THE INVASION OF CENTRAL EUROPE BY *SENECIO INAEQUIDENS* DC. – A COMPLEX BIOGEOGRAPHICAL PROBLEM

With 5 figures, 4 tables and 1 photo

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Zusammenfassung: Die Einwanderung des Schmalblättrigen Greiskrautes (*Senecio inaequidens* DC.) nach Mitteleuropa – Analyse eines komplexen biogeographischen Problems

Das aus Südafrika stammende Schmalblättrige Greiskraut *(Senecio inaequidens* DC.) hat sich seit den 1970er Jahren, von Westen (Raum Aachen) und Nordwesten (Bremen) einwandernd, sehr schnell in Deutschland ausgebreitet und dringt weiter ins östliche Mitteleuropa vor. Bevorzugte Wuchsorte sind Ruderalstellen an Verkehrswegen (Bahnanlagen, Autobahnen), Stadtbrachen, Abraumhalden, Baustellen und weitere anthropogen gestörte Standorte, auf denen die Pflanze vor allem im Spätsommer aspektbildend in Erscheinung tritt. Die außergewöhnliche Ausbreitungsgeschwindigkeit und die möglicherweise zunehmende Konkurrenzfähigkeit in verschiedenen Pflanzengesellschaften geben Anlass, dieser invasiven gebietsfremden Art besonderes Augenmerk zu widmen. Wir analysieren den Einwanderungsprozess mit Hilfe eines konzeptionellen Modells zur Erklärung von biologischen Invasionen, dem INVASS-Modell ("Model of Invasion Steps and Stages").

Summary: Since the 1970's, the neophyte Narrow-leafed Ragwort (*Senecio inaequidens* DC.) has spread rapidly in Central Europe, particularly in Germany. The species grows on roadsides and railway embankments, on urban wasteland, slag heaps, construction sites and other disturbed locations. This study reviews literature on the invasion of *S. inaequidens* in Central Europe with a focus on Germany, and analyses the factors determining the species' success. The analysis is based on a conceptual invasion model, termed the "model of invasion steps and stages" (INVASS model). Using an organism-centred approach, the model names problems which may arise during a plant invasion. The present study discusses factors which may have influenced the spreading of *S. inaequidens*. Species characteristics and favourable conditions contributing to the success of the invasion steps are named. Unresolved questions are identified, and major subjects for further research are recommended.

1 Introduction

One of the basic questions concerning biological invasions is: What makes a species able to survive (or even prosper) within a foreign environment? The 'biological foreignness' of a species to an ecosystem can obstruct a potential invader in many different ways: The abiotic conditions may not be suitable, e.g. due to inappropriate temperatures; there may be competitors hindering the establishment, or necessary mutualists may be missing. Thus, most of the species arriving in a foreign area fail to establish (e.g. MACK et al. 2000). The systematic search for problems encountered by a foreign species in a new area might help to reveal the principal factors determining invasion processes (TUCKER a. RICHARDSON 1995; RICHARDSON et al. 2000). Several current papers address the mechanisms of invasions (e.g. HIGGINS a. RICHARDSON 1998; REJMÁNEK 1999; SHER a. HYATT 1999; DAVIS et al. 2000; KEANE 2002; SHEA a. CHESSON 2002), and some of them emphasize the importance of dissecting the process into several stages (e.g. MACK 2000; RICHARDSON et al. 2000; KOLAR a. LODGE 2001).

The rapid spread of the South African neophyte Narrow-leafed Ragwort (*Senecio inaequidens* DC.) in Central Europe is well documented (e.g. ERNST 1998 for the Netherlands, DANCZA a. KIRÁLY 2000 for Hungary, BÖHMER et al. 2001 for Germany, PYŠEK et al. 2002 for the Czech Republic). Based on a review of existing knowledge (with a focus on Germany), we show the species' characteristics and environmental conditions that help to avoid or overcome potential obstacles. For the systematic analysis of the invasion process we use a conceptual model, the "model of invasion steps and stages" (INVASS model, HEGER 2004) which takes up the idea that 'biological foreignness' is the crucial feature of biological invasions. As a basis for this analysis, we suggest a scheme that visualizes the invasion process as a "staircase". The model postulates that a plant must overcome several steps to advance from one invasion

stage to the next. The invasion steps, which are partly similar to elements of classic succession theories (CLEMENTS 1916; MACARTHUR a. WILSON 1967; cf. MUELLER-DOMBOIS 2001), are designed in a way to encompass the main problems that may arise for a plant continuing in an invasion process (Fig. 1, for a definition of the steps and stages see below, and in detail HEGER 2001; a discussion of other proposed schemes can be found in HEGER a. TREPL 2003).

The INVASS model systematically analyses the main factors influencing the course of an idealized invasion during each of the four steps (i.e. transportation, growth, and reproduction of the first individuals in the new area; population growth, and colonization of new localities). An organism-centred approach explores problems that might cause a crucial obstacle for the invader during each invasion step, and which species characteristics or features of the new environment might enable the plant to avoid or overcome these obstacles. The suggestions of the model, summarized in four tables describing the potential problems as well as favourable species characteristics and environmental conditions (HEGER 2004), are appropriate as a framework for the analysis of invasion cases. In the following, they are used as checklists leading step-by-step through the investigation of the invasion of Central Europe by *Senecio inaequidens*. It is shown that, with the help of the tables, this complex invasion process can be described in a clear and transparent manner, highlighting the important factors which led to the success of the species.

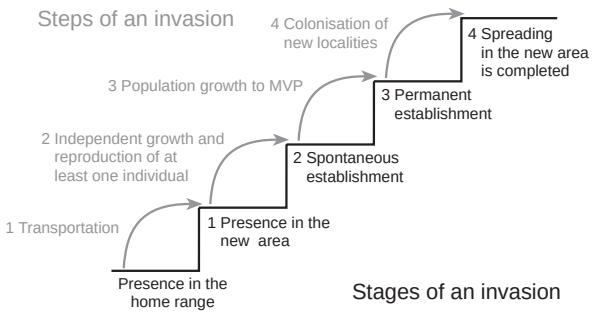


Fig. 1: Chronological discrimination of an idealised invasion process into steps and stages. Different stages are reached by overcoming a sequence of steps in the course of an invasion. The height of each step depends on the ability of the species to overcome environmental limitations. MVP: Minimum viable population (from HEGER 2001)

Chronologische Abfolge der Schritte und Stufen eines idealisierten Invasionsprozesses. Neue Phasen werden durch die Überwindung einer Reihe von Hürden erreicht. Die Höhe einer Stufe hängt von der Fähigkeit einer Art ab, limitierende Umweltfaktoren zu überwinden. MVP: Mindestpopulationsgröße (nach HEGER 2001)

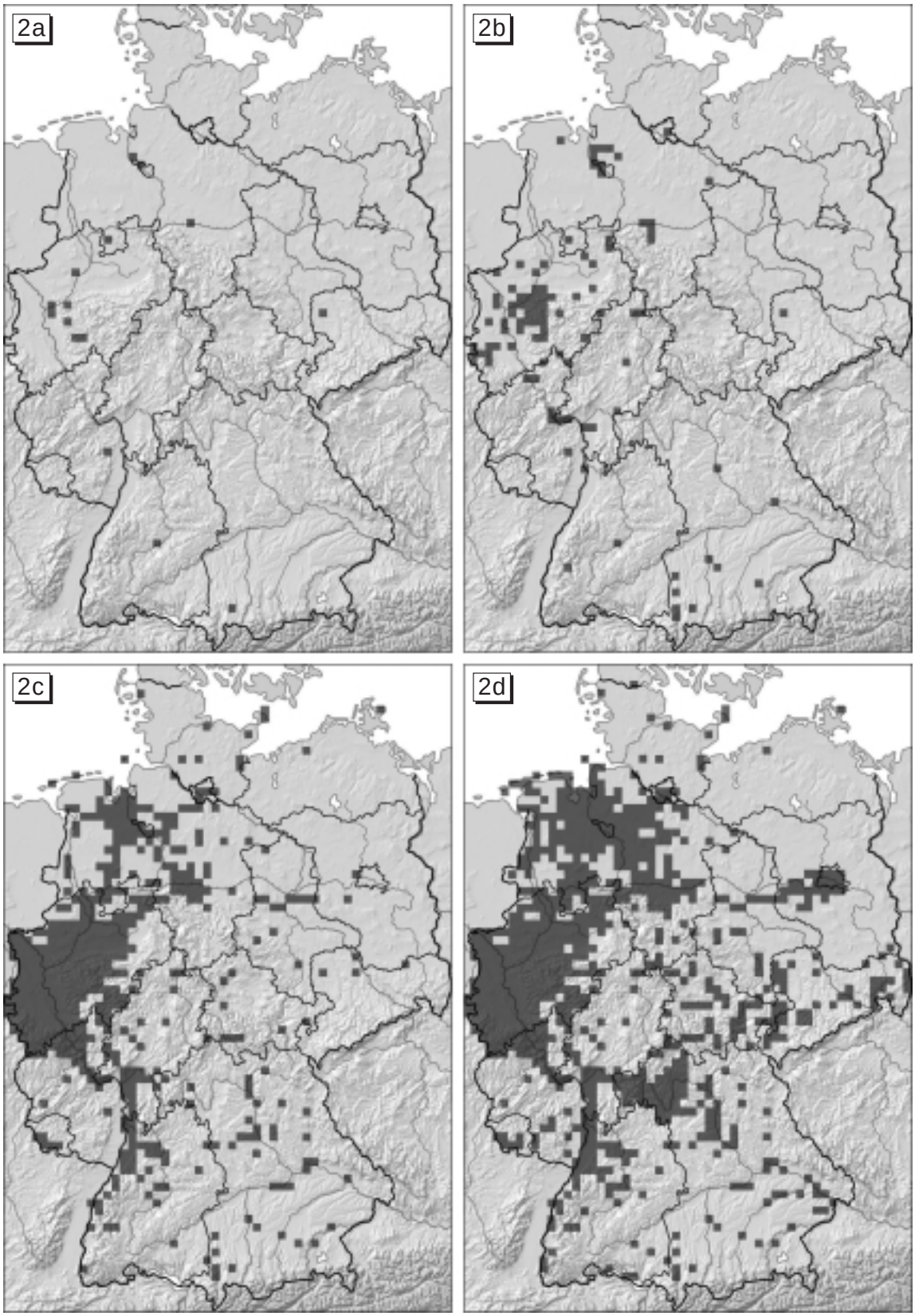
2 Senecio inaequidens in Central Europe and South Africa

Senecio inaequidens is a perennial shrubby herb about 60–80 cm tall. The lemon-yellow flower heads contain 80 to 100 flowers (GUILLERM et al. 1990), leading to a production of up to 29,000 achenes per plant (ERNST 1998). The plants – as are all *Asteraceae* – are protandrous. They are highly self-fertile (ERNST 1998); clonal reproduction has not been observed. The achenes are small (3 mm) with relatively long pappus hairs (5 mm), helping them not only to be transported by wind, but also to stick to many different structures.

The species is native to South Africa's "Highveld"; its original range covers approximately the provinces of North-West, Northern Province, Gauteng, Mpumalanga, Free State and Kwazulu-Natal, at elevations between 1,400 and 2,850 m (WERNER et al. 1991; MEUSEL a. JÄGER 1992). Thus, the original range lies within the region of summer rainfall: more than 80% of the annual precipitation occurs between October and March. Winter (during the European summer) is sunny and dry, with daily maxima of temperatures around 20 °C. The temperature does usually not fall below –4.5 °C (but locally reaches –11 °C; JACKSON 1961; THOMPSON 1965; LOW a. REBELO 1996; MURREY et al. 1996).

Occurring within grassland and savannah biomes (LOW a. REBELO 1996), *S. inaequidens* originally colonizes skeletal sectors on steep, moist and grassy slopes, as well as sandy and gravelly banks of periodic streams (HILLIARD 1977). A noteworthy phenomenon is that *S. inaequidens* has extended its range in South Africa to anthropogenic locations with weak competition (particularly on the verges of roads and areas damaged by fire, but also on coastal dunes; HILLIARD a. BURTT 1987). The species is currently colonizing a wide ecological range of areas, from dry to humid habitats, stone to clay soils, exposed to shaded locations (WERNER et al. 1991).

The first occurrence in Europe was detected near Hannover in 1889 (ERNST 1998), followed by a finding at the port of Bremen in 1896 (KUHBIER 1977). Since the early 1970s, the species spread rapidly in Germany (see Fig. 2 a-d). The wave of its eastward propagation from the centre of dispersal at Liège (since 1955) attained the western border of Germany at Aachen around 1970, followed by the first reports in West Germany. It also spread from an older population near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Düsseldorf, and reports of sites east of the Rhine became frequent a little later. The plant has been reported from the Cologne area since about 1980. OBERDORFER (1983) was the first to term the plant as naturalized. It has colonized the eastern Ruhr area (around Dortmund) since about 1990. At this time, its German range was mostly restricted to the western part of North Rhine-Westphalia and the area around Bremen (HAEUPLER a. SCHÖNFELDER 1989). In 1985, *S. inaequidens* appeared in northern Hessen on railway gravel. The gap in distribution between the Liège and Bremen areas was closed by the mid-1990s. Isolated occurrences were reported by the early 1990s from the upper Rhine Valley, the Neckar region, and Bavaria. ADOLPHI (1992) detected the first occurrence of *S. inaequidens* on the Baltic island of Rügen, and KÖNIG (1995) in Berlin. BRENNENSTUHL (1995) reported isolated pioneers in Saxony-Anhalt, eastern Thuringia and the area of Lower Lausitz, and HENKER (1996) in Mecklenburg-West Pommerania. IHL (1997) judged that *S. inaequidens* had become established in Saxony. The latest reports have come from Thuringia, from Greifswald, and from Bavaria, so that it may be assumed that the range of the species is spread throughout Germany, at least along railway tracks (for a detailed review of literature on the invasion process see BÖHMER et al. 2001).

In Europe as well as in South Africa, stony sites are preferred (ERNST 1998; BÖHMER et al. 2001). *Senecio inaequidens* can be found up to elevations of 1,000 m within the Alps (BÜSCHER 1989). It appears early in the course of succession (ASMUS 1988), but usually is displaced during later stages. Nevertheless, the species – in Central Europe as well as in South Africa – is able to build up large dominant stands (ADOLPHI 1997).

Fig. 2a–d: Documentation of the spread of *Senecio inaequidens* in Germany, as an example for its rapid range expansion in Central Europe

Dokumentation der Ausbreitung von *Senecio inaequidens* in Deutschland als Beispiel für die rasche Ausbreitung der Art in Mitteleuropa

Fig. 2a: Distribution of the species in 1979 (after RADKOWITSCH 1997)

Verbreitung im Jahr 1979 (nach RADKOWITSCH 1997)

Fig. 2b: Distribution in 1989 (after RADKOWITSCH 1997)

Verbreitung im Jahr 1989 (nach RADKOWITSCH 1997)

Fig. 2c: Distribution in 1997 (after RADKOWITSCH 1997)

Verbreitung im Jahr 1997 (nach RADKOWITSCH 1997)

Fig. 2d: Documented range extensions of *S. inaequidens* until 2003 (data taken from http://www.floraweb.de, WEISS 1999, ZAHLHEIMER 2000, 2001, MEIEROTT 2001, BORNKAMM 2002, LANG a. WOLFF 2002, WOLFF a. LANG 2002, KUHBIER 2003, expanded by own observations as well as written notifications by H.-U. PIONTKOWSKI, Eckernförde and H.-E. SALKOWSKI, Vallendar)

Dokumentierte Vorkommen von *S. inaequidens* im Jahr 2003 (Daten aus http://www.floraweb.de, WEISS 1999, ZAHLHEIMER 2000, 2001, MEIEROTT 2001, BORNKAMM 2002, LANG a. WOLFF 2002, WOLFF a. LANG 2002, KUHBIER 2003, ergänzt um Beobachtungen von H.-U. PIONTKOWSKI, Eckernförde, und H.-E. SALKOWSKI, Vallendar)

2.1 'Foreignness' of the species

As a basis for the forthcoming analysis it is important to know how 'foreign' the new environment actually is to *S. inaequidens*, i.e. what important differences exist between the home range and the new range. Those differences are:

– postponement of the growing season due to a transportation from the southern to the northern hemisphere

– less extreme seasonal differences in precipitation in Central Europe than in South Africa (for instance no serious drought in the Central European winter)

– lower temperatures during the year in Central Europe, especially during winter

– biocoenoses composed of different species and genera; this is indicated

(1) by the different inhabited vegetation types

(2) by the different biogeographical realms of the areas (Paleotropica as opposed to Holarctica).

3 The first step: transportation to Europe

In any invasion, the first obstacle faced by the prospective invader is to leave its home range and to reach a new area; it has to overcome a barrier to dispersal (cf. RICHARDSON et al. 2000). In the case of *S. inaequidens*, the propagules either have to pass the whole continent of Africa as well as the Mediterranean Sea, or surmount a distance of about 11,000 km across the Atlantic Ocean. *Senecio inaequidens* overcame this difficulty by transportation of sheep wool from South Africa to Europe. Other modes of transportation are also conceivable, but every one of the reported five primary centres of origin are connected to the wool processing industry (i.e. Mazamet, France; Calais, France; Verona, Italy; Liège, Belgium and Bremen, Germany; WERNER et al. 1991), which supports this assumption.

Table 1: Main factors determining the first step of invasion according to the INVASS model, differentiated into potential problems, favourable species characteristics and favourable environmental conditions (after HEGER a. TREPL 2003). Highlighted are those factors which might have caused a failure in the case of Senecio inaequidens in Central Europe. "?": further research needed. For more details see text

Entscheidende Faktoren der ersten Stufe einer biologischen Invasion gemäß dem INVASS-Modell, unterteilt in potentielle Probleme, günstige Arteigenschaften und günstige Umweltbedingungen (nach HEGER a. TREPL 2003). Hervorgehoben sind jene Faktoren, die im Falle von *Senecio inaequidens* eine Erschwernis verkörpert haben könnten. „?": Weitere Forschung nötig. Nähere Erläuterungen im Text

Step 1:	Determining factors					
Transportion	Potential problems for an invader	Did it occur?	Favourable species characteristics	Were they given?	Conditions favourable for transportation	Were they given?
	• Lack of suitable pathways	no	• Adaptations for long-distance dispersal	yes	• Suitable pathway is available	yes
	• No association with a potential pathway	no	• Production of many descendants	yes	• Pathway is used with big volume and high frequency	yes
	• Transport and storage are difficult to survive	no	• Seeds with high longevity compared to duration of transport	yes	• Transportation starts during fruiting time	yes
	• Pest management procedures may harm the species	no	• Robust seeds	not necessary	• **Predominance in the area of origin**	**(no?)**
	• No possibility to be transferred to a suitable habitat	no			• Occurrence on sites in contact to a potential pathway	yes
					• **Transportation lasts shortly**	**no**
					• No extreme conditions during transportation	yes
					• No pest management procedures	yes
					• Associated commodity is imported to many destinations	yes
					• Points of entry, transfer, and destination are near to suitable sites	yes
					• Time of entry is during a period suitable for germination and establishment	not necessary
					• **Associated commodity is intended for planting**	**no**

Table 1 summarizes the factors that drive unintentional transportation according to the INVASS model, and indicates which of them have contributed to the success of *S. inaequidens* during this step. In the following section, the statements of the table will be discussed in detail.

3.1 Availability and accessibility of a pathway

Transportation of *S. inaequidens* from South Africa to Europe was possible because sheep wool has been imported to Europe since the 19th and the beginning of the 20th century (see REEKEN 1996). The question why such a pathway exists is a cultural one, which cannot be answered here. A main problem *S. inaequidens* had to overcome is establishing contact with exported wool in South Africa.

To achieve this, five factors are implicated (cf. ISPM 11, 2001). The first one is the volume and frequency of movements along the pathway. Since the 1840s, Germany developed from a wool exporting to an importing country, and South Africa became one of the main exporters. Within two decades, sheep wool became a very important commodity world-wide (REEKEN 1996). It is not known how much wool has been imported from South Africa to Europe per year during this time and how many sheep were needed to produce this amount of wool, but it is clear that the pathway was exploited quite frequently and to a large extent during this decade. The transportation of achenes by this pathway therefore was quite likely.

A second question is whether there was a seasonal timing of diaspore production and movements along the pathway, increasing the probability of a transportation. Since grazing of the South African grassland and bush savannah took place during southern summer (WELLINGTON 1955) and *S. inaequidens* flowers mainly from October to February, a coincidence of the availability of diaspores and sheep grazing was also likely.

An association of diaspores with a pathway is more likely if the species is dominant in its area of origin. As mentioned above, *S. inaequidens* is able to build up large dominant stands, but this seems to happen only locally.

Presumably, this has not contributed to a frequent association of the species with sheep. It is supposed that usually only a few achenes would be found in the wool of a flock of sheep (cf. ERNST 1998).

The probability of dispersal is further increased if the species occurred at sites with a connection to the potential pathway. The original sites inhabited by *S. inaequidens* are steep and stony, and thus not very suitable for agricultural utilization, except for sheep grazing. Thus, an association of the species with sheep wool was likely.

A last important question is how it was possible for diaspores of *S. inaequidens* to become attached to the wool of grazing sheep. The essential characteristic for overcoming this obstacle is the morphology of the achenes described above, i.e. originally an adaptation for long-distance dispersal which was useful for human-mediated transportation in this case. Moreover, the species is able to produce many seeds (see above), which also increases the probability of transportation.

3.2 Survival during transport and storage

The transportation of wool from South Africa to Europe took place by ships and afterwards by railway (REEKEN 1996). It can be assumed that transportation took up to several months. Nevertheless, the conditions during transportation presumably were not extreme. It can also be assumed that there were no special treatments of the wool (such as freezing) during storage or transportation. Therefore, the duration of the transportation might have been the only problem connected to this sub-step. From the reviewed literature, longevity of seeds is not apparent and has to be explored in future investigations, but ERNST (1998) observed a dormancy lasting several months. Therefore, the longevity seems to be great enough to survive a period of at least several months.

3.3 Survival of existing pest management procedures

A crucial situation for the achenes arriving with sheep wool would have arisen if there had been pest management procedures during the process of harvesting and importation of wool. Before spinning, the wool was washed and combed, both of which presumably took place without the use of chemicals, thus providing no preclusion of the invading species.

3.4 Transfer to suitable habitats

The last problem for the arriving achenes of *S. inaequidens* during the first step of invasion was reaching a suitable habitat. Within the new area, transportation could have taken place due to adaptations of the achenes to anemochory, but even more probable was a transfer due to human-aided transportation (hemerochory). The wool imported to Europe was sent to different wool processing factories in Germany, France, Italy, and the Netherlands. Obviously, the seeds would have been teased out of the wool and deposited in the vicinity of these factories, in many cases finding conditions suitable for growth (see below). Therefore, hemerochory favoured the transfer to a high degree.

3.5 What is the likelihood of overcoming the first step of invasion?

The summary in table 1 shows that none of the potential problems of the first step of invasion actually arose during the transportation of *S. inaequidens* to Europe. This is due to some favourable species characteristics, and especially to several favourable conditions during transportation. Therefore, overcoming the first invasion step was apparently not a singular, rare event; instead, it is likely that the transportation of *S. inaequidens* from South Africa to Europe took place repeatedly.

4 The second step: growth and reproduction

Similar to the 'ecesis' coined by CLEMENTS (1928) for successions, the second step of invasion is the process of growth and establishment of a single individual arriving at a new site. The founder individuals, which have no chance to adapt to the new environment, have to germinate, mature and reproduce; these three substeps again resemble the ones proposed by CLEMENTS (1928).

4.1 Dormancy and germination

Problems during dormancy and germination of the diaspores result from seed predators, and from adverse abiotic conditions that hinder germination or the survival of dormancy. Some species, moreover, need a trigger to end dormancy and start germination. As a third problem, this might not be available in the new environment (see Tab. 2).

Thus, the first question to be answered is whether there are seed predators harming *S. inaequidens*. In Europe, several indigenous species of birds and phytophagous insects (e.g. species of the genera *Nysius* and *Stictopleurus*) have been observed feeding on the species' fruits (WERNER 1994; ERNST 1998; SCHMITZ a. WERNER 2000). Some of these insects are specialists for

Table 2: Main factors determining the second step of invasion in the case of Senecio inaequidens, see Table 1

Entscheidende Faktoren während der zweiten Stufe der Invasion von *Senecio inaequidens*, vgl. Tabelle 1

Step 2:	Determining factors					
	Potential problems for an invader	Did it occur?	Favourable species characteristics	Were they given?	Favourable conditions which might be given in the new area	Were they given?
a) Dormancy and germination	• **Seed predators**	**yes**	• Defence against generalist predators	?	• No specialized seed predators because of 'foreignness' of the plant	yes
	• Environmental conditions are not suitable to survive dormancy / for germinantion	no	• **Production of vegetative propagules**	**no**	• **New environment is similar to the home range concerning climate**	**no**
	• Trigger necessary for germination is not available	?	• Robust diaspores	yes (?)		
			• Broad ecological amplitude concerning necessary conditions for germination	?	• Favourable microhabitat	yes
			• **Competitive strength**	**no**		
			• Dormancy with no necessary / easy available trigger	?		
b) Growth to maturity	• Competitors	no	• **Competitive strength**	**no**	• Existence of a safe site	yes
	• **Predators**	**yes**	• Defence mechanism against generalist predators	yes	• Few specialist predators because of 'foreignness'	yes
	• Necessary mutualists are not available	?	• Ability to tolerate loss of tissue	yes	• **Absence of related species**	**no**
	• **Unfavourable abiotic conditions**	**yes**	• No mutualists necessary	?	• Presence of potential mutualists	?
	• Shortage of resources	no	• Mutualism with a cosmopolitan partner	?	• **New environment climatically similar to the home range**	**no**
			• Spread of mutualist partner with diaspore	?	• Origin and new area have similar disturbance regimes	in places
			• **Broad ecological amplitude**	**limited**		
c) Independent reproduction	• Trigger or necessary conditions for production of flowers not available	no	• **Vegetative reproduction**	**no**	• **New environment is similar to the home range concerning climate**	**no**
	• **Lack of sexual partners**	**yes**	• No special demands concerning fruiting and flowering	yes		
	• Lack of suitable pollinators	no	• **Dispersal leading to big founder population**	**no**	• **Large founder population due to favourable conditions of transportation**	**no**
	• Fruiting and ripening of seeds is not possible	no	• **Autogamy or agamospermy**	**no**		
			• **Monoecism**	**no**	• Presence of generalist pollinators	yes
			• Self-fertility	yes		
			• Hermaphroditism	yes		
			• Unspecific pollinators	yes		
			• Attractive flowers	yes		
			• Longevity of the plant	?		
			• Prolonged flowering period	yes		

the genus *Senecio*, and some are generalists (SCHMITZ a. WERNER 2000). So, it can be assumed that the first arriving achenes already had some generalist enemies which might have eaten them. On the other hand, specialist predators would be lessened due to the 'biological foreignness', which might have been an advantage for the plant (see e.g. KEANE 2002). An open question is whether the achenes have some possibility to defend against generalist predators (e.g. due to alkaloids that can be found in adult plants, see ERNST 1998). The production of vegetative propagules, which provides an escape from seed predators, is not a possible solution for *S. inaequidens*.

Dormant achenes of *S. inaequidens* encounter lower winter temperatures in Europe than in South Africa. Surprisingly, the achenes are able to cope with this problem, as ERNST (1998) observed achenes (of European individuals, which might have adapted) that survived two European winters and frost of –15°C.

The next question is why the first achenes to arrive were able to germinate in the new environment. Not much is known concerning this question. Further research (with South African achenes) will have to clarify the conditions required for germination and whether a trigger is necessary to end dormancy. The requirement of a trigger (as e.g. a certain daylength) could explain the ability of the species to adapt its life cycle to the postponed growing period in Europe. It is known that during germination, competitors may inhibit the appearance of seedlings (ERNST 1998). *S. inaequidens* is thus a weak competitor during this phase which requires a suitable microhabitat to meet its demands; unfortunately, the habitat of the first successfully germinating achenes is unknown.

4.2 Growth to reproductive maturity

During the growth to reproductive maturity, crucial situations for the invader may arise due to competitors, predators, a lack of mutualists, adverse abiotic conditions, and a shortage of requisite resources (see Tab. 2).

Seedlings of *S. inaequidens* – as well as growing and adult individuals – do not seem to be strong competitors (ERNST 1998). This assumption is based upon the observation that the species requires open sites with little competition for light and nutrients (see above). Thus, the success of the species is favoured to a high degree by the abundance of safe sites due to anthropogenic disturbance. It is assumed that *S. inaequidens* met an underexplored niche: its preferred sites are poorly occupied by indigenous competitors (BÖHMER et al. 2001, and references therein).

Up to now, 62 phytophagous insects have been observed feeding on *S. inaequidens* in Europe (SCHMITZ a. WERNER 2000). Of these, 11 only feed on flowers and fruits, therefore 51 affect the growth of the plants. Three of these species are specialists for the genus *Senecio*, and three for *Asteraceae*. These numbers would have to be compared to the phytophagous complex of the species in its home range, but a comparison with the indigenous species *Senecio jacobea* (96 phytophagous insects) supports the assumption that *S. inaequidens* again has an advantage due to its 'foreignness'. The presence of closely related species moderates this: specialized predators had (and will have in the future) the possibility of switching to the new host (STRONG et al. 1984; but see FRENZEL et al. 2001).

The impact of phytophagous insects on the growth of *S. inaequidens* in Europe seems negligible until now. This may be due to the ability of the plant to produce alkaloids (ERNST 1998). Another favourable species characteristic especially concerning grazers is the ability of the species to regenerate lost tissue (see GUILLERM et al. 1990).

Not much is known concerning non-insect predators of *S. inaequidens*. An alien rust (*Puccinia laenophorae* Cooke) grows on the plant, and an indigenous fungus (*Coleosporium senecionis* (Pers.) J. J. Kickx) has also been observed (SCHMITZ a. WERNER 2000). An open question is what influence these and other pathogens have on the plant in Europe and the home range.

There is also a lack of knowledge concerning possible mutualists *S. inaequidens* might need during growth to maturity. Further research is required to clarify whether the species is mutualistic in South Africa, and whether a problem might have occurred because of its biological foreignness in Europe.

Concerning the abiotic conditions, during the period of growth to maturity, problems may arise especially due to the differences in temperatures between the European and the South African range of the species (see above). A shortage of resources may not be a problem, because water supply is usually better in Europe than in its home range, especially during winter.

A crucial obstacle to the establishment of seedlings is low winter temperatures (ERNST 1998). This is a problem for individuals germinating in late autumn (i.e. during South African spring), which seems to happen rarely (GUILLERM et al. 1990; ERNST 1998). In addition to the demand for suitable temperatures, the seedlings seem to need a certain degree of moisture (ERNST 1998).

The plants' demands during their growth to maturity are not well studied. Most of the knowledge is concluded from physical conditions predominating the occupied sites. As described above, these cover a wide range, suggesting a broad ecological amplitude for the species (e.g. concerning available nutrients). Nevertheless, there are some limitations. The species prefers open sites, which indicates a demand for light (MOLL 1989; KEHREN 1995; ERNST 1998). It is discussed whether the species requires high temperatures during summer (average minimum temperatures during July not below 12 °C, RADKOWITSCH 1997; cf. WERNER et al. 1991; ADOLPHI 1997). Further studies will have to prove this assumption, and it has also to be examined whether this demand could be met by a choice of suitable microsites (despite possibly lower average temperatures). The woody stem base as well as the ability to regenerate from the main roots (GUILLERM et al. 1990) contribute to the species' ability to tolerate frost (KUHBIER 1977; GRIESE 1996; ADOLPHI 1997). Nevertheless, the extreme frosts in winter 2002/2003 in Central Europe caused a noticeable loss of *S. inaequidens* populations, e.g. in the City of Leipzig (P. Gutte, oral comm.).

Successfully invading species sometimes profit from an adaptation to a disturbance regime which resembles the one in the new area (GROVES 1991). In some respects this also applies to *S. inaequidens*. Within the South African range, fire and grazing are the main factors driving the ecosystems (LOW a. REBELO 1996), both being unusual for the sites occupied in Central Europe. But, from the viewpoint of the organisms, these disturbances may resemble those present in some of the European sites in some respect: It has variously been observed that *S. inaequidens* is promoted by mowing (BÖHMER et al. 2001). The plant is also able to resist the application of herbicides and to tolerate heavy metals in the soil (WERNER et al. 1991; HARD 1993), but these characteristics are not obviously connected to the disturbance regime of its home range.

4.3 Reproduction

The next range of problems faced by plant invaders is connected to their reproduction. The question is: How did the first individuals in Europe manage to reproduce despite a lack of reproductive partners and without prior adaptation to the new conditions? *Senecio inaequidens* is unable to reproduce vegetatively, which would have been one way of easily overcoming this problem.

For alien species lacking this possibility, several problems may emerge (see Tab. 2). One of them is the production of flowers. Since climatic conditions differ between the Central European and the South African ranges, and the growing season is postponed, the production of flowers might have been hindered in Europe. This has not been the case, and the question is why. In Kwazulu-Natal *S. inaequidens* flowers from October to February, but some plants may flower throughout the year (ADOLPHI 1997). In Europe, the species has two main periods of flowering, one starting in July and one in September (BÖHMER et al. 2001). Its flowering period locally lasts to December or even January (GERSTBERGER 1978; GUILLERM et al. 1990; MAZOMEIT 1991; KUHBIER 1996; ADOLPHI 1997; ERNST 1998). Apparently, the species has almost kept its South African flowering period (which in Central Europe now takes place in autumn and the beginning of winter) and has added a second one during the European spring. This second flowering period seems to be caused by an ongoing adaptation, as the onset of flowering has continuously shifted „forward" during recent years to the beginning of May (BÜSCHER 1989; MOLL 1989). To sum up the existing knowledge, *S. inaequidens* seems to require no particular daylength, no vernalisation, and to have no special demands concerning the abiotic conditions.

Pollination of an alien species may be hindered due to a lack of sexual partners, or of suitable pollinators. The first problem does not arise if the founder population is large, due to favourable conditions of transportation. As discussed above, this has apparently not been the case for *S. inaequidens*. One reason for this is the condition of transportation, another is the missing ability to disperse clustered seeds (e.g. with fruits containing many seeds). Further possibilities to explain the crucial lack of partners are autogamy, agamospermy, or monoecism, which are not applicable in the case of *S. inaequidens*. Nevertheless, even single individuals are able to reproduce because of its protandric (thus hermaphrodite) flowers coupled with high self-fertility (see ERNST 1998).

In Europe, there are several generalist pollinators, which probably facilitated a pollination of even the first flowers produced by this insect-pollinated species. Several syrphids and other insects have been observed to visit the flowers (ERNST 1998), and the species does not seem to depend on specialist pollinators. An alien species starting with a small population has a higher probability of being pollinated if its flowers are especially attractive for some reason (cf. CHITTKA a. SCHURKENS 2001). Few flowers are available to insects in Europe during autumn, and the late flowering of *S. inaequidens* provides a competitive advantage. Pollination becomes even more probable, if the species has a long life span (further research has to clarify this for *S. inaequidens*) or if it is – like *S. inaequidens* – flowering for a long period (BARRET a. RICHARDSON 1986).

A last problem which might have hindered the reproduction is the ripening of seeds under foreign climatic conditions. Flowers that pollinated after the end of November are not able to produce viable achenes (ERNST 1998). Therefore, again the crucial question is how the species managed to postpone its life cycle according to the European growing season. The ripening of seeds during the European summer and autumn seems to provide no problem for the plant.

4.4 What is the likelihood of overcoming the second step of invasion?

Compared to table 1, the summary in table 2 indicates more factors which might have caused a problem during the second step of invasion. *Senecio inaequidens* lacks some convenient characteristics, e.g. competitive strength, the ability to reproduce vegetatively, and also a broad amplitude of light requirement. Moreover, several environmental conditions were unfavourable, above all the climatic differences between Europe and the home range. *Senecio inaequidens* nevertheless was successful in overcoming this step, which can be attributed mainly to the following factors:

– the self-fertility of the species coupled with its protandrous flowers,

– the flexibility in the beginning of flowering, and particularly,

– the availability of abundant sites with low competition ('empty niches') due to anthropogenic changes, coupled with the ability of the species to occupy those sites despite the locally extreme conditions.

5 The third step: population growth to a minimum viable population

After overcoming the problems associated with growth and reproduction in Europe, the founder individuals of *S. inaequidens* faced the next invasion step:

attaining a critical self-supporting population size (the minimum viable population) to minimize the probability of extinction due to demographic, genetic or environmental stochasticity (see Tab. 3). An examination of the species' invasion history in Europe reveals that several problems actually did emerge during population growth: ERNST (1998) for instance, reports that several populations of *S. inaequidens* persisted for some years in the vicinity of Dutch sites with wool processing, but later disappeared again. According to ADOLPHI (1997), the plant has been ephemeral in Germany for many decades. It has been introduced repeatedly, but started establishing itself not before the 1960s. Many small populations of *S. inaequidens* have obviously been unable to overcome the third step of invasion.

5.1 Problems for single plants within the growing population

Population growth is only possible if each individual of the population manages to overcome the problems of growth and reproduction. These problems have been discussed above, but there are some differences for the generations descending from the founder population.

As discussed above, the first arrivals of *S. inaequidens* in Europe had to face many different problems. It could therefore be assumed, that the first settlement of some individuals was due to a coincidence of rare events ("good luck"), and an establishment was only possible due to genetic adaptation (but see HARPER 1982). This possibility is plausible especially because of the supposed small population at the beginning of the invasion, which might have led to a founder effect (cf. MACARTHUR a. WILSON 1967).

Unfortunately, no genetic comparison between different populations of *S. inaequidens* within Europe or South Africa has been undertaken as of yet. Nevertheless, some observations seem to support the assumption. One was already mentioned above; the continuous shift of the beginning of flowering, which could be interpreted as an adaptation to European climate (BÖHMER et al. 2001). Another notable fact is that the achenes of *S. inaequidens* show quite a complex pattern of dormancy. Achenes ripening in early summer have low dormancy and are able to establish a new generation in the same year, whereas those of late autumn have high dormancy and germinate the next spring. ERNST (1998) suggests that this pattern has evolved in adaptation to the climatic conditions in Europe, because low dormancy of early summer achenes is not suitable in the South African climate. It would be interesting to know whether the species has a special genetic predisposition which might have led to a quick genetic change in the beginning of the invasion.

The growing population is more attractive to predators than single plants (or achenes), and the longer the species is present in the area, the more predators might switch to the new host. This seems to be the case for *S. inaequidens*, since some specialized insects can be found in the flower heads (SCHMITZ a. WERNER 2000), and it can be assumed they did not feed on the first arriving achenes. Again, the presence of congeners from the genus *Senecio* in Europe seems to be a disadvantage for the plant (SCHERBER et al. 2003).

Table 3: Main factors determining the third step of invasion in the case of Senecio inaequidens, see Table 1

Entscheidende Faktoren während der dritten Stufe der Invasion von *Senecio inaequidens*, vgl. Tabelle 1

Step 3:	Determining factors					
	Potential problems for the plant	Did it occur?	Favourable characteristics of the plant	Were they given?	Favourable conditions which may be given in the new area	Were they given?
Population growth	• First settlement was due to "good luck"	?	• Ability for genetic adaptation	?	• **Absence of specialized predators despite a longer time of presence in the new area**	**no**
	• **New Predators because higher attractivity or long period of presence**	**yes**	• Adaptations for directed short-distance dispersal	(yes)	• **Absence of related species**	**no**
	• Control measures	no	• Persistent seed bank	?	• No control measures	yes
	• Lack of suitable safe sites in the immediate vicinity of the founder individuals	no	• Production of many seeds	yes	• Presence of generalists facilitating directed short-distance dispersals	not necessary
	• **Small size of initial population leads to demographic, genetic, and environmental stochasticity**	**yes**	• Short reproduction cycle	yes	• Suitable sites in the vicinity of the founder individuals	yes
			• High genetic variation of the population	?	• **Large founder population due to favourable conditions of transportation**	**no**
			• Self-fertility	yes	• Repeated secondary introductions	yes

Alien plants may not be able to establish in a new area if effective control measures hinder the growth and reproduction of individuals. This was not the case for *S. inaequidens* in Europe.

An aggregation of individuals, which is one requirement of population growth, can be achieved through directed short distance dispersal or dispersal by wind, the latter being the case for *S. inaequidens*. Achenes blown over an open site have a good chance to aggregate at some higher structure at the edge of the site. Another possibility to assure aggregation is the assembling of a persistent seed bank. Whether this is the case for *S. inaequidens* has to be determined in future studies.

Population growth is in any case not possible if the descendants do not find suitable sites for establishment in the vicinity of the founder individuals. For *S. inaequidens*, the preference of anthropogenic sites has led to an abundance of appropriate locations with low competition (such as railway tracks and stations, industrial sites, and sites along highways).

Photo 1: Senecio inaequidens DC. in Fuerth/Bavaria (near Nuremberg, 2001); photo: H. J. BÖHMER

Senecio inaequidens DC. in Fürth/Bayern (bei Nürnberg, 2001); Aufnahme: H. J. BÖHMER

5.2 Problems of the population

Small populations, such as those most likely produced by *S. inaequidens*, have to face a set of problems resulting from demographic, genetic, and environmental stochasticity (e.g. SHAFFER 1981; SOULÉ 1987; SIMBERLOFF 1988). Since *S. inaequidens* is now established in Central Europe, some populations must have been able to grow fast enough to survive. One prerequisite for a fast population growth is the ability to produce many descendants. Individuals of *S. inaequidens* produce even more descendants in Europe than in South Africa. This is remarkable if we consider the seemingly adverse climatic conditions, and it might be due to the absence of enemies or a prolonged flowering period.

A reproductive cycle of only 96 days has been observed for single individuals. So, an individual is capable of producing two generations within a vegetation period (WERNER et al. 1991; ERNST 1998). This is another characteristic favouring fast population growth. The successful establishment of *S. inaequidens* was further supported to a high degree by repeated introductions of diaspores. Without these, the small founder populations would have vanished and the species would not have been able to establish (cf. KOWARIK 2003).

Additionally, the probability of becoming extinct due to some kind of stochasticity is lessened if the populations are genetically variable. For *S. inaequidens* some morphological features hint at such variability (ADOLPHI 1997), but further research will have to clarify this. The high self-fertility of the species has probably also minimized the problems connected to genetic stochasticity (see OOSTERMEIJER et al. 1996).

5.3 What is the likelihood of overcoming the third step of invasion?

The determining factors for the step of population growth are summarized in table 3. An obviously crucial problem for the species was the small size of the initial population. This obstacle has been overcome mainly due to

- the ability of *S. inaequidens* to produce many propagules quickly, and (probably even more decisive),
- secondary introductions of diaspores, providing new founder populations again and again over multiple decades.

The latter circumstance made overcoming the third step of invasion quite probable.

6 The fourth step: colonization of new localities

Starting from single established populations at wool processing sites, *S. inaequidens* managed to spread in Europe (for details see BÖHMER et al. 2001). Thus, it had to overcome the fourth step of invasion, which is the colonization of new localities. Again, an alien species must overcome a series of obstacles during this step (see Tab. 4). They have to be differentiated into two groups: necessary conditions (if they are not fulfilled a colonization of new localities is impossible), and factors which influence the extent and velocity of the spreading.

6.1 Necessary conditions

A colonization of new localities is impeded if the alien species is not able to produce enough descendants. As discussed above, this is not the case with *S. inaequidens*. Dense stands (cf. e.g. BRANDES 1993; REIDL 1995) produce "enormous seed quantities" (ADOLPHI 1997), creating great colonization pressure, even in unusual habitats (e.g. lawns, and the façade of the cathedral at Cologne). Although, in the beginning of the invasion the production of just a few descendants might have protracted the spread.

Apart from this, the spread of an alien species is hindered if no suitable habitats are within reach. This, in turn, may be due to (a) a lack of suitable habitats or (b) an inability of the propagules to be transported to a suitable location. As mentioned repeatedly, there is no lack of suitable sites for *S. inaequidens* in Central Europe, although climatic conditions differ from the home range. This is not only due to the high abundance of anthropogenic sites (e.g. BORNKAMM 2002 a, b), but also to a broad ecological amplitude, enabling the species to colonize e.g. woodland clearings. On the other hand, the demand for high light limits its spread. Further studies will have to reveal whether, additionally, a genetic adaptability of the species or a high genetic variation within and between the European populations favoured the colonization of new localities.

Since *S. inaequidens* is adapted to dispersal via wind, a lack of dispersal means has probably never been a problem. Its eastward propagation from Belgium and the Netherlands was obviously facilitated by the prevailing westerly winds (GERSTBERGER 1978; WERNER et al. 1991). A further means of dispersal within Europe might be animals; the ability of the achenes to stick to fur has been demonstrated. Transportation by water may also be possible. Nevertheless, the availability of a dispersal means does not guarantee an effective transportation, i.e. having a high probability of leading to a site suitable for the growth of the species. None of the modes of dispersal mentioned fulfills this precondition.

However, why might *S. inaequidens* have been able to spread despite this deficiency? Two favourable conditions can give an answer to this question. At first, repeated introductions to different wool processing sites

Table 4: Main factors determining the fourth step of invasion in the case of Senecio inaequidens, see Table 1

Entscheidende Faktoren während der vierten Stufe der Invasion von *Senecio inaequidens*, vgl. Tabelle 1

Step 4:	Determining factors					
	Potential problems for the plant	Did it occur?	Favourable characteristics of the plant	Were they given?	Favourable conditions which may be given in the new area	Were they given?
Colonization of new localities	• Not enough descendants are produced	no	• Ability to produce many seeds or vegetative propagules	yes	• **Climatic conditions similar to the home range**	**no**
	• Lack of suitable sites	no	• **Broad ecological amplitude**	**limited**	• Anthropogenic changes create suitable sites	yes
	• Lack of appropriate means of dispersal	no	• Genetic adaptability of the individuals	?	• Natural disturbances create suitable sites	not necessary
	• **Transportation has low chance to reach suitable site**	**yes**	• High genetic variation within and between populations	?	• Presence of generalist dispersers	not necessary
	• Spread is hampered due to competitors, increasing appearance of enemies or missing mutualisms	?	• **Adaptations to hydrochory**	**no**	• Repeated secondary introductions	yes
			• **Adaptations to dispersal by generalist animals**	**no**	• Human aided dispersal within the new range	yes
	• Change of abiotic conditions has negative effects on the performance of the species	in the past: no	• **Competitive strength**	**no**	• **Predators which may switch to the new host are absent**	**no**
	• Control measures may hamper the spread	no			• Mutualists which may switch to new hosts are present	?
					• Changes of abiotic conditions have positive effects	in the past: yes
					• No control measures	yes

all over Europe led to different focal points of spread, thus stimulating the expansion (cf. MOODY a. MACK 1988). Recently, the species has been recommended for planting by beekeepers (ADOLPHI 1995); such a usage would intensify this effect. Secondly, human-aided transportation within Europe provides a very effective means of dispersal. An indicator for this is the observable pattern of expansion, since in Europe the plant is found mainly along linear anthropogenic structures such as railways and highways (RADKOWITSCH 1997; ADOLPHI 1998). A transportation of achenes sticking to trains, in the profile of tyres or on transported goods are some possible modes of hemerochory (cf. BRANDES 1993; GRIESE 1996; RADKOWITSCH 1997), others are listed in BÖHMER et al. (2001).

6.2 Factors influencing the extent and velocity of spreading

The factors mentioned until now are those which may have totally prevented the spread of *S. inaequidens* in Central Europe. Additionally, it could be asked which factors determine how fast and to what extent the species is spreading. The arguments listed above favour the suggestion that a genetic change has accelerated the expansion. Further research is necessary to establish whether this was the case, and to explore the probability of future change (e.g. due to hybridization, cf. ELLSTRAND a. SCHIERENBECK 2000).

Extent and velocity of spread can, moreover, be strongly influenced by the effect of competitors, predators or mutualists. What is known about the effect of these biotic factors up to now has been stated above. It is hypothesized that phytophagous insects (especially seed predators) may have a stronger effect on *S. inaequidens* in the future (ERNST 1998; SCHMITZ a. WERNER 2000). As the species is not a strong competitor, the extent of the spread is limited – and might be strongly affected if a strong competitor suddenly dominates its preferred sites. But summing up, not very much is known about the influence of biotic factors on the process of spreading in the past, at present and in the future.

Abiotic conditions, especially climatic ones, may strongly influence the process of spreading. It has been stated repeatedly that the rapid expansion of *S. inaequidens* was parallel to a period of dry and warm summers and mild winters in Europe (BÜSCHER 1989; WERNER et al. 1991; BÜSCHER a. LOOS 1993; HARD 1993; RADKOWITSCH 1997; ERNST 1998). It is probable that climate shows a strong positive (or negative) influence on the extent and velocity of the species' spread, but its demands concerning temperature and humidity are not known in detail.

6.3 What is the likelihood of overcoming the fourth step of invasion?

Table 4 shows that the lack of effective natural dispersal (i.e. leading to directed dispersal) was the only serious problem which might have prevented the species from spreading. This deficiency was overcome due to hemerochory. Another very important favourable condition for step 4 is, again, the anthropogenic creation of suitable sites. Extent and velocity of spreading moreover seem to be influenced strongly by climatic conditions. It remains to be explored whether the rapid expansion during the 1970s can be ascribed to climatic factors alone, or whether other factors (genetic or biotic ones) also contributed.

7 Conclusions

The invasion of *S. inaequidens* in Central Europe has not been an uncomplicated and highly probable incidence. Instead, the process is quite complex and a number of crucial obstacles have occurred, which had to be surmounted. During the four steps of invasion proposed by the INVASS model, different species characteristics and favourable conditions of the new environment (or during transportation, respectively) helped to avoid potential problems, or to overcome emerging crucial situations. Therefore, the reason for the success of the species in Europe is the coincidence of a range of different factors, indicated in tables 1 to 4.

It has been shown that a conceptual model can offer a useful framework for the description and explanation of the complex interplay of factors determining invasion cases. Using the scheme of steps and stages as a basis, the four tables can be used as a guideline for a detailed analysis. Thus, the INVASS model provides a heuristic tool to systematize case studies of plant invasions.

Although the invasion of Central Europe by *S. inaequidens* seems to be studied quite well, some interesting questions remain to be answered. Perhaps the most urgent one is if a genetic adaptation has occurred, and whether the species is genetically variable in Europe and South Africa. To be able to assess future trends for the ongoing spread of the species it would be helpful to know more about the conditions necessary for germination, and about the influence of predators in the home range as well as the European range.

Still, almost all reports on *S. inaequidens* are records of range extensions. The number of detailed ecological research is correspondingly small; not much is known about the ecological consequences of the invasion. In recent years, it has been observed that *S. inaequidens* is

probably threatening indigenous species of importance to nature conservation (e.g. blue lettuce, *Lactuca perennis;* Adolphi, oral comm.). The spreading to cereal cultures (e.g. wheat) may entail another problem, not just due to the species' competitive capacity, but particularly because of its poisonous quality. According to BROMILOV (1995), *S. inaequidens* is a crop weed in South Africa and repeatedly finds its way into bread. In Germany, *S. inaequidens* has been found on fallow fields (according to ADOLPHI 1997), but it has not yet been detected on cultivated surfaces. The poison has repeatedly been detected in milk as well, even though *S. inaequidens* is usually avoided by grazing animals. Therefore, a monitoring program is advisable in those parts of the range of *Senecio inaequidens* where the species has either begun to exert massive colonization pressure on locations outside the ruderal sites preferred in the past or is capable of doing so (BÖHMER et al. 2001).

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