

A comparison of native and introduced populations of the South African Ragwort *Senecio inaequidens* DC. in the field

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Synopsis

Two hypotheses that have been put forward to explain the success of invasive plants, the enemy release hypothesis and the evolution of increased ability (EICA) hypothesis, are based on observations of greater vigour of invasive plants in their range. In this study, we found support for this phenomenon in field populations of the invasive South African Ragwort, *Senecio inaequidens*: In the introduced range, plants were individually larger and built up larger populations than in the native range. Moreover, invasive populations showed a reduced incidence of parasitizing insects suggesting that enemy release may play a role in the success of this invader. We also found that among-population variation in seed mass was significantly reduced in European population, implying that the species underwent a population bottleneck when introduced to Europe. These first results will serve as a starting point for further studies on the influence of herbivory in this invasive species.

Keywords: alien plants, biological invasions, enemy release hypothesis, EICA hypothesis, herbivory

1. Introduction

The invasion of nonindigenous species is recognized as a major threat to global biodiversity, the composition of native communities, and the structure and functioning of ecosystems (DRAKE & al. 1989; UNEP 1995; VITOUSEK & al. 1996). Humans have accidentally or intentionally promoted the world-wide spread of organisms and thereby torn down the biogeographic barriers that had separated floras and faunas for millions of years (VERMEIJ 1991). Thus, besides their relevance for conservation and management, biological invasions might be regarded as “grand but unplanned experiments” (AUGE & al. 2001; CLELAND 2001; SAKAI & al. 2001) that can be used to address basic questions on the stability of food webs, on ecosystem functioning, and on the role of evolutionary processes in shaping natural communities.

A frequent notion about plant invaders is that they grow more vigorously in their invasive than in their native range (e.g. CRAWLEY 1997). To explain this phenomenon, a number of hypotheses have been put forward, in particular the enemy release hypothesis (e.g.

CRAWLEY 1987), according to which escape from natural enemies is responsible for this increased growth, and the evolution of increased competitive ability (EICA) hypothesis (BLOSSEY & NÖTZOLD 1995): if there is a trade-off between plant resource allocation to growth and defence, then the reduced herbivore impact in the invasive range should favour selection of poorly defended but competitively superior genotypes. According to the EICA hypothesis, the increased vigour of invasive plants would thus be genetically determined rather than a plastic response to the environment.

There has been much debate about the validity and generality of these hypotheses (e.g. MARON & VILÀ 2001; KEANE & CRAWLEY 2002) and a number of experiments have been carried out to test its predictions (e.g. DAEHLER & STRONG 1997; MEMMOTT & al. 2000; WILLIS & al. 1999; 2000; SIEMANN & ROGERS 2001). However, surprisingly little attention has been paid to the phenomenon that these hypotheses are based on. Apart from a handful of case studies (e.g. PRITCHARD 1960; STARFINGER 1990) and two flora comparisons with ambiguous outcomes (CRAWLEY 1987; THÉBAUD & SIMBERLOFF 2001) the available literature does not provide sufficient empirical data yet to actually suggest that increased vigour in invasive populations is a common phenomenon. The aim of our study was to collect such empirical data for one of the most rapid current invaders of Europe, the South African Ragwort, *Senecio inaequidens*.

2. Material & Methods

The South African Ragwort *Senecio inaequidens* DC. (Asteraceae) is a dwarf shrub from the mountainous regions of Eastern South Africa, where it is a typical colonizer of primary habitats such as rocky slopes and gravelly river beds. The species has become a ruderal both in South Africa and in Australia, South America and Europe, where it has been introduced presumably as a wool alien (ERNST 1998). First records in Germany date from 1890, but only in the 1970's *S. inaequidens* began to spread rapidly. However, apart from its distribution history and associated plant communities in Europe (see e.g. ASMUS 1988; BORNKAMM & PRASSE 1999), and an observational study on its insect herbivores (SCHMITZ & WERNER 2000), little is known so far about the population biology and ecological interactions of this species.

In February and March 2002, we collected field data in eighteen South African populations that covered a large geographical area and included both natural and ruderal habitat types (Table 1). We estimated population sizes either by counting all flowering individuals, or in the case of large populations by counting a fraction and multiplying by the total area over which *S. inaequidens* occurred. In each population we determined plant height and the number of flowering heads on up to twenty flowering individuals. In addition, we counted the percentage of flowering heads parasitized by insects on ten individuals with at least ten flowering heads. Finally, we collected seeds from up to twenty individuals per population and estimated average seed mass based on thirty seeds per individual. In summer 2002, the same measurements were taken in five European populations and seeds were collected from these and another five populations (Table 1). The data were analysed with nested analysis of variance.

Table 1List of sampled populations of *Senecio inaequidens* in South Africa and Europe.

Location (Province or Country)	Elevation a.s.l. [m]	Coordinates	Habitat	Number of Indi- viduals	Plant height (cm ± s.e.)	No of flower heads (± s.e)	Infesta- tion rate (% ± s.e) ¹
South Africa							
Bethlehem (Free State)	1700	28.15E 28.19S	Roadside	42	42.2 ± 2.6	130.1 ± 39.8	56.8 ± 9.3
Boshof (Free State)	1250	28.32E 25.15S	Roadside	387	43.8 ± 2.3	19.5 ± 4.9	47.8 ± 5.2
Bultfontein (Free State)	1340	28.16E 26.08S	Roadside	62	42.8 ± 1.9	39.3 ± 12.4	49.1 ± 9.1
Dealesville (Free State)	1240	28.40E 25.46S	Roadside	150	61.3 ± 2.8	31.9 ± 7.3	39.7 ± 12.0
Dewetsdorp (Free State)	1550	29.35E 26.40S	Roadside	208	44.8 ± 2.2	84.6 ± 26.6	59.7 ± 8.4
Giant's Castle (KwaZulu-Natal)	1950	29.20E 29.30S	River bed	11	51.0 ± 3.1	60.1 ± 15.8	52.6 ± 8.9
God's Window (Mpumalanga)	1550	24.50E 30.50S	Roadside	278	42.0 ± 1.3	85.6 ± 47.0	65.3 ± 5.1
Golden Gate I (Free State)	2150	28.31E 28.25S	River bed	102	81.2 ± 5.8	99.2 ± 35.7	22.9 ± 4.9
Golden Gate II (Free State)	2050	28.31E 28.25S	Rocks	17	54.1 ± 4.5	173.5 ± 47.9	64.4 ± 6.8
Golden Gate III (Free State)	2000	28.32E 28.39S	Roadside	73	41.5 ± 2.6	141.9 ± 27.5	70.0 ± 8.2
Graskop (Mpumalanga)	1450	24.58E 30.49S	Residential area	432	58.1 ± 3.1	63.4 ± 11.6	54.2 ± 4.6
Joel's Drift (Lesotho)	2000	28.46E 28.25S	Roadside/Pasture	472	30.9 ± 1.0	54.3 ± 7.2	63.2 ± 6.4
Lydenburg (Mpumalanga)	1500	25.10E 30.01S	Roadside	11	61.8 ± 3.5	84.1 ± 18.7	9.2 ± 4.1
Memel (Free State)	1741	27.41E 29.35S	Roadside	675	23.8 ± 1.3	8.6 ± 1.2	76.7 ± 4.2
Mt. Lebanon I (KwaZulu-Natal)	1800	29.35E 29.40S	Pasture	40	48.7 ± 3.5	225.6 ± 35.8	63.4 ± 8.4
Mt. Lebanon II (KwaZulu-Natal)	2130	29.35E 29.40S	Alpine pasture	54	27.6 ± 2.1	109.6 ± 62.9	49.0 ± 6.7
Port St. Johns (Easter Cape)	10	31.37E 29.32S	Roadside/Ruderal	396	53.4 ± 4.2	30.5 ± 6.1	64.8 ± 4.6
Semonkong (Lesotho)	2200	29.49E 28.03S	River bed	256	55.4 ± 4.0	114.3 ± 25.2	32.8 ± 4.4
Mean				108.1	48.02	86.44	52.33
Europe							
Amersfoort (Netherlands)	5	52.09N 5.23E	Ruderal vegetation	300	n.a.	n.a.	n.a.
Amsterdam (Netherlands)	0	52.21N 4.54E	Road ditches	1000	n.a.	n.a.	n.a.
Basel (Switzerland)	254	47.33N 7.36E	Railway tracks	5000	56.0 ± 2.7	98.8 ± 24.1	11.5 ± 5.2
Bremen (Germany)	15	53.05N 8.48E	Railway tracks	15000	45.3 ± 2.7	111.5 ± 24.1	34.7 ± 5.3
Halle (Germany)	104	51.28N 11.58E	Car park	235	74.3 ± 3.1	172.3 ± 27.8	23.0 ± 5.5
Hamburg (Germany)	11	53.33N 10.00E	Car park	112	n.a.	n.a.	n.a.
Karlsruhe (Germany)	115	49.00N 8.24E	Railway tracks	1000	n.a.	n.a.	n.a.
Kiel (Germany)	10	54.20N 10.08E	Railway tracks	800	n.a.	n.a.	n.a.
Köln (Germany)	46	50.56N 6.57E	Ruderal vegetation	500	53.3 ± 3.1	122.9 ± 27.8	13.1 ± 5.9
Weissenfels (Germany)	159	51.12N 11.58E	Railway tracks	600	52.3 ± 2.7	82.9 ± 24.1	57.1 ± 4.8
Mean				813.5	56.23	117.67	27.89

¹ Infestation rate was measured as the proportion of flower heads parasitized by insects

3. Results

The average size of European populations was about eight times greater than that of South African populations, although there was considerable overlap in the ranges (Tab. 1, Fig. 1a). Plant individuals were larger in European populations, both in terms of plant height (+15.0%; Fig. 1b) and the number of flowering heads (+44.5%; Fig. 1c), whereas infestation rates of flowering heads were markedly higher in native South African populations (+87.6%; Fig. 1d). There was significant variation among populations in terms of plant height ($F_{21, 335} = 17.4$; $P < 0.001$), the number of flowering heads ($F_{21, 335} = 2.916$; $P < 0.001$) and their infestation rate ($F_{21, 251} = 7.970$; $P < 0.001$). Seed mass did not differ significantly

Fig. 1

Comparison of South African (native) and European (invasive) populations of *Senecio inaequidens* in the field. Mean \pm standard error of **a**) population size measured as the number of flowering individuals, **b**) plant height, **c**) individual plant size measured as the number of flower heads, **d**) infestation rate measured as the proportion of parasitized flower heads by insects. *F*- and *P*- values refer to the comparison between continents.

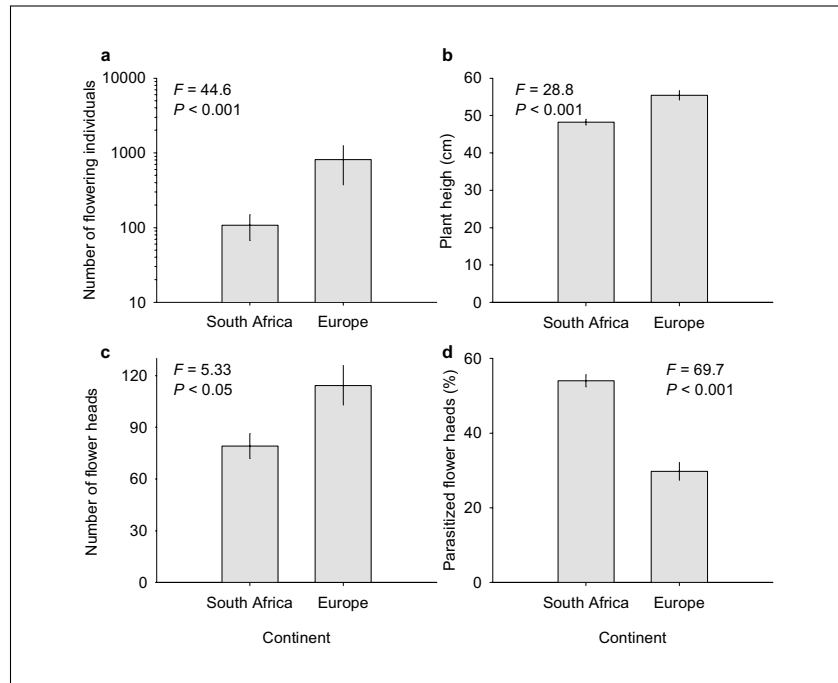
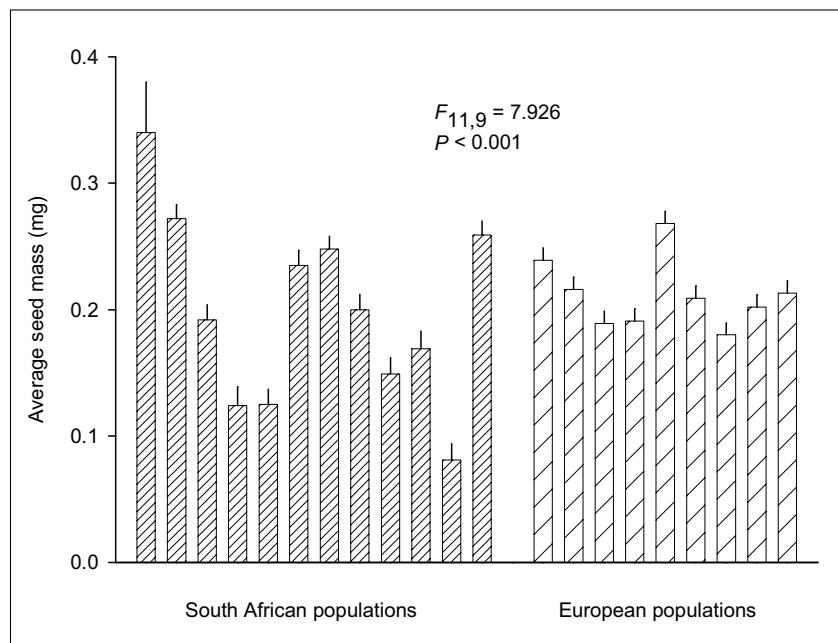


Fig. 2

Comparison of the average seed mass of South African (native) and European (invasive) populations of *Senecio inaequidens*. Population means and standard errors are given. *F*- and *P*- values compare the among-population variation of continents based on variance components.



between continents ($F_{1, 20} = 0.241$; $P < 0.628$), but the variance component among South African populations (75%) was significantly larger than the corresponding component among European populations (32%; Fig. 2).

4. Discussion

Two hypotheses that have been put forward to explain the success of invasive plants, the enemy release hypothesis and the evolution of increased ability (EICA) hypothesis, are based on observations of greater vigour of invasive plants in their range. In our study, we

found support for this phenomenon in field populations of the invasive South African Ragwort, *Senecio inaequidens*: In the introduced range, plants were individually larger and built up larger populations than in the native range. Moreover, invasive populations showed a reduced incidence of parasitizing insects suggesting that enemy release may indeed play a role in the success of this invader.

To rigorously test the enemy release hypothesis, however, it would be necessary to do insect enclosures in the native and introduced ranges (MARON & VILÀ 2001). If invasive plants experience an enemy release then excluding herbivores should have a lesser impact on plant performance in European populations of *S. inaequidens*. In addition, the data by SCHMITZ & WERNER (2000) could serve as a starting point for a quantitative survey of the insect fauna on *S. inaequidens* in its native and introduced range, similar to the work by MEMMOTT & al. (2000) on *Cytisus scoparius*. Such an approach might not only indicate those enemies the species is actually released from, but it might also identify switches of herbivorous insects from other *Senecio* species to *S. inaequidens* and thus provide insight into the ecological interactions and food-web consequences of this invader. To address the EICA hypothesis, common garden experiments are necessary. If there has been evolution of increased competitive ability, then plants from the invasive range should grow significantly better under herbivore-free conditions, but they should do worse where herbivores are present. We will use the collected seeds for addressing, among others, this question in greenhouse experiments.

We found reduced among-population variation in seed mass in the introduced as compared to the native range, a pattern that one would expect for a species that was introduced only a limited number of times and thus underwent a population bottleneck. Although ERNST (1998) reported multiple introductions of *S. inaequidens* to Europe, our data suggest that the introduced seeds may have come from geographically close rather than distant regions of the species' distribution. There is great need for molecular marker studies that address these and other issues, including the apparently still difficult taxonomic demarcation of *S. inaequidens* from other *Senecio* species (K. BALKWILL, University of Witwatersrand, pers. comm.), the variation in ploidy levels in the native range (L. LAFUMA, University of Montpellier, pers. comm.) and how these factors may relate to the invasion process.

In its native range, *Senecio inaequidens* appears to be particularly successful in two types of habitats: First, it occurs in pioneer habitats that are characterised by low vegetation cover and at least temporary drought conditions, and it seems to be the species' ability to tolerate such environments that makes it a successful invader of roadsides and railway tracks. Second, it is extremely abundant and most vigorous on pastures where it is obviously avoided by most of the browsing animals. At present, the spread of *S. inaequidens* in Central Europe is restricted to ruderal habitats of the first type that are usually of little conservation or agricultural value, and it is an intriguing question why the species has not (yet?) invaded grazed habitats. While the closely related *S. madagascariensis* appears to be avoided by mammals in its invasive Australian range (SCOTT & al. 1998), it is not clear yet to what extent mammalian herbivory may limit the spread of *S. inaequidens* in Europe. Future research should address this question in order to be able to predict the species' potential for invading natural communities and out-competing native species in Europe.

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