezählt, womit sich eine Samenproduktion pro Pflanze von 14.522 (± 8.884) ergibt. Die Dichte fruchtender Pflanzen wurde auf Ruderalflächen in Frankfurt am Main mit 45,8 (± 27,5) pro m² bestimmt. Eine Beweidung durch Kaninchen (*Oryctolagus cuniculus*) führte nicht zu einer Verminderung der Samenproduktion pro Individuum. (7) Die Keimung erfolgte auf innerstädtischen Ruderalflächen in Frankfurt am Main zwischen September und Dezember sowie in geringerem Maße im März. Während des Winters kann die Zahl der Jungpflanzen (Keimblattstadium bis 1–2 Blattpaare) sehr hoch sein. Im Januar 2010 stellten wir in 12 Probeflächen von 10 cm × 10 cm Größe 299 (± 266) Jungpflanzen fest. Zwischen April und Juni sind sterile Pflanzen mit etlichen Blattpaaren vorhanden. Die Blüte- und Fruchtzeit liegt zwischen Juli und September (Abb. 9). Die Pflanzen sind gegen Trockenperioden empfindlich, überstehen aber mehrwöchige Überschwemmungen oder Schneeüberdeckung. Im Gartenversuch keimte *E. brachycarpum* sowohl auf Gartenerde wie auf einer Sand-Erde-Mischung im Herbst 2010 in sehr hohen Anteilen und erwies sich bei Konkurrenzversuchen *Epilobium lamyi* und *Senecio inaequidens* deutlich überlegen.

(8) *Epilobium brachycarpum* hat Eigenschaften, die es als wahrscheinlich erscheinen lassen, dass die Art als Schädling in landwirtschaftlichen Ökosystemen auftreten kann: (i) Unkraut im natürlichen Verbreitungsgebiet, (ii) Vorkommen in Ruderalgesellschaften, (iii) annuelle Lebensform, (iv) hohe Samen-Produktion, (v) Schwimmfähigkeit der Samen, (vi) sehr gute Ausbreitung über Wind, (vii) schnelle Ausbreitung und wahrscheinlich (viii) Profiteur des Klimawandels.

Diskussion – So weit bekannt fand eine Phase gelegentlicher Einbringung ohne Ausbreitung in Mitteleuropa nicht statt. In Deutschland bestand die Phase lokaler Einbürgerung 1994–1998; die Jahre 1999–2001 waren durch regionale Einbürgerung charakterisiert. Seit 2002 verhält sich *E. brachycarpum* in Mitteleuropa invasiv (Definition nach PYŠEK et al. 2004). Bei gleichbleibender Ausbreitungsgeschwindigkeit wird *E. brachycarpum* die Schweizer Grenze im Rheintal 2030 und die deutsche Nordostgrenze 2080 erreichen. Durch das Entstehen neuer lokaler Ausbreitungszentren durch Ferntransport wird die Ausbreitung aber wahrscheinlich schneller verlaufen. Über die Einwanderung bestehen keine sicheren Erkenntnisse. Die Nähe früher Funde zu Einrichtungen der US-Armee lässt aber einen Zusammenhang mit militärischen Transporten vermuten. In Mitteleuropa sind heute mindestens zwei Wege für Ferntransporte nachgewiesen (i) durch Lastwagen zwischen Abbaugebieten und (ii) durch Zugverkehr.

Bei Annahme einer Nischenkonstanz zwischen Nordamerika und Europa wäre eine deutlich stärkere Ausbreitung im Mittelmeerraum zu erwarten (Abb. 5). Eine mögliche Erklärung für die unerwartete Ausbreitung in Europa ist, dass sich die ökologische Nische geändert hat. Molekulare Studien und reziproke Transplantationsexperimente können hier Aufklärung bringen.

Ähnlichkeiten zum *Sisymbrion* in der ökologischen Klassifikation machen es wahrscheinlich, dass *E. brachycarpum* Gesellschaften des *Fumario-Euphorbion* besiedeln und insbesondere im Weinbau zum Problemunkraut werden kann. Auch Waldschlaggesellschaften (*Carici piluliferae-Epilobion angustifoliae*) und Bidention-Gesellschaften könnten von *E. brachycarpum* besiedelt werden. Gesellschaften des *Sisymbrion* verändern sich nach der Einwanderung von *E. brachycarpum* deutlich. Die Vegetation wird dichter und höher. Auf Ruderalflächen in Frankfurt am Main wurde dadurch das in Vorjahren festgestellte Brüten des Flussregenpfeifers (*Charadrius dubius*) verhindert.

Die in Europa festgestellten Dichten an Pflanzen pro m² und die Samenproduktion pro Pflanze liegen deutlich über den aus Nordamerika bekannten Werten. Risikoabschätzungen nach für Australien (PHELOUNG et al. 1999) und Mitteleuropa (ESSL et al. 2011) entwickelten Systemen ergaben jeweils ein mittleres Risiko. Diese Systeme berücksichtigen jedoch nicht die bereits erkennbare Nischen-Änderung und unterschätzen daher wahrscheinlich das Potential von *E. brachycarpum* als invasiver Pflanze.

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Supplements and Appendices

Supplement 1. Table 1. Vegetation relevées of *Epilobium brachycarpum* from the Rhine-Main area and northern Bavaria.

Beilage 1. Tabelle 1. Vegetationsaufnahmen mit *Epilobium brachycarpum* aus dem Rhein-Main-Gebiet und dem nördlichen Bayern.

Appendix 1. Geographic origin of the relevés in Table 1. Plot numbers correspond to sequential numbers in Table 1.

Anhang 1. Geographische Herkunft der Aufnahmen in Tabelle 1. Die Aufnahmenummern entsprechen den laufenden Nummern in Tabelle 1.

6328/41 – German ordinance map 1:25 000 (10' longitude × 6' latitude) / numbering of quadrants in lines from top to bottom. (3469164/5543580) – Georeference with Gauss-Krüger coordinate system.

6328/41 – Deutsche topographische Karte 1:25 000 (10' Breite × 6' Länge) / mit fortlaufender Quadranteilung; Nummerierung der Quadranten jeweils zeilenweise und von oben nach unten. (3469164/5543580) – Georeferenzierung mit Gauß-Krüger-Koordinaten.

1: 6328/41 Markt Bibart, railway station
2: 6030/144 s Stettfeld, dredging lake
3: 6030/413 nw Trunstadt, sandpit and landfill
4: 6231/41 nw Lauf,sandpit and landfill with sand
5: 6428/43 Bad Windsheim-South, parking ground and fallow land
6: 5917/32 Frankfurt airport, CargoCity Süd, fallow land with sand and gravel (3469164/5543580)
7: 6032/13 n Scheßlitz, land fill
8: 6328/41 Markt Bibart, storage area for wood
9: 6330/14 Uehlfeld, garden
10: 5917/41 Frankfurt airport, CargoCity South (3468907/5543574)
11: 6030/413 nw Viereth, sandpit and gravelpit
12: 6328/41 Markt Bibart, railway station
13: 6230/44 e Höchstadt, disabandoned pits, partly used as landfill
14: 6332/12 w Kersbach, sandpit near highway
15 6329/32 ne Baudenbach, landfill for building site rubble
16: 6330/12 w Mailach, sandpit and landfill
17: 6328/41 e Markt Bibart, commercial area and railway track
18: 6328/23 Grappertshofen, building site rubble
19: 6329/33 se Langenfeld, railway line Nürnberg - Würzburg, railway track
20: 6232/14 n Forchheim, flattened sandy area prepared for development
21: 5817/44 Frankfurt/Main, former freight yard, sand and gravel (3473804/5552383)
22: 6330/34 s Linden, fallow field
23: 5917/41 Frankfurt airport, CargoCity South, sandy fallow land (3470555/5543706)
24: 6330/33 Between Bundesstrasse 470 and Göttelhöf, fallow field
25: 6328/14 sw Altmannshausen, railway line
26: 6018/43 Messel pit, pile of oil shale (3482900/5531319)
27: 5917/121 Frankfurt/Main, Schwanheim, Leuna-Straße (3468080/5550143)
28: 6329/43 s Kleinsteinach, dumping site "Gutenstetten"
29: 6328/42 s Frankenfeld, railway line Nürnberg - Würzburg
30: 6330/21 sw Lonnerstadt, sand pit
31: 6332/12 n Baiersdorf, storage area for sand
32: 6018/43 Messel pit, pile of oil shale (3482915/5531300)
33: 6328/33 nw Ingolstadt, landfill for building site rubble
34: 6232/13 s Neuses/R., sand pit and land fill
35: 5817/443 Frankfurt/Main, former freight yard (3474244/5552513)
36: 5817/443 Frankfurt/Main, former freight yard (3473242/5552590)
37: 5817/434 Frankfurt/Main, former freight yard (3473031/5552461)
38: 5817/434 Frankfurt/Main, former freight yard (3473077/5552468)
39: 5817/44 Frankfurt/Main, former freight yard, very sandy gravel (3474107/5552451)
40: 5817/443 Frankfurt/Main, former freight yard (3473221/5552571)
41: 5818/33 Frankfurt/Main, Eastern harbour, industrial area at the right side of Main, ca. 100 m east of Deutschherrnbrücke, grus (3478915/5552457)
42: 5817/44 Frankfurt/Main, former freight yard, flattened rubble (3474204/5552510)
43: 5817/443 Frankfurt/Main, former freight yard (3473192/5552534)

44: 5817/443 Frankfurt/Main, former freight yard (3473202/5552551)
45: 5817/432 Frankfurt/Main, Rebstock, urban waste land (3472829/5553151)
46: 5817/443 Frankfurt/Main, former freight yard (3474327/5552522)
47: 5817/443 Frankfurt/Main, former freight yard (3474297/5552519)
48: 5817/443 Frankfurt/Main, former freight yard (3473231/5552521
49: 5817/432 Frankfurt/Main, Rebstock, urban waste land (3472858/5553156)
50: 6018/43 Messel pit, open ruderal vegetation on crushed oil shale (3482700/5531070)
51: 5817/44 Frankfurt/Main, Hanauer Landstraße / Grusonstraße, landfill used as industrial area, ruderal, rich in Conyza canadensis, very open, fine gravel (3479073/5552869)
52. 6018/43 Messel pit, short-lived ruderal vegetation on crushed oil shale (3482697/5531331)
53: 6429/31 Diespeck, industrial area, green space
54: 6018/43 Messel pit, open ruderal vegetation on crushed oil shale (3482812/5531486)
55: 6018/43 Messel pit, open ruderal vegetation on crushed oil shale (3482622/5531337)
56: 6018/43 Messel pit, open ruderal vegetation on crushed oil shale (3482733/5531678)
57: 6429/21 Neustadt a. d. Aisch, Karl-Eibl-Straße, garden
58: 6429/21 Neustadt a. d. Aisch, railway station
59: 6018/43 Messel pit, basalt cover in center of pit (3482564/5531281)
60: 6018/43 Messel pit, basalt cover in center of pit (3482592/5531309)
61: 6018/43 Messel pit, basalt cover in center of pit (3482625/5531305)
62: 6328/43 Markt Sugenheim; waste disposal site
63: 6429/21 Neustadt a. d. Aisch, abandoned clay pit
64: 6427/223 e Weigenheim, Mittelwald (coppice-with-standards forests)
65: 6018/43 Messel pit, open ruderal vegetation on crushed oil shale (3482679/5531310)
66: 6330/33 Göttelhöf, fallow field
67: 6018/43 Messel pit, open ruderal vegetation on crushed oil shale (3482595/5531225)
68: 6018/43 Messel pit, basalt cover in center of pit (3482545/5531300)
69: 6018/43 Messel pit, basalt cover in center of pit (3482645/5531272)

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