

Original article

Life-history traits of alien and native *senecio* species in the Mediterranean region

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Abstract

Two related shrubs, *Senecio inaequidens* and *S. pterophorus*, both introduced to western Mediterranean Europe from South Africa, were compared with a native Mediterranean shrub, *S. malacitanus*, to identify life-history traits that confer invasive ability. We examined ecological interactions that affect seedling emergence and establishment, flowering time, growth and reproduction and competitive ability in these three closely related species. Seeds were planted, the seedlings were then transplanted and individual performance was evaluated with respect to: (1) competition with plant neighbours and (2) resource addition. *Senecio inaequidens* had higher rates of seedling establishment and a shorter pre-reproductive period. Competition with neighbours had a considerable impact on *S. malacitanus*, delaying flowering time and reducing growth and reproduction. *S. pterophorus* showed inefficient seedling establishment compared to the other two species, but performed better in terms of growth and reproduction. The two alien species were markedly more competitive than the native one. However, differences in competitiveness among *S. malacitanus* and the two aliens varied depending on resource availability. Thus, *Senecio inaequidens* and *S. pterophorus* were more affected by competition in subplots with resource addition and by competition in those without addition, respectively. The latter showed a greater capacity to respond to additional resources in competitive environments and, in addition, its reproductive effort was unrelated to habitat conditions. The invasive potential of the alien species was higher than that of the native. This was a result of various biological characteristics and specific interactions between invader and environment, which made the invasiveness of alien species unpredictable.

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1. Introduction

Invasion has been defined as the introduction, establishment and expansion of a new species in a community in which it was previously absent (Mack, 1985; Groves, 1986). The process is distinguished from colonisation on the basis of the biogeographical origin of the invading species and the detrimental effects that its expansion has on the new community (Mack, 1996; Drake et al., 1989). Invasion by alien species causes major problems in most regions of the world. Invasive species can alter natural communities by competing with and displacing native ones (Drake et al., 1989; Vitousek and Walker, 1989; Vitousek, 1990; Gordon 1998), modifying function (Blank and Young, 2002), and, in addition, they

cause economic loss (Pimentel et al., 2000). Plant invasion can be viewed in the context of global change, as they have a considerable impact on biodiversity (Mack et al., 2000; Chapin et al., 2000).

Many studies on plant invasion have focused on the life-history traits responsible for the invasive nature of a species (Baker, 1965, 1974; Noble, 1989; Roy, 1990; Rejmánek and Richardson, 1996), while others have examined the invasibility of habitats and communities (Crawley, 1986, 1987; Lonsdale, 1999; Levine and D'Antonio, 1999). Recently, several authors have proposed the hypothesis that the successful establishment of an alien species depends on complex interactions between the species and its target community, so that biological invasions are essentially context-specific processes (Thébaud et al., 1996; Levine, 2000; Alpert et al., 2000). The implication of this theory is that small differences in the life-history traits of certain species, such as germina-

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tion, establishment ability, length of the juvenile period (D'Antonio, 1993; Rejmánek and Richardson, 1996; Dietz et al., 1999) and competitive ability (Thébaud et al., 1996), may interact with habitat characteristics to produce distinct distribution and abundance patterns throughout a new range. Moreover, since invasive species are usually released from the pressure of herbivores and parasites in the invaded region (Keane and Crawley, 2002), there is an increased allocation of resources for growth as a result of a reduction in resources used for defence against herbivores (Blossey et al., 1994). This increased growth can confer invasive species superior competitive ability than that of natives (Bakker and Wilson, 2001). Studies within genera have produced a clearer picture of this scenario than those conducted within entire floras. However, although comparative studies of life-history events conducted among related species can provide information that partly explains differences in performance, invasiveness is essentially unpredictable because of the specific interactions between the invader and its new range (Radford and Cousens, 2000). Therefore, rather than seeking global explanations of invasiveness, which may not exist, it is more meaningful to examine the life-history traits of a group of closely related species (Mack, 1985, 1996; Grotkopp et al., 2002) within a single habitat or environmental gradient (Radford and Cousens, 2000), thereby avoiding the confounding effect of phylogeny on the traits analysed.

To our knowledge, few experimental studies in which environmental factors are manipulated have been conducted to examine the ecological interactions that affect the performance of closely related invaders and native perennial taxa (Thébaud et al., 1996). There is considerable evidence that the emergence and establishment of plant invaders are generally favoured when communities are subject to disturbance (Burke and Grime, 1996; Crawley, 1986, 1987; Mack, 1985). Moreover, disturbance can produce nutrient enrichment or a release of resources in the disturbed habitat, thus favouring the proliferation of the invading species (Davis and Pelsor, 2001). Most exotic species grow in disturbed and nutrient-rich ecosystems (Fox and Fox, 1986; Hobbs and Huenneke, 1992; Meiners et al., 2002). Studies on the potential influence of established vegetation on invasibility are few, but some have shown that invasion potential and competitive ability are positively related (Thébaud et al., 1996). Competition plays a key role in structuring communities, and its intensity may depend on resource availability (Grime, 1979). Moreover, fluctuation in the latter may greatly contribute to controlling the invasibility of communities (Davis et al., 2000). The circumstances under which *Senecio jacobaea*, a biennial or short-lived perennial herb, becomes invasive have been reported using a combination of factorial experiments (manipulating plant competition, and natural enemies) and structured population models (McEvoy et al., 1993; McEvoy and Coombs, 1999).

The genus *Senecio* L. includes native and alien perennial species that grow in the Mediterranean region. The invaders *S. inaequidens* and *S. pterophorus* from South Africa and the

native *S. malacitanus* provide a good biological model for comparing respective life-history traits because they are taxonomically related and ecologically similar. Moreover, there is no information available on the ecology of *S. pterophorus* or on *S. malacitanus*, while data on the ecology and life-history attributes of *S. inaequidens* are scarce (Werner et al., 1991; Ernst, 1998; López and Maillet, 1998).

Here we studied the differences in the life-history traits of the alien invasive *S. inaequidens* and *S. pterophorus* and the native *S. malacitanus*. We also determined the effects of the addition of resources and competition with neighbours on interaction strength and the impact on seedling emergence and establishment, time to first reproduction, growth, and reproduction. To determine whether the invaders have advantages over the native, this study focused not only on the invaders but also on the recipient community.

The experiment was based on simulated colonisation by means of planting seeds and transplanting seedlings of the three *Senecio* species in an experimental field. Two factors, competition by neighbouring vegetation and resource addition, were manipulated to assess the extent to which ecological interactions affect species performance. Although the three species are shrubs, and long-term studies are required to examine their life-history traits, we focused on the first stages of the life cycle, which are the most crucial in determining successful establishment of a species in a new site. Here we addressed the following questions:

- (i) Is seedling emergence and establishment affected by competition and resource availability? Does the response of the three species differ?
- (ii) To what extent are growth and reproduction affected by competition and availability of resources? Do growth and reproduction rates of the three species differ? If so, what causes these differences?
- (iii) Does the intensity of competition vary with availability of resources? Do these species show any differences in this respect?

2. Material and methods

2.1. Study species

The three species studied were *Senecio pterophorus* D.C., *S. inaequidens* D.C. and *S. malacitanus* Huter (Asteraceae). The latter is native to the Mediterranean area, while the first two are alien invaders, native to the province of Natal, South Africa. The three species are ecologically similar and all colonise disturbed ruderal habitats, though they differ in their geographical distribution and in the density and abundance of their populations.

The introduction of *S. pterophorus* into mainland Europe is recent; it was first recorded in 1995 around the metropolitan area of Barcelona and in recently burned areas (Pino et al., 2000), and it has also been reported in the British Isles (Stace, 1997). It forms dense populations of around

3 individuals/m². It has also been reported in southern Australia from 1930 (Parsons and Cuthbertson, 1992). In Europe, *S. pterophorus* is mainly found in disturbed riverbeds and waste nitrophilous areas. *Senecio inaequidens* was introduced into Europe via sheep wool at the end of the nineteenth century (Ernst, 1998), and today it is widely distributed in many countries of Europe. It has been found in the NE of the Iberian Peninsula since the second half of the 1980s (Casasayas Fornell, 1990). *Senecio inaequidens* is currently establishing itself as a weed of considerable significance in southern France (López and Maillet, 1998) and northern Catalonia because its high toxic alkaloid content (Ernst 1998) is rejected by cattle. It forms dense populations ranging from 5 to 15 individuals/m². The native *S. malacitanus* forms sparse populations (around 0.1 individuals/m²) and colonises dry and nitrophilous disturbed habitats such as dry riverbeds and waste ground in SE Spain. It is also found in parts of Morocco and Algeria (Bolós and Vigo, 1995).

2.2. Seed germination trials

Seeds from 20 randomly selected individuals of three populations of *S. inaequidens*, two of *S. malacitanus* and one of *S. pterophorus* were collected from September to December 1998. Ripe seeds were cleaned and stored at room temperature in darkness until use. Seeds were exposed to eight constant temperature regimes, from 5 to 40 °C, with a 12:12 h (dark: light) photoperiod in a growth chamber. Illumination intensity was 12000 µmol PAR (Photosynthetically Active Radiation) m⁻²s⁻¹. We used four replicates of 50 seeds for each population and temperature regime. Seeds were placed in Petri dishes with a moist filter paper to assure water availability (we used distilled water for this purpose). Germinated seeds were counted and removed daily. Radicle protrusion was considered to be the criterion for germination.

2.3. Site manipulation and experimental design

This study was carried out between March and November 1999 at an experimental field at the University of Barcelona (41° 20' N, 2° 05' E, 120 m above sea level). The climate is Mediterranean, with rainfall averaging 600 mm per year, and with mean monthly temperatures ranging from 29°C in July to 10°C in January.

In March 1999, a uniform area of 10 x 12 m was delimited. This area was ploughed and divided into four 5 x 4 m blocks 1 m apart. The surrounding 50 cm border acted as a buffer zone in which the vegetation received the same treatment as the subplot immediately adjacent to it, thereby reducing edge effect from surrounding vegetation. Each block was subdivided into two equal 1.5 x 5 m plots 1 m apart. In one of these plots, nutrients and water were periodically added to the soil (R) while no additions were made in the other (NR). Each block was further divided into two 2 x 4 m plots spaced 1 m apart. In one of these plots, vegetation was periodically removed so there was no aboveground competition from

neighbouring plants (NC), while natural vegetation was left intact in the other (C) after the first ploughing. The combination of these two factors, availability of resources and interspecific competition, produced a total of four 1.5 x 2 m treatment plots. Each of these contained three equal 1 x 0.5 m subplots 0.5 m apart and one of the target species was randomly assigned to each. The randomisation of treatments between plots and target species within plots reduced the systematic effect of species or treatments on species estimators or treatment responses.

For the vegetation removal treatment, all emerged neighbouring seedlings were periodically removed by hand over the course of the experiment. For the resource addition treatment, we applied fertiliser in granular form (15:15:15 N-P-K) in two applications, equivalent to 77 Kg/Ha of each element. Plots were irrigated at regular intervals from one to three times per week. We applied a total of 649 mm of water over the study period. Plots were watered with a hose with a fine sprinkler attachment to allow the water to soak into the soil and to minimise lateral movements of water.

In summary, the effects of neighbourhood competition and resource addition on species performance were analysed by means of a split-plot experimental design (Snedecor and Cochran, 1966), with vegetation removal and water and nutrient addition as the main factors and with species as the split-plot factor.

The floristic composition of each subplot and the abundance of each neighbour species were evaluated in July by a relative abundance index for each species, with a ranking from one to five.

2.4. Transplantation of seedlings

Seeds from 20 individuals were collected from selected natural populations of each species between November and December 1998. *Senecio malacitanus* seeds were collected from sparse shrubland at Rambla del Rambuchar, Alicante (38° 28' N, 0° 14' E). *Senecio inaequidens* seeds from roadside waste ground at El Figaró (41° 43' N, 2° 17' E), 30 Km north of Barcelona while those of *S. pterophorus* were collected from the Ripoll river bank, near Barcelona (41° 29' N, 2° 11' E).

Seeds were air-dried and stored at room temperature in paper bags until sowing. For convenience of manipulation, pappus was removed from achenes prior to storage. In February 1999, the seeds were sown in Petri dishes in a solution of 10⁻³ M gibberellic acid, to stimulate simultaneous germination. Seeds with an emerged radicle were transplanted in bedding cells filled with a 1:1 mixture of sterilised sand and peat. Trays were placed on a greenhouse bench under optimal conditions (20 °C and natural photoperiod). In March 1999, 6 seedlings per 1 x 0.5 m species subplot were transplanted in a regular pattern with a constant 0.5 m interplant spacing (see site manipulation and experimental design section). Seedlings were planted at a density intended to minimise intraspecific competition. Seedlings and their vicinity were sprayed

with water on the day of transplantation to minimise transplant shock. None of the 288 transplants died in the first few weeks of the experiment.

2.5. Germination, emergence and establishment in the field

Two 9 cm diameter circular plots were located in each 1 x 0.5 m species subplot to compare emergence and establishment among species. Circular plots were placed to avoid competition for resources and light with transplants. Each surface was surrounded by a plastic ring (3 cm in height) to prevent seed movements caused by rainfall or watering. On 23rd April 1999, 25 seeds were surface sown on each circular plot.

2.6. Seedling emergence and establishment

Seedling emergence was evaluated 7 days after sowing, and the exact location of the seedlings on each circular surface was mapped. From March onwards, new seed emergence and establishment were mapped weekly, although no emergence was recorded after May. Successful establishment was noted at the transition between the four-leaf stages. Seedlings were removed after their establishment and were recorded. There was no contribution from pre-existing seeds in the seed bank and there was no input of new seeds during the experiment.

2.7. Growth and reproduction of established plants

The flowering time of each transplant was recorded at weekly or two-weekly intervals from the time of transplanting to the end of the experiment. Death from desiccation was assumed when shrivelled plants were found. We observed no other apparent cause of mortality over the course of the experiment. No signs of predation on leaves, stems or seed heads were detected.

The growth pattern of species within each treatment was evaluated from the final dry weight of each plant and the reproductive output was evaluated by counting the number of seed heads per plant monthly. Reproductive strategy was evaluated from the relationship between reproductive and vegetative dry weight. In November 1999, plants were uprooted and separated into roots and aerial parts. These two parts were dried at 100°C for 48 h and weighed. To evaluate the dry mass of reproductive structures, 20 ripe seed heads were randomly collected for each species and treatment, dried at 100°C for 48 h and weighed. The reproductive biomass of each plant was estimated as the product of mean seed head dry weight and the number of seed heads of each individual. Aboveground vegetative dry biomass was calculated as the difference between total dry aboveground and reproductive dry biomasses.

2.8. Statistical analysis

Because no significant differences in seed germination rates were found among populations for *S. inaequidens* and for *S. malacitanus* in each temperature, these populations were pooled for each species and temperature combination. The germination rates were statistically compared among species for each temperature by means of one-way analysis of variance. Differences among species were analysed using the LSD method. The degree of significance was $P < 0.05$.

The split-plot model (Snedecor and Cochran, 1966) with vegetation removal and resource addition as the main factors and species as the split-plot factor was used to analyse: (1) The effect of competition and resource addition on the proportions of seedling emergence and establishment, (2) the mean flowering time, and (3) the total dry weight and seed head number per transplant. The performance of target species within each treatment was a result, therefore, of the combination of competition and resource availability.

To avoid pseudo-replication, in each analysis we computed the mean flowering time, the mean dry weight and the mean seed head number for each species subplot within the treatment plot (Hurlbert, 1984). Assumptions of normality were checked by applying the Kolmogorov-Smirnov test with the Lilliefors correction (SPSS, 1999). Data were transformed, where necessary, to achieve normality and homoscedasticity of residuals. Non-proportional data were log-transformed and arcsine square root transformation was applied for proportional data.

The analysis of reproductive allocation pattern was performed following Samson and Werk (1986) and Weiner (1988), who proposed that for several species a large proportion of variation in reproductive effort is due to intrinsic size effect. This effect can be analysed by examining the ratio between reproductive and vegetative biomass, called reproductive effort, by means of regression techniques (Klinkhamer et al., 1990; Sans and Masalles, 1994; Schmid and Weiner, 1993; Pino et al., 2002). Allometric regressions between reproductive and vegetative biomass were calculated for each species and environmental condition by linear regressions. Note that vegetative instead of total biomass was used as the independent variable so as to avoid autocorrelation in the regression analysis. The degree of variation of reproductive biomass among species within each treatment and among treatments within each species were tested by means of a coincidence test, which consists of two consecutive tests to compare, respectively, the slope and the y-intercept of the regression lines (Cuadras, 1991).

Competition intensity, calculated as the reduction in performance caused by the presence of neighbours in comparison to the level of performance achieved in their absence (Wilson and Keddy, 1986; Campbell and Grime, 1992), was also compared among species and between resource addition treatments. We used the relative form because the responses of plants to environmental gradients can be separated from their responses to one another (Wilson and Tilman, 1993;

Grace, 1995). The relative competition intensity was calculated as

$$RCI = (B_{NC} - B_C) / B_{NC}$$

where B_{NC} and B_C represent the plant performance expressed as mean final dry weight, in C and NC subplots, respectively. RCI was calculated in each block for species in R subplots (RCI_R) and in NR subplots (RCI_{NR}). The statistical significance of a difference between the two RCIs, among the three species, and the interaction between these two factors was tested with a two-way analysis of variance. One RCI value of *S. inaequidens* and one of *S. pterophorus* were rejected because they were suspected outliers.

3. Results

3.1. Environmental data

Although no differences were recorded in the floristic composition of R/C and NR/C subplots, these subplots differed in their vegetation cover and in the relative abundance of each species (Table 1). Vegetation cover in NR subplots was 60.83% and was dominated by annuals such as *Urtica urens*, *Lamium amplexicaule* and *Amaranthus retroflexus*, whereas in R subplots cover was as high as 80% and the perennial grass *Dactylis glomerata* was dominant.

3.2. Seed germination

The three species displayed a high percentage of germination in a wide range of temperatures, from 5 to 30 °C, and the germination rate did not differ significantly among species. While the rate of seed germination was also high at 35 °C for *S. inaequidens*, the percentage of germination was significantly lower for the other two species (Fig. 1a). For all species, a small percentage of seeds germinated at 40 °C (Fig. 1a). At all the temperatures tested *S. pterophorus* was the last species to start germination and had the slowest germination rate, as shown by the shape of the germination curve (see at 20 °C as an example; Fig. 1b).

Table 1
Mean vegetation cover (%) of the most abundant species in vegetated plots. Nomenclature follows Bolòs and Vigo (1995)

Resources added (R)		No Resources added (NR)	
<i>Dactylis glomerata</i>	46.25	<i>Urtica urens</i>	25.83
<i>Urtica urens</i>	20.63	<i>Lamium amplexicaule</i>	23.13
<i>Lolium rigidum</i>	19.17	<i>Amaranthus retroflexus</i>	10.29
<i>Lamium amplexicaule</i>	11.89	<i>Dactylis glomerata</i>	6.67
<i>Amaranthus retroflexus</i>	4.20	<i>Medicago lupulina</i>	2.98
<i>Amaranthus blitoides</i>	2.93	<i>Polygonum aviculare</i>	2.74
<i>Medicago lupulina</i>	1.29	<i>Lolium rigidum</i>	2.36
<i>Convolvulus arvensis</i>	0.71	<i>Chenopodium album</i>	1.46
<i>Melilotus officinalis</i>	0.69	<i>Erodium malacoides</i>	1.27
<i>Sonchus tenerrimus</i>	0.68	<i>Convolvulus arvensis</i>	0.50
<i>Senecio vulgaris</i>	0.31	<i>Senecio vulgaris</i>	0.47
<i>Lactuca serriola</i>	0.28	<i>Sonchus oleraceus</i>	0.43

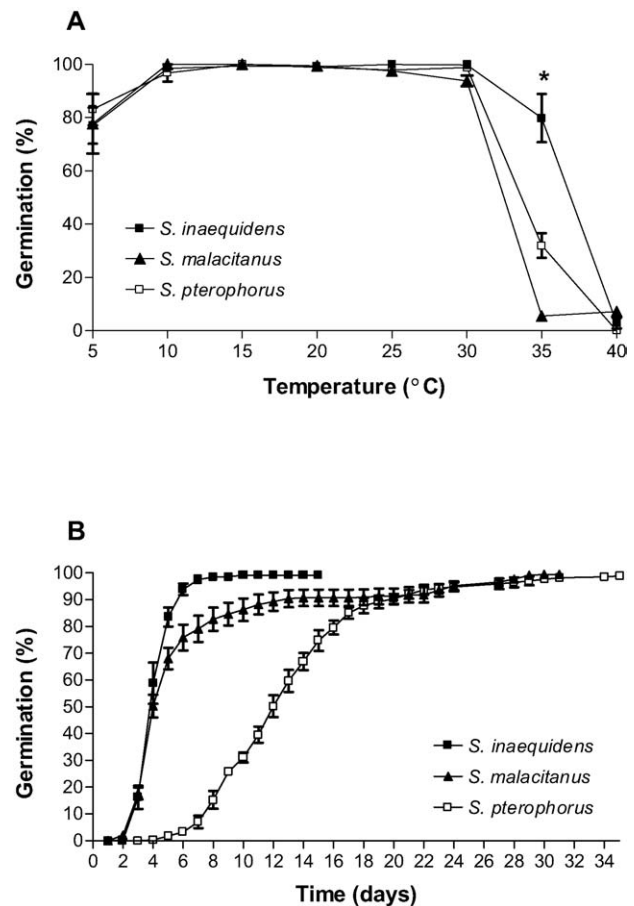


Fig. 1. Percentage (Mean \pm S.E.) of seed germination according to temperatures for each species (a) and seed germination of the three species in a growth chamber, at 20 °C and 12:12 h (light: dark) photoperiod (b). Data shown are mean of three populations for *Senecio inaequidens*, mean of two populations for *S. malacitanus* and a single population for *S. pterophorus*.

3.3. Seedling emergence and establishment

Seedling emergence of the three species was mainly recorded in R subplots (Fig. 2a). No *S. malacitanus* seedlings and only 0.5 ± 0.5 % (Mean \pm S.E.) of those of *S. pterophorus* emerged in NR/NC subplots, and the emergence of *S. inaequidens* seedlings ranged from 21 ± 7.60 % to 3 ± 2.37 % in NR/C subplots and in NR/NC subplots, respectively. Seedling emergence differed significantly among species in R/NC subplots (Fig. 2a). Thus, while about 45% of *S. inaequidens* and 30% of *S. malacitanus* seedlings emerged, the emergence of *S. pterophorus* was about 3-times lower (Fig. 2a). The emergence of *S. inaequidens* was significantly higher than that of the other two species in NR/C subplots. Our data show that the presence or absence of additional resources was a more determining factor than the presence or absence of competition because the differences in emergence were higher when resource availability varied than when competition varied.

Because of dramatic seedling mortality of the three species in C subplots, the pattern of seedling establishment related to resource availability differed markedly from that of seedling emergence (Fig. 2b). Only about 5% of

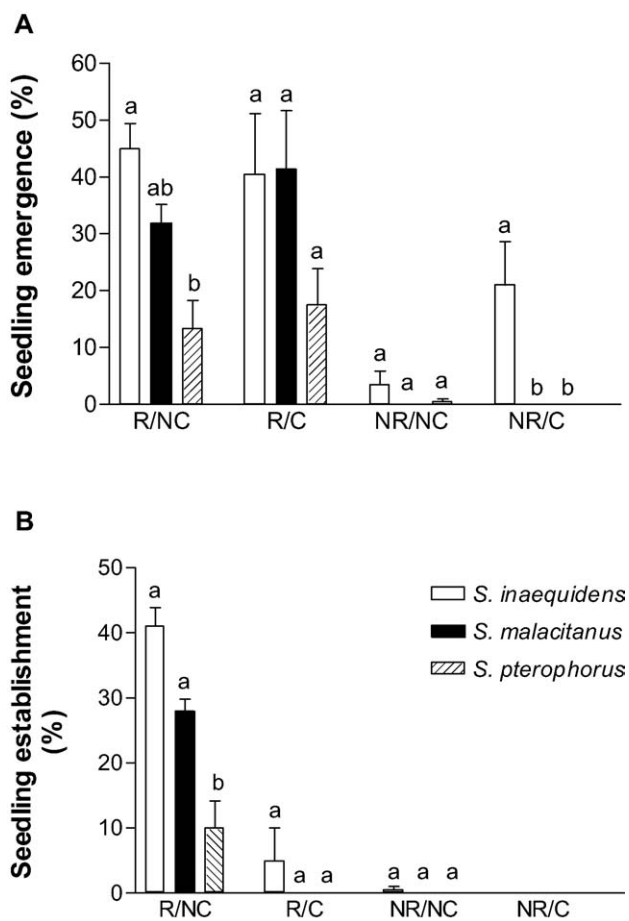


Fig. 2. Proportion of seeds sown that produced seedlings (a) and established plants (b) for each species in relation to the presence (C) and absence (NC) of competition, and with additional resources (R) and without (NR). Data represent means \pm S.E. of replicate subplots in each case. Columns within each treatment with the same letter above are not significantly different ($P < 0.05$) by the Tukey test.

S. inaequidens seedlings established in R/C subplots. The establishment of *S. inaequidens* and *S. malacitanus* was 4 and 3 times higher than *S. pterophorus* in R/NC subplots (Fig. 2b).

3.4. Flowering time

The pattern of flowering clearly varied among species (Fig. 3). Maturity occurred very early in *S. inaequidens*; most plants started flowering 7 to 8 weeks after transplanting in all treatments (Fig. 3a). However, that of *S. malacitanus* and *S. pterophorus* was more gradual. The flowering of the latter started 10 to 11 weeks after transplanting (Fig. 3b), while the length of the pre-reproductive period of *S. malacitanus* was the longest of the three (Fig. 3c). In the latter, a small number of plants started flowering 19 weeks after transplanting, but most flowered after between 25 and 27 weeks, depending on the treatment. While the flowering pattern of *S. inaequidens* was unaffected by resource availability and competition, small changes were detected in that of *S. malacitanus* and *S. pterophorus* related to environmental conditions.

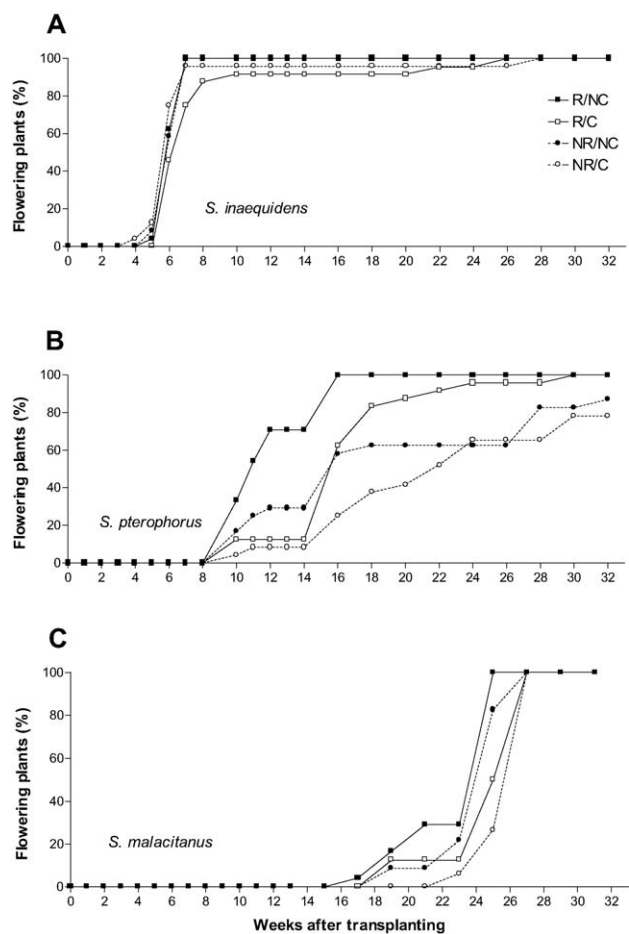


Fig. 3. Proportion of flowering plants from April till August of *Senecio inaequidens* (a), *S. pterophorus* (b) and *S. malacitanus* (c) in relation to the presence (C) and absence (NC) of competition, and with additional resources (R) and without (NR).

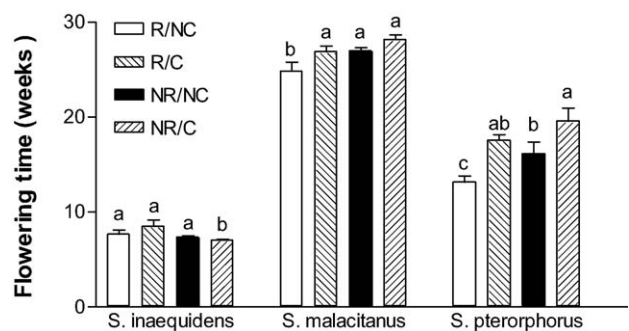


Fig. 4. Mean flowering time for each species and treatment. Treatments are presence (C) and the absence (NC) of competition, and with additional resources (R) and without (NR). Data represent means \pm S.E. of replicate subplots in each case. Columns within each species with the same letter above are not significantly different ($P < 0.05$) by the Tukey test.

The mean flowering time differed significantly among species ($F_{(2, 36)} = 773.28$, $P < 0.001$) and the pattern of variation related to competition and resources also differed among species (Fig. 4). While the mean flowering time of *S. inaequidens* was unaffected by competition, small changes were detected by resource addition ($F_{(1, 12)} = 8.23$, $P < 0.05$) because mean flowering was one week earlier in

NR/C subplots than in R/C subplots. The mean flowering time of *S. malacitanus* varied in response to competition ($F_{(1, 12)} = 9.05$, $P < 0.05$) and resources ($F_{(1, 12)} = 9.72$, $P < 0.05$). Thus, it flowered 2–3 weeks earlier in R/NC subplots than in the other experimental conditions. The flowering time of *S. pterophorus* was significantly affected by competition ($F_{(1, 12)} = 14.25$, $P < 0.01$) and resources ($F_{(1, 12)} = 5.68$, $P < 0.05$). It flowered 4–5 weeks earlier in NC subplots in both resource treatments and was also favoured by resource addition in NC subplots.

Overall, our results show that the effect of competition and resources on flowering time was very small in *S. inaequidens* and *S. malacitanus*, whereas the flowering time of *S. pterophorus* was delayed by a lack of resource addition, although it started earlier in conditions of no competition.

3.5. Growth and reproduction

Growth, assessed as total dry weight at the end of November, differed significantly among species ($F_{(2, 36)} = 63.51$, $P < 0.001$). The mean dry weight of *S. pterophorus* was two and three times higher than that of *S. inaequidens* and *S. malacitanus* in R/C subplots ($F_{(2, 9)} = 23.62$, $P < 0.001$) and R/NC subplots ($F_{(2, 9)} = 8.53$, $P < 0.01$) respectively (Fig. 5a). While mean dry weight did not differ significantly among

species in NR/NC subplots, the growth of *S. pterophorus* was significantly higher than that of *S. inaequidens* and the mean dry weight of the latter was also significantly higher than that of *S. malacitanus*.

The growth of *S. inaequidens* was more sensitive to competition ($F_{(1, 12)} = 10.64$, $P = 0.007$) than to resource addition ($F_{(1, 12)} = 6.47$, $P = 0.026$). For this species, growth was significantly reduced by competition in R subplots (Fig. 5a). In contrast, it was not affected by competition in NR subplots. The mean dry weight of *S. malacitanus* was significantly lower in C than in NC subplots in both resource treatments ($F_{(1, 12)} = 48.96$, $P < 0.001$). The addition of resources led to a significant increase in dry weight only in NC subplots ($F_{(1, 12)} = 20.48$, $P < 0.001$). Reduction in the growth of *S. pterophorus* caused by competition was not statistically significant, either in NR or R subplots (Fig. 5a). However, growth was statistically enhanced by R treatment at both competition levels.

Overall, competition had a greater effect on *S. inaequidens* and *S. malacitanus* than resource availability. In contrast, the opposite was observed for *S. pterophorus*.

Reproductive output, assessed as the mean number of seed heads per plant, was analysed only in those plants that flowered (Fig. 5b). The number of seed heads varied among species ($F_{(2, 36)} = 18.22$, $P < 0.001$). While reproductive output did not differ among species in NR subplots, the number of seed heads of *S. pterophorus* was significantly higher than that of the other two species in R/C subplots ($F_{(2, 9)} = 8.88$, $P < 0.01$), and the number of seed heads of *S. inaequidens* was significantly lower than that of the other two species ($F_{(2, 9)} = 9.19$, $P < 0.01$) in NR/NC subplots.

The pattern of seed head production in response to competition and resource addition also varied among species (species \times treatment interaction, $F_{(6, 36)} = 3.32$, $P = 0.011$). The reproductive output of *S. inaequidens* was unaffected by resource addition and by competition. In contrast, that of *S. malacitanus* was significantly reduced by competition in both resource treatments and significantly enhanced by resource addition in NC subplots. In *S. pterophorus*, reproduction was significantly enhanced by resource addition ($F_{(1, 12)} = 26.09$, $P < 0.001$) but unaffected by competition (Fig. 5b).

Overall, our results show that the effect of competition on reproductive output of *S. inaequidens* is in the same range as that of resource availability, and for *S. pterophorus* resource availability had a greater effect than competition. Finally, competition had a greater effect than resource availability for *S. malacitanus* because reproductive output was unaffected by resources addition in vegetated plots.

3.6. Reproductive effort

3.6.1. For distinct treatments within each species

There was a significant and positive linear relationship between reproductive biomass and vegetative biomass for each species and each treatment (Table 2).

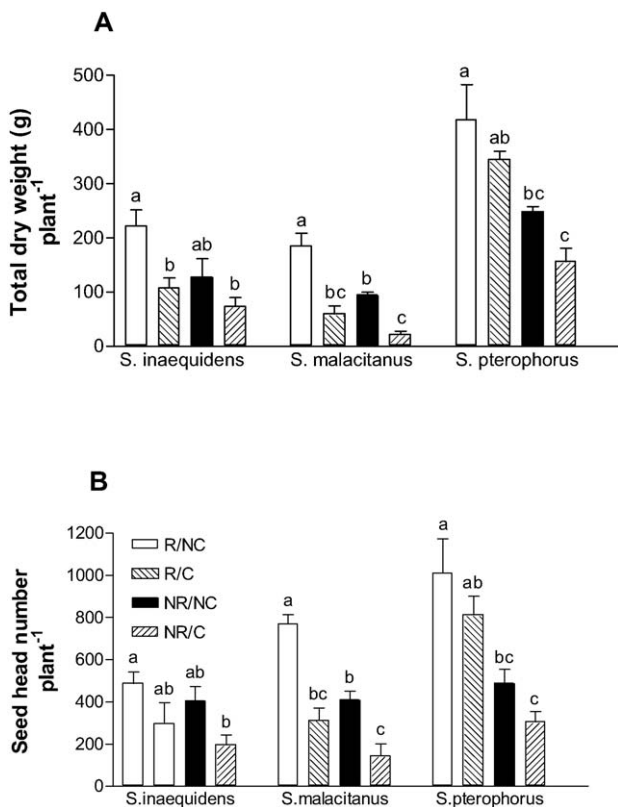


Fig. 5. Mean total dry weight (a) and mean seed head number (b) for each species and treatment. Treatments are presence (C) and the absence (NC) of competition, and with additional resources (R) and without (NR). Data represent means \pm S.E. of replicate subplots in each case. Columns within each species with the same letter above are not significantly different ($P < 0.05$) by the Tukey test.

Table 2

Parameters of linear regression between reproductive and vegetative biomass

	y-intercept	Slope	r ²
R/NC			
<i>S. inaequidens</i>	8.462**	0.075**	0.64***
<i>S. malacitanus</i>	8.363*	0.108*	0.48***
<i>S. pterophorus</i>	7.06	0.090**	0.58***
R/C			
<i>S. inaequidens</i>	-2.643	0.155*	0.70***
<i>S. malacitanus</i>	3.076**	0.150*	0.78***
<i>S. pterophorus</i>	8.408	0.085*	0.52***
NR/NC			
<i>S. inaequidens</i>	9.936**	0.098*	0.56***
<i>S. malacitanus</i>	0.576	0.180*	0.60***
<i>S. pterophorus</i>	5.582	0.073*	0.31*
NR/C			
<i>S. inaequidens</i>	0.464	0.140**	0.89***
<i>S. malacitanus</i>	0.06	0.296*	0.75***
<i>S. pterophorus</i>	-2.507	0.110**	0.73***

R: resources added; NR: no resources added; C: competition with neighbouring vegetation; NC: no competition with neighbouring vegetation.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.0001$.

Senecio pterophorus showed the same regression function in all treatments and no significant differences were found among slopes ($F_{(3, 75)} = 0.36$, $P = 0.776$) or y-intercepts ($F_{(3, 78)} = 1.64$, $P = 0.185$). This finding indicates that the pattern of size-dependence of RE and RE itself did not differ among the four treatments. In the other two species, the slopes of the regression lines of the four treatments were significantly different ($F_{(3, 72)} = 4.95$, $P = 0.0035$ for *S. inaequidens* and $F_{(3, 77)} = 2.80$, $P = 0.045$ for *S. malacitanus*; Fig. 6). Thus, the relationship of RE to size differed with treatments, and we therefore we could not test for differences among y-intercepts.

In *S. inaequidens*, our statistical results did not provide us with an insight into the environmental factors that affected the relationship between reproductive biomass and size. However, competition resulted in changes in slope (Fig. 6), which implies that the pattern of size-dependence of RE was related to habitat conditions.

In *S. malacitanus*, slope was affected by resources, but only when there was competition. However, this was only marginally significant, as shown by the small p-value of only 0.045 when comparing the four lines. The only treatment that altered slope significantly was that of the most extreme conditions (NR/C) (Fig. 6). The other three regressions were not statistically different ($F_{(2, 64)} = 1.67$, $P = 0.197$ for slope; $F_{(2, 66)} = 0.23$, $P = 0.797$ for y-intercept).

3.6.2. For distinct species within each treatment

The reproductive effort among species was compared only in the extreme environmental conditions, NR/C and R/NC. A comparison among species within each treatment (Fig. 7) shows that there were no differences among slopes ($F_{(2, 66)} = 0.58$, $P = 0.564$) or y-intercepts ($F_{(2, 68)} = 1.90$, $P = 0.157$) when plants were grown under optimal conditions

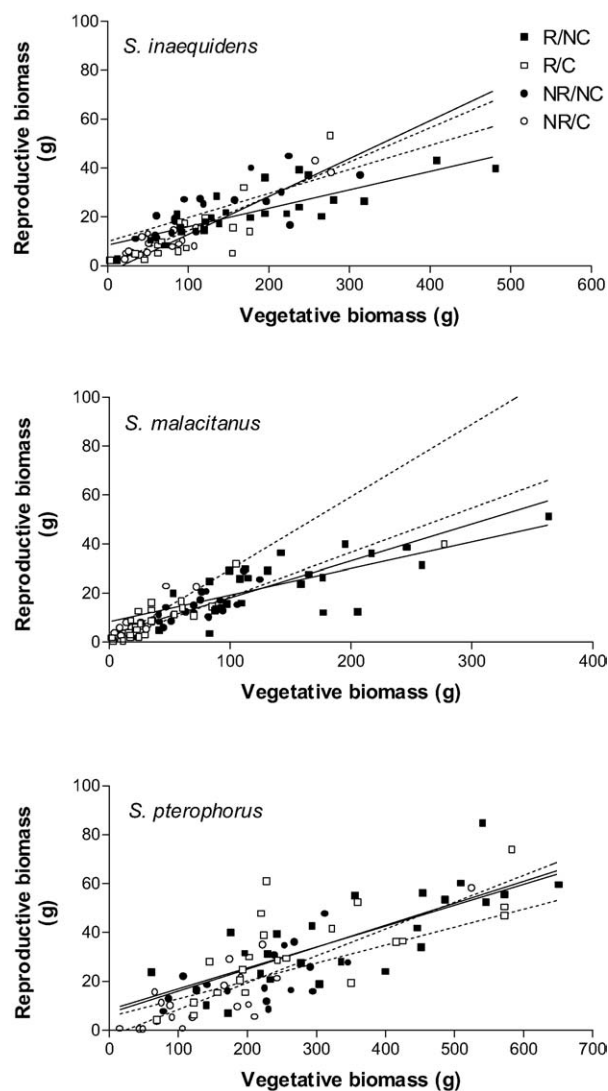


Fig. 6. Relationship between vegetative and reproductive dry weight for each species in the four treatments. The treatments were the presence (C) and the absence (NC) of competition and with additional resources (R) and without (NR).

(R/NC), revealing that reproductive effort was the same for all species. In contrast, when plants were grown under more stressful conditions (NR/C), the slopes differed ($F_{(2, 46)} = 3.78$, $P = 0.03$) and y-intercepts could not be tested. The pattern of size-dependence of RE among species differed when they were grown under extreme environmental conditions, with the highest slope for *S. malacitanus* and the lowest for *S. pterophorus* (Fig. 7). *Senecio malacitanus* invested most resources in reproduction under these conditions, while *S. pterophorus* had the lowest RE. Although we did not test the differences among the species' y-intercepts, small individuals of *S. malacitanus* invested as much as larger individuals of the other two species in proportion to resources (Fig. 7).

3.7. Competition intensity

Competition intensity differed significantly among species ($F_{(2, 16)} = 14.00$, $P < 0.001$) but not between resource

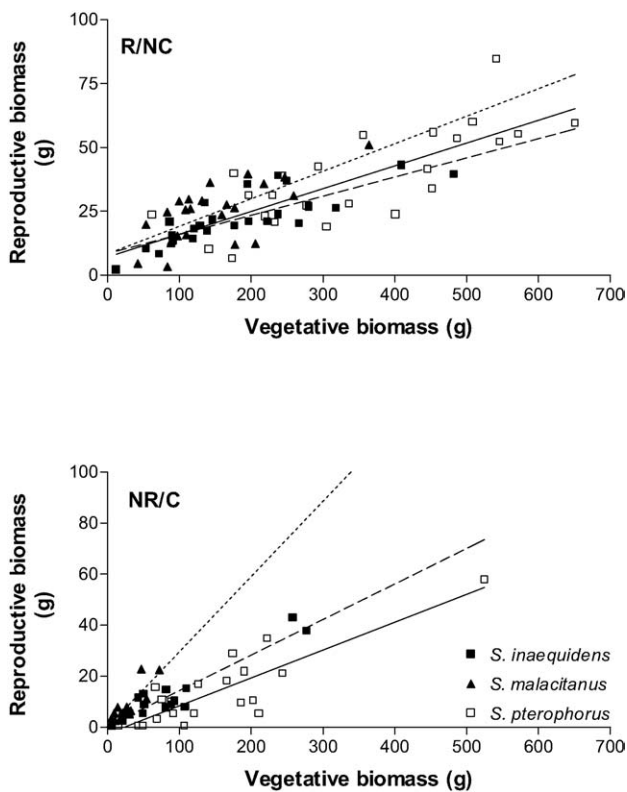


Fig. 7. Relationship between vegetative and reproductive dry weight comparing the three species in two contrasting environmental conditions: subplots without additional resources and competition (NR/C) and subplots with additional resources and without competition (R/NC).

Table 3

Relative Competition Intensity for each species in subplots with additional resources (R) and in subplots without additional resources (NR). Mean \pm S.E. followed by an asterisk indicates significant differences among species within a treatment

	R	NR
<i>S. inaequidens</i>	0.466 \pm 0.176	0.185 \pm 0.102 *
<i>S. malacitanus</i>	0.687 \pm 0.094	0.659 \pm 0.121
<i>S. pterophorus</i>	0.195 \pm 0.116 *	0.428 \pm 0.129

treatments ($F_{(1, 16)} = 0.002$, $P = 0.95$). Moreover, interaction between species and resources was only marginally significant ($F_{(2, 16)} = 3.05$, $P = 0.08$), showing that the mean RCI varied among species in response to resources. The mean RCI was significantly higher in *S. inaequidens* and *S. malacitanus* than in *S. pterophorus* in R subplots, and was significantly higher in *S. pterophorus* and *S. malacitanus* than in *S. inaequidens* in NR subplots (Table 3). Note that the mean RCI of *S. malacitanus* was the highest in both resource treatments, while the mean RCI of *S. pterophorus* and *S. inaequidens* were the lowest in R and NR subplots, respectively (Table 3).

4. Discussion

This study shows that water and nutrients are limiting factors for seedling emergence, as long as temperature does

not prevent germination, as shown by germination trials over a range of temperatures. While seedling emergence of the three species occurred when resources were added, regardless of competition, our results on establishment ability indicate that all three can colonise a new site only under low competition from neighbours and in conditions of resource addition. Other studies have shown the importance of environmental stress on the establishment of invasive species (Alpert et al., 2000) and for many species, establishment is more sensitive to stress than emergence (Turnbull et al., 2000). Our results confirm the inability of these three species to establish in undisturbed natural communities. The role of disturbance in favouring the establishment of *S. inaequidens* has also been reported by Cottrel et al. (1998) and López and Maillet (1998) in southern France. These studies agree with natural patterns of distribution and with the predominance of these species in disturbed sites, such as recently abandoned fields, river banks, and road margins. Many species cannot establish under a closed vegetation cover (Hobbs and Atkins, 1988), especially when they are small-seeded (Burke and Grime 1996). Moreover, there is strong evidence that disturbance enhances the invasibility of natural communities (Mack, 1985; Crawley, 1987) by increasing the availability of resources (McConnanghay and Bazzaz, 1991; Davis and Pelsor, 2001) and free space (Johnstone, 1986), or by decreasing competition with established vegetation (Hobbs, 1989; Hobbs and Huenneke, 1992; Wilson and Tilman 1995). The establishment of distinct species is higher when disturbance coincides with eutrophication (Burke and Grime, 1996). Our results also show a better performance of the three target species in “disturbed” (without neighbours) and “eutrophic” (with additional resources) conditions.

The presence of neighbouring vegetation enhanced the germination of *S. inaequidens* in the presence of additional resources. This effect, known as facilitation, is, like competition, a key factor in structuring communities (Callaway, 1995; Sans et al., 1998). However, when seedlings grow, they compete for resources with established vegetation, and therefore competitive interactions dominate.

Our results show no differences in emergence and establishment between the invader *S. inaequidens* and the native *S. malacitanus*, which contrasts with results obtained by Radford and Cousens (2000), who found that the alien *S. madagascarensis* emerged and established better than the native *S. lautus*. Under conditions without vegetation, it is surprising that *S. pterophorus* had the lowest establishment ability of the three species, even below that of the native *S. malacitanus*. However, the reproductive output of this species was the highest of the three; consequently, this could compensate, from a demographic point of view, for its low establishment ability. The small number of individuals that establish is not related to seedling mortality, but rather to a low seedling emergence rate. Our germination trials showed that the germination of *S. pterophorus* was always slower than that of the other two species. This may explain why, in Mediterranean conditions, where water availability is limited

even under an additional resource treatment, this slower germination rate limited seedling emergence.

A short pre-reproductive period may be particularly beneficial during colonisation events (Rejmánek and Richardson, 1996), as it allows a plant to reproduce early and to leave progeny even if another disturbance occurs (Cohen, 1966). Radford and Cousens (2000) found that alien invasive *Senecio* species in Australia flowered earlier than native ones. In our study, we also found that the pre-reproductive period was much shorter for the two alien species than for the native, and there were a higher proportion of individuals flowering early for the invaders. The age of first reproduction may be critical in determining the colonisation success of an alien species, especially *S. inaequidens*, in a new habitat subjected to periodic disturbances.

Abiotic and biotic factors may restrict invasion processes. The growth of alien species is more favoured by the availability of resources than that of natives in serpentine grasslands (Huenneke et al., 1990). Resource addition has a more positive effect on the growth and survival of alien than on native annual *Asteraceae* in Australia (Milberg et al., 1999). Furthermore, the invasive *Conyza sumatrensis* has a greater ability to survive in more extreme conditions than the less invasive *C. canadensis* (Thébaud et al., 1996). In our experiment, competition with neighbouring plants had a stronger impact on *S. malacitanus* than on the alien species, both in terms of growth and reproduction. The greater ability to uptake water in a competitive environment was also supported in our experiment in the case of *S. pterophorus*. Our results show that resource addition enhances the growth and competitive intensity in *S. pterophorus*.

Our analysis of growth and reproduction in terms of RE, defined as the resource investment in reproduction that results in its diversion from vegetative activities, show that there is no clear pattern of response to the presence of competitive vegetation and resource addition. In the case of *S. pterophorus*, there was no significant effect of treatment, while in *S. inaequidens* and *S. malacitanus* there was a trade-off between growth and reproduction under situations of stress, but responses varied among treatments. No clear pattern of RE variation related to environmental constraints emerged as there was as much difference between the native species and one of the aliens as there was between the two alien species.

Senecio pterophorus showed a similar reproductive effort over the range of competition and resource addition conditions tested. The energy allocation of this species was relatively inflexible, determining the proportion of resources to invest in reproduction regardless of environment. Therefore, its success in invasion can be explained better in terms of growth than reproduction because of its fixed reproductive strategy. In our experimental conditions, the addition of resources led to an increase in resource availability for *S. pterophorus*. However, instead of increased reproductive structures, these additional resources enhanced its competitive ability.

Senecio malacitanus displayed the highest proportion of resources allocated to reproductive biomass. The reproductive effort of this species varied slightly in distinct environmental conditions. In the presence of neighbouring vegetation, absolute values of RE were higher with additional resources. When resources were available, *S. malacitanus* assigned them to reproduction in detriment of growth, as shown by the lower competitive ability of the native species.

Plastic responses in reproductive strategy to environmental variation may confer *S. inaequidens* advantages in invasion, enhancing its success over a considerable gradient of environmental conditions. In the absence of competitive vegetation, the lack of resources leads to a higher reproductive effort of the species. However, in competition with neighbours, availability of resources enhanced growth and also, consequently, the competitive ability of this species. Thus, *S. inaequidens* is more competitive than *S. malacitanus*, but less than *S. pterophorus*.

In terms of RCI, competition had less effect on the two alien species than on the native one, as we hypothesised at the outset. However, differences in competitiveness among *S. malacitanus* and the two aliens varied depending on resource availability. Thus, while *S. inaequidens* was more affected by competition in R subplots, *S. pterophorus* was more affected by competition in NR subplots.

5. Conclusion

Our results allow us to rank the three species according to their invasive potential. The least invasive was the native *S. malacitanus*, which showed good establishment ability in open and disturbed habitats, but growth and reproduction of established adults were highly affected by environmental conditions (mainly competition with established vegetation). The invasiveness of *S. inaequidens* and *S. pterophorus*, on the other hand, was achieved in a different manner. While the former displayed better establishment ability, established adults of *S. pterophorus* were more resistant to environmental constraints. Responses to environmental shifts were more plastic in *S. inaequidens*, while *S. pterophorus* had narrower plasticity in terms of reproductive effort. Major differences were found among the two alien and the native species, but no clearly defined pattern was identified, while the considerable differences between the two aliens prevent us from presenting a linear classification according to an invasive/non-invasive gradient. However, our results show that invasion depends on the life-history traits of the invading species, the recipient habitat, and the interactions between the invader and its new habitat. Our study provides further evidence that there are no specific attributes that characterise invaders in general. Some authors have noted that there are few differences in life history-traits among native and alien invasive plants, and that colonisation success depends, in these cases, on the interaction with habitat (Thompson et al., 1995). The spread of the aliens *S. inaequidens* and *S. pterophorus*

throughout Europe has been the result of advantageous biological traits over native vegetation. The mechanisms that provide these traits are diverse, and include distinct parts of the biological cycle of each species. Therefore, these life-history traits respond in particular to each environmental condition.

On the basis of our results we highlight the need for invasion studies that combine ecological and biological features of habitat and species introduced.

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