

Generalist versus Specialist Herbivores on the Invasive *Senecio inaequidens* and a Native Related Species: What Makes the Difference?

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ABSTRACT

We compared herbivory pressure in the native *Jacobaea vulgaris* (formerly *Senecio jacobaea*) and the alien invasive *S. inaequidens* in sites where they co-occur in Belgium. We predicted that the alien species experiences relaxed herbivory pressure by specialist herbivores (enemy release hypothesis ERH) whereas it is still attacked by generalist herbivores. Impacts of two generalist (gastropods and rabbits) and one specialist (the caterpillar *Tyria jacobaeae*) herbivores were assessed with field observations and exclusion experiments. The generalist herbivores had a higher impact on the biomass and survival of the seedlings of the alien *S. inaequidens* than on the native *J. vulgaris*. On the contrary, the specialist *Tyria jacobaeae* attacked exclusively the adults of the native species, supporting one of the main predictions of the ERH. These results are discussed in relation to differences in pyrrolizidine alkaloid profiles between the two species.

Keywords: Enemy Release; Biotic Resistance; Invasive Plant; Invasive Success; Pyrrolizidine Alkaloids

1. Introduction

Natural enemies play a key role in hypotheses explaining the invasive success of alien plant species when introduced outside their native range [1-5]. First the enemy release hypothesis (ERH) proposes that the proliferation of an introduced plant species is due to the relaxed pressure by coevolved herbivores and pathogens [6,7]. The ERH has been tested in many different ways including comparisons between native and alien congeners (community approach), or between aliens in their native and introduced range (biogeographical approach) [5,8,9]. The ERH has been confirmed in many cases, as the invasive plants were less attacked in their new range than indigenous counterparts or than in their native range [2,9-13]. In contrast, the biotic resistance hypothesis (BRH) predicts that native generalist herbivores will suppress alien plants because these are naive, *i.e.* have not been selected to deter those herbivores [6,14]. Alien species are in this case considered to be more vulnerable than native species to attacks by native herbivores [1,15-18]. These two hypotheses could be complementary as differences in herbivore damage can exist between generalist and specialist herbivores [19-21]. In the introduced range, gen-

eralist and specialist herbivores are expected to differently interact with a new alien plant. Generalists feed on a wide range of plants, possibly including introduced species [14]. In contrast, specialists are not expected to feed on introduced plants, except in the case of host-switching from native to introduced plant. Moreover, introduced species with congeners in the resident flora are more likely to acquire enemies from them, partly due to chemical similarity [16,22].

In the present study, we compared damage of generalist versus specialist herbivores on two closely related *Senecionae* species (Asteraceae): *Jacobaea vulgaris* Gaert. (syn. *Senecio jacobaea* L.) native to NW Europe and the invasive *Senecio inaequidens* DC. We chose these species because they occasionally co-occur in open grasslands in Europe. *S. inaequidens* is troublesome in Europe while the native European species is invasive in other parts of the world. They thus represent an adequate system for testing hypotheses about herbivore influence on alien species success.

Senecio inaequidens, the narrow-leaved ragwort, native to South Africa and Lesotho, was accidentally introduced at several locations in Europe at the end of the 19th century as a contaminant of sheep wool [23,24]. The species is now considered as one of the most aggressive

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alien invasive species in Europe [25,26]. The species is a perennial polycarpic suffrutescent herb, mostly occurring, in its introduced range, as a pioneer of well-drained soil, also occurring occasionally in closed mesic grassland [23, 24].

Jacobaea vulgaris (formerly *Senecio jacobaea*), the tansy ragwort, is native to Europe. It is a biennial to short-lived perennial monocarpic species which forms a rosette during the first year and a flowering shoot in the second year [27]. It is usually found in later successional stages (closed grasslands on humus-rich soil) compared to *S. inaequidens*, but both species can occasionally co-exist in open grasslands on dry soils [27-29].

In this paper, we assessed herbivore damage at different life stages for generalist and specialist herbivores. We focused on two types of generalist herbivores, *i.e.* gastropods and rabbits that are known to feed on seedlings [30, 31]. On the other hand, we assessed damages due to the specialist caterpillar *Tyria jacobaeae* (Lepidoptera, Arctiidae), the cinnabar moth, which attacks *J. vulgaris* shoots mainly at the flowering stage. We did not estimate damages from other herbivores as they remained rare with very low damages on our sites (even the specialists *Botanophila seneciella*, Diptera, seed-head fly or *Longitarsus jacobaeae*, Coleoptera, flea beetle or *Aphis jacobaeae*, Hemiptera, aphid).

All *Senecionae* species contain pyrrolizidine alkaloids (PAs) of the senecionine type as constitutive defences against herbivores [32,33]. Some adapted co-evolved insects can detoxify and even sequester and use PAs for their own defence against predators [33] like the specialist moth *Tyria jacobaeae*. We thus attempted to relate patterns of herbivory to the PA defences at the different life stages.

We addressed three questions: 1) Is the alien *S. inaequidens* less attacked by generalists and/or specialists than the native *J. vulgaris*? Based on the ERH and the BRH, we predict that *S. inaequidens* should experience lower rates of foliar damage than the native congener by specialist herbivores and equal to higher pressure by generalist herbivores; 2) Are the two species equally affected by herbivores throughout their whole life cycle? We predict that the most critical life stages (seedlings) are those affected by generalist herbivores; 3) Can differences in the pattern of herbivory between the two species be explained by their profiles of pyrrolizidine alkaloids? We predict that the concentrations of PAs are higher in the alien than in the native species.

2. Material and Methods

2.1. Study Sites

Observations and field experiments were conducted in

two field sites where both species co-occurred. Such sites were chosen to ensure that the two species are subjected to the same herbivore community. The first field site was a rough mesic mown grassland on a SW-facing slope on a roadside situated in Nossegem (50°52'18.30"N, 4°30'39.44"E), central Belgium. Vegetation was dominated by *S. inaequidens*, *J. vulgaris*, *Bromus mollis* and *Daucus carota*, with scattered alien shrubs (*Buddleja davidii*). This site was studied in 2005 and was thereafter destroyed by road works. Therefore, a second site was selected in Antwerp (51°14'36.40"N, 4°23'15.03"E), northern Belgium, for field observations and experiments in 2006 and 2007. There, the vegetation was a rough grassland on sandy soil dominated by *S. inaequidens*, *J. vulgaris*, *Festuca rubra*, *Plantago lanceolata* and *Cirsium arvense*.

2.2. Generalist Herbivores on Early Stages

We collected seeds in a total of seven populations of either species in Belgium. Seeds were pooled per species and sown in 3 L pots filled with a mixture of sand and compost (1:3, v:v) in a glasshouse. After emergence, the number of seedlings per pot was equalized to 30 and transferred to the field.

In June 2007, 80 pots were distributed in five blocks in the field site at Antwerp, separated from each other by approximately 10 m. In each block, four treatments were applied, *i.e.* exposed to both gastropods and rabbits, exposed to gastropods only, exposed to rabbits only and exposed to neither gastropods nor rabbits. Rabbit protection consisted of 60 cm high fences (mesh: 2.5 cm), buried to 20 cm deep, forming an enclosure of 70 × 120 cm around the pots. Gastropod protection consisted of copper tapes (Adalia®) glued around the pots, thus preventing gastropods from reaching the seedlings. The fully protected (neither gastropods nor rabbits) pots were protected both by the rabbit fence and the copper tape. The unprotected pots had no copper tape and were placed outside the fence. Surviving seedlings per pot were counted twice a week. After six weeks, surviving seedlings in each pot were cut at soil level, pooled in a paper bag, and dried at 50°C for 6 days. The mean individual biomass was calculated as the total biomass per pot divided by the final number of surviving seedlings.

2.3. Specialist Herbivores at Flowering Stage

The number of flowering individuals of *J. vulgaris* and *S. inaequidens* attacked by *Tyria jacobaeae* caterpillars, and the number of caterpillars per plant, were counted from July to October, in the sites Nossegem (in 2005, 400 individuals per species) and Antwerp (2006 and 2007). In Antwerp the populations of both species were too large

for an exhaustive survey. Plants were thus monitored within five permanent plots of approximately 0.75 m² for each species. These plots initially contained a total of 50 individuals per species. Damage of *T. jacobaeae* was estimated (percent leaf damage) and the number of remained flowering heads per plant was counted.

2.4. Pyrrolizidine Alkaloid Analysis

We sampled both species at different life stages. The seedlings were collected twice, *i.e.* at 2 weeks old (one true leaf) and 2 weeks later (2 - 4 true leaves), from plants used in the generalist herbivore field experiment. For later stages, plant material was randomly sampled at the Antwerp site in early July 2008. Leaves were harvested from non flowering plants (6 plants per species) and 5 flowering heads (all florets open) on flowering plants. All samples were individually dried at 50°C for 6 days, except for seedlings pooled in 2 bags per species.

Chemical analyses of pyrrolizidine alkaloids (PAs) were performed by Klaas Vrieling at the Institute of Biology, Leiden University, The Netherlands, using previously described method. Composition and concentration in PAs were determined by gas chromatography (HP 6890, 30 m × 0.25 µm HP-1) with split injector (1 - 30), Exterlut columns, PND detector and N₂ as carrier gas at 0.9 ml/min. The temperature program was 0-22-5- 250°C and pressure 56 kPa. The total PA concentration was calculated by summing the area of all the peaks in the chromatogram.

2.5. Statistical Analyses

Survival rate and remaining biomass were tested by 4-way ANOVA with all factors fixed. The effects of species, rabbit protection, gastropod protection, block and interactions were tested. Survival rates of seedlings were arcsin transformed and seedling biomass data were log-transformed to achieve normality. PA composition was tested with 2-way ANOVA with species and life stage as main factors. All statistical analyses were performed with SAS Enterprise version 4.1. Data are shown as means ± SD.

3. Results

3.1. Generalist Herbivores

In fully protected pots and in pots exposed to gastropods only, nearly all seedlings of the two species survived. In fully exposed pots and in pots exposed to rabbits, survival rates were significantly lower (**Figure 1**). Rabbit grazing significantly decreased survival rate, but gastropods did not (**Table 1**). Rabbit grazing had a higher negative impact on the survival of *S. inaequidens* than on *J.*

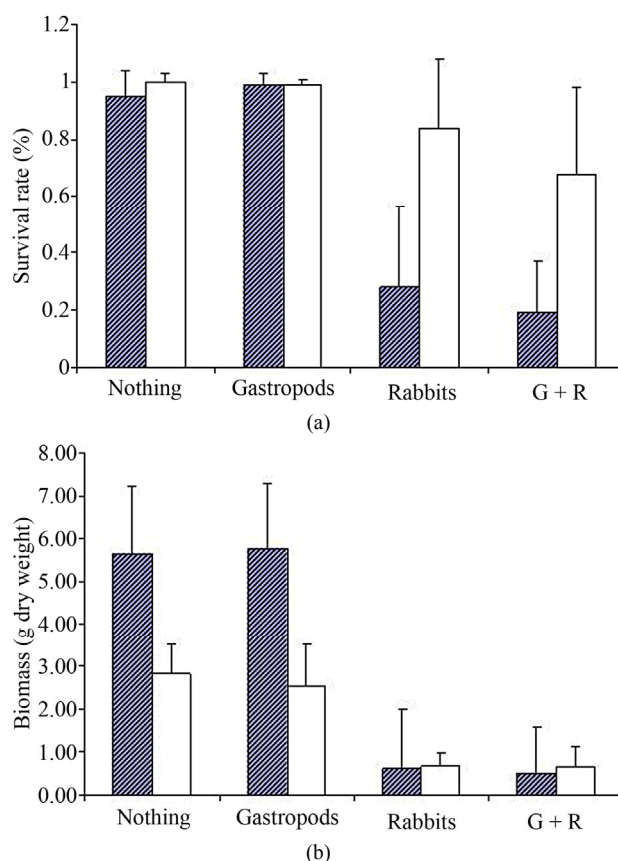


Figure 1. Survival rate (a) and biomass (b, in g dry weight) of *S. inaequidens* (hatched) and *J. vulgaris* (white) seedlings in the field experiment at Antwerp. G + R = Gastropods + Rabbits.

vulgaris (significant rabbit * species interaction; **Table 1**).

Gastropod grazing, obviously not very important in our study site, had no effect on the remaining biomass of both species (**Figure 1** and **Table 1**). Rabbit grazing significantly decreased the remaining biomass, and this effect was larger on *S. inaequidens* than on *J. vulgaris*, accounting for the significant rabbit * species interaction. Biomass loss due to rabbits reached approximately 90% for *S. inaequidens* and 75% for *J. vulgaris*.

3.2. Specialist Herbivores

No caterpillar was observed feeding on *S. inaequidens* over the three years at both field sites. In contrast, caterpillars were often observed feeding on *J. vulgaris* but their impact varied highly among years and sites (**Table 2**). At Nossegem in 2005, caterpillars were found on only 10 individuals of *J. vulgaris* (*i.e.* 4% of the population). In Antwerp in 2006, caterpillars were mainly observed in dense patches of *J. vulgaris*. In several patches, the plants were completely defoliated and their flowering

Table 1. Seedling herbivory by gastropods and rabbits in the field. Results of ANOVA for effects of gastropod protection, rabbit protection, species and block on the survival rate and the remaining biomass of *S. inaequidens* and *J. vulgaris*.

Source of variation	d.f.	Survival rate			Remaining biomass		
		SS	F	p	SS	F	p
gastropod-protection	1	0.020	0.23	0.72	0.001	2.38	0.11
rabbit-protection	1	12.32	138.7	<0.001	0.064	162.7	<0.001
species	1	3.39	38.02	<0.001	0.018	44.73	<0.001
block	4	0.60	1.70	0.12	0.009	5.53	0.002
gastropod-prot.*species	1	0.052	0.58	0.35	0.002	4.66	0.061
rabbit-prot.*species	1	2.62	29.51	<0.001	0.011	29.06	<0.001
rabbit-prot* gastropod-prot	1	0.15	1.70	0.12	0.001	2.70	0.10
rabbit* gastropod* species	1	0.001	0.01	0.92	0.0003	0.85	0.36

Table 2. Monitoring of *Tyria jacobaeae* caterpillar attacks in two natural populations from 2005 to 2007.

		Nossegem 2005	Antwerp 2006	Antwerp 2007
Flowering plant density in July (m ⁻²):	<i>S. inaequidens</i>	0.38	0.56	5.55
	<i>J. vulgaris</i>	1.25	0.87	0.09
Caterpillars per flowering shoot (maximum):	<i>S. inaequidens</i>	0	0	0
	<i>J. vulgaris</i>	3	55	80
Percentage of individuals beheaded before seed maturation:	<i>S. inaequidens</i>	0	0	0
	<i>J. vulgaris</i>	1	14	86

heads have been eaten, with only stems remaining ungrazed. Approximately half of these individuals showed compensatory growth, and produced secondary flowering heads and set fruit in September, when caterpillars had pupated. In Antwerp in 2007, caterpillars were very abundant and attacked nearly all the *J. vulgaris* plants (Table 2), so that a very small part of the population was able to set fruit in July. Seven out of 50 monitored individuals of *J. vulgaris* produced on average 6 flowering heads only and set fruit in 2007. Only 10% of the grazed plants produced secondary flowering heads (1 to 4 for per plant). On average (over the three years), impacts of *T. jacobaeae* prevented flowering in 34% of the individuals. For *S. inaequidens*, all the monitored individuals produced an average of 122 flowering heads per plant and successfully set fruit.

3.3. Pyrrolizidine Alkaloids

For all stages pooled, a total of 13 and 14 different PAs were detected in *S. inaequidens* and *J. vulgaris*, respectively and 7 were shared (Table 3). Only five of these PAs corresponded to known compounds, i.e., senecionine, seneciphylline, integerimine, jacobine and erucifoline. The PA profile of *S. inaequidens* was dominated (56%) by an unknown compound not detected in *J. vulgaris*. The profile of *J. vulgaris* included jacobine (37%), erucifoline (28%) and senecionine (14%).

The PA concentration significantly increased ($F = 38.2$, $p < 0.001$) across the successive life stages from seed-

lings to flowering heads, except for the rosettes of *J. vulgaris* which contained higher PA than adult flowering plants. The composition also varied with life stages as 7 - 8 different PAs were detected in seedlings and 12 - 13 different alkaloids were present in flowering heads (Table 3). The total concentrations were not significantly different between the two species at the adult stage ($F = 2.37$, $p = 0.11$) while they were higher in the flowering heads of *S. inaequidens* than in those of the native species ($F = 9.64$, $p = 0.011$).

4. Discussion

Previous work showed that the alien *Senecio inaequidens* does not escape herbivory in Europe, with more than 62 species of insects feeding on it in Germany [34, see also 35]. Heteropteran species and rabbits had a significant negative effect on fitness [31]. In Spain snails and slugs had impacts on the alien species too [36]. In our sites, gastropods had almost no effect whereas rabbits negatively impacted survival and biomass of seedlings. Nevertheless, gastropods had a negative impact in an experimental garden experiment with potted plants of both species [37]. Rabbits had a more pronounced negative effect on the alien *S. inaequidens* than on the native species.

On the contrary, the specialist caterpillar *Tyria jacobaeae* had no effect on the alien species while it can destroy all the flowering population of the native species, thus having a great negative impact on the reproductive

Table 3. Pyrrolizidine alkaloids (PA) composition and contents (in µg/mg dry weight) for the different life stages of *S. inaequidens* and *J. vulgaris*. tr= traces (<0.02 µg/mg).

Retention time	PA	<i>S. inaequidens</i>			<i>J. vulgaris</i>			
		Seedling	Adult stem	Flowering head	Seedling	Rosette	Adult stem	Flowering head
3.88	unknown	tr	tr	tr	0.02 ± 0.003			
4.7	unknown	tr	tr	tr	tr	tr	tr	tr
6.72	unknown				tr			
7.37	unknown							0.01 ± 0.03
7.55	unknown	tr	0.16 ± 0.06	1.05 ± 0.40				
7.67	senecionine	tr	0.18 ± 0.22	2.03 ± 2.49	0.06 ± 0.08	0.35 ± 0.50	0.15 ± 0.13	0.83 ± 0.76
7.90	seneciophylline				0.05 ± 0.06	0.13 ± 0.22	0.09 ± 0.13	0.75 ± 0.43
8.11	unknown	tr	tr	0.01 ± 0.02	0.03 ± 0.05	0.01 ± 0.02		0.02 ± 0.04
8.50	integerimine	tr	0.16 ± 0.14	1.43 ± 0.92	tr	0.09 ± 0.15	0.02 ± 0.06	0.36 ± 0.10
9.75	unknown		tr	0.03 ± 0.04				
9.92	jacobine					1.35 ± 0.81	1.17 ± 1.69	1.37 ± 0.87
10.41	unknown					0.03 ± 0.07	0.02 ± 0.04	0.06 ± 0.08
10.83	unknown			tr		0.15 ± 0.13	0.12 ± 0.20	0.23 ± 0.15
11.37	unknown	tr		0.04 ± 0.06				
11.52	erucifoline					1.12 ± 0.17	0.23 ± 0.22	1.69 ± 0.74
11.55	unknown	tr	1.05 ± 0.65	6.25 ± 2.68				
12.41	unknown		0.03 ± 0.07	0.03 ± 0.07				
12.97	unknown		0.16 ± 0.30	0.97 ± 0.52				tr
13.80	unknown					tr		0.12 ± 0.29
total			1.75 ± 1.06	11.8 ± 3.84	0.16 ± 0.23	3.22 ± 1.67	1.80 ± 2.21	5.44 ± 1.30

success. These results are in agreement with some studies [31], but contradictory with others [28] where caterpillars have been sporadically observed feeding on *S. inaequidens*.

4.1. Influence of Alkaloids

Explanation for differences in herbivore preferences may lie in PA concentrations for flowering life stages. PA defences are synthesized in roots and translocated to shoots; as for most plant defences, reproductive organs usually show the highest concentrations [33]. The high PA concentrations in flowering heads of both species are consistent with previous results showing that 79% of PA in those species is located in inflorescences [38]. We did not detect any difference in total PA concentrations between the two species in adult leaves like in [9]. Nevertheless, differences in concentrations among populations have been reported [9,32,39,40]. Extracts of *S. inaequidens* are considered to stimulate oviposition of *T. jacobaeae* females [41]. However, larvae fed with *S. inaequidens* under controlled conditions did not survive [32]. The absence of some PAs (including jacobine or erucifoline for example) might explain why *T. jacobaeae* did not consume the alien species [19,41].

For both species, seedlings contained only traces of PA and represented the most palatable stage. Therefore,

differences in rabbit damages between the two species cannot be ascribed to PA defences. Differences in seedling morphology might be more important. Seedlings of *S. inaequidens* possess erect leaves while those of *J. vulgaris* form a rosette closely pressed onto the soil, thus being less easily grazed by mammalian herbivores including rabbits [42].

4.2. Herbivore Impacts throughout the Life Cycle

Based upon assessments of herbivore damage, we tentatively calculated an overall estimate of the global effect of herbivory on the whole life cycle for both species (**Figure 2**). The initial number of seedlings for the estimation was fixed to 100. Germination rates are 67% for *S. inaequidens* and 57% for *J. vulgaris* [36]. Adult plants of the invasive *S. inaequidens* typically have several ramified flowering shoots and produce on average 122 flower heads per plant, even in the first year following germination and each flowering head bears on average 59 seeds [29,43]. The survival of *J. vulgaris* rosettes to the adult stage was estimated as ca. 76% [44]. There are on average 6 flowering heads per plant and 32 seeds per flowering head for *J. vulgaris* [29,45]. Even if the native *J. vulgaris* suffers from lower damage at the seedling stage and the survival rate remains high during the first year,

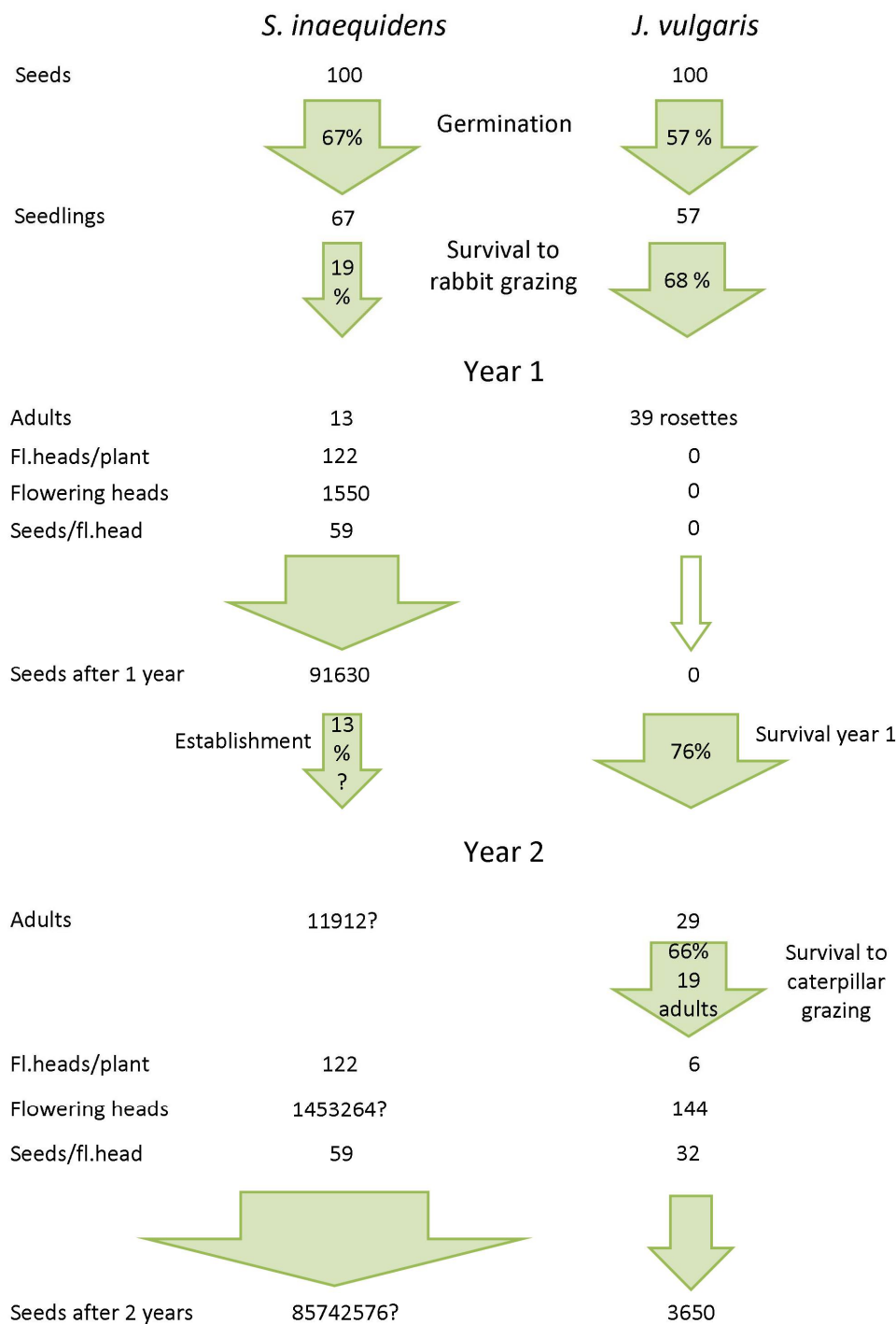


Figure 2. Global estimation of herbivore damage on the life cycle of *S. inaequidens* and *J. vulgaris*.

lower flowering head production, high damage due to the specialist caterpillar and lower seed set per flowering head explain the mean seed production that only reaches 3650 seeds after two years. This huge difference in seed production can explain the invasive success of *S. inaequidens* in Europe.

Several other studies already suggested that invasive-

ness may be the result of different combinations of particular functional traits such as high reproductive success [46], dispersal ability [47], increased size or competitive ability [12]. Moreover, multiple introductions, environmental preadaptation and high gene flow along invasion routes also contributed to the success of this rapid *Senecio* invader [48].

5. Conclusion

Senecio inaequidens suffers from herbivory mostly at the seedling stage, due to generalist herbivores, i.e. rabbits in this study. For *J. vulgaris*, the flowering stage was the most heavily affected, due to the attacks from the specialist moth *Tyria jacobaeae*. Finally, the global estimation of herbivory pressure throughout the life cycle suggests that populations of *S. inaequidens* can still grow faster compared to *J. vulgaris*, and that herbivore pressure cannot control the invasion. This conclusion is in line with the rapid expansion of *S. inaequidens* in Europe.

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