A comparative growth analysis between alien invader and native Senecio species with distinct distribution ranges

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Abstract: A good way to check hypotheses that explain the invasion of ecosystems by exotic plants is to compare congeneric alien and native species. To test the hypothesis that alien invaders grow faster than natives, the maximum relative growth rate and its components were compared in controlled growth conditions between four Senecio species, two aliens introduced from southern Africa (S. inaequidens and S. pterophorus) and two European natives (S. malacitanus and S. jacobaeus). The four species colonize similar habitats, but the frequency and abundance of their populations and their distribution ranges differ. The two aliens showed a higher relative growth rate than the natives, and although there were differences between species for leaf area ratio, leaf dry matter content, and dry matter partition between stems, leaves, and roots, no clear pattern was detected to explain the differences in growth rates: several combinations of the components of the relative growth rate can give similar results. The higher relative growth rate of the alien species, combined with other ecological and life-history traits, may enhance their invasive capacity.

Keywords: alien, interspecific comparisons, invasion, native, relative growth rate, Senecio.

Résumé : Une bonne façon de tester les hypothèses expliquant l’invasion des écosystèmes par des plantes exotiques est de comparer les espèces étrangères et indigènes appartenant à un même genre. Nous avons utilisé le taux de croissance relatif maximal afin de tester l’hypothèse que les espèces exotiques envahissantes croissent plus rapidement que les espèces indigènes. Le taux de croissance relatif maximal et ses composantes ont été comparés en conditions contrôlées chez quatre espèces de Senecio, soit deux espèces introduites provenant d’Afrique du Sud (S. inaequidens et S. pterophorus) et deux espèces indigènes européennes (S. malacitanus et S. jacobaeus). Les quatre espèces colonisent des habitats similaires, mais la fréquence d’apparition et l’abondance de leurs populations ainsi que leur répartition sont différentes. Les deux espèces exotiques montrent un taux de croissance relatif supérieur à celui des espèces indigènes. Il existe des différences entre les espèces au niveau du rapport de la surface de la feuille, du contenu en matière sèche de la feuille et du partage de la matière sèche entre les tiges, les feuilles et les racines, mais aucun patron bien défini ne semble expliquer les différences dans les taux de croissance. Plusieurs combinaisons des composantes du taux de croissance relatif peuvent donner des résultats similaires. Le plus haut taux de croissance relatif des espèces exotiques combiné à d’autres caractéristiques écologiques ou du cycle vital peuvent favoriser ces espèces lorsqu’elles envahissent de nouveaux milieux.

Mots-clés : comparaisons interspécifiques, espèce exotique, espèce indigène, invasion, Senecio, taux de croissance relatif.


Introduction

Invasion by alien species can have both a detrimental effect on ecosystems (Vitousek & Walker, 1987; Mack et al., 2000) and a great economic impact (Pimentel et al., 2000). Some alien species can outcompete and displace native species or hinder their regeneration (Vitousek, 1990), thereby lowering the diversity of invaded ecosystems or modifying ecosystem characteristics and function (Vitousek & Walker, 1987; Blank & Young, 2002). Consequently, biological invasion is a threat to biodiversity and an important agent of global change (Vitousek et al., 1996; Chapin et al., 2000; Mack et al., 2000). Habitat disturbance and nutrient enrichment of soils, often after a disturbance, may favour the proliferation of alien invasive species (Davis & Pelsor, 2001). Actually, most exotic species grow in disturbed and nutrient-rich ecosystems (Fox & Fox, 1986; Hobbs & Huenneke, 1992; Meiners, Pickett & Cadenasso, 2002).

Although many studies have addressed this topic, there is no clear consensus as to the traits that make a species invasive (Roy, 1990; Alpert, Bone & Holzapfel, 2000). Since invasive alien species are usually released from the pressure of their native herbivores and parasites.
in the invaded region (Keane & Crawley, 2002), there is an increased allocation of resources to growth because of a reduction in allocation to herbivore defence (Blossey & Nortzhold, 1995; Torchin et al., 2003). This increased growth can confer a superior competitive capacity to aliens relative to that of natives (Baker, 1965; Noble, 1989; Bakker & Wilson, 2001). The competitive ability of seedlings is related to seedling size, which depends on seed size and relative growth rate (Marañón & Grubb, 1993). Furthermore, for species or populations of comparable seed size, the time to reach a critical seedling size is an important component of fitness because large seedlings may capture a larger share of resources and can survive better, since smaller seedlings are more susceptible to environmental constraints (Solbrig & Solbrig, 1984; Pino, Sans & Masalles, 1986). This has led numerous authors (Grime, 1973; Baker, 1974; Grime & Hunt, 1975; Bazzaz, 1986; Davis, Grime & Thompson, 2000; Davis & Pelsor, 2001) to hypothesize that a high relative growth rate (RGR) favours plant colonization, especially in resource-rich and disturbed ecosystems.

Few studies have compared the growth of alien and native species (Garnier et al., 1989; Pattison, Goldstein & Ares, 1998; Baruch, Pattison & Goldstein, 2000; Grotkopp, Rejmanek & Rost, 2002) and, except for the study by Garnier et al. (1989) on two species of Bromus and the studies reviewed by Maillet and López (2000) on several American aliens invading France, they have usually found higher growth rates in aliens than in natives. With the exception of the studies by Garnier et al. (1989) and Grotkopp, Rejmanek, and Rost (2002), comparisons were made between species from different genera and even families, and there can be a confounding effect of phylogeny on the traits analyzed. Therefore, it might be more meaningful to study closely related species, which can yield clearer results in the comparisons due to the minimization of differences due to phylogeny (Mack, 1996; Radford & Cousens, 2000).

Here we compared the growth of two alien and two native species within the same genus, and we tested the hypothesis that the alien invasive species have higher growth rates than the natives. Furthermore, we compared the components of RGR (ULR, LAR, LMR, and SLA; see Table I for abbreviations and measurement units) in order to improve our understanding of the underlying causes of differences in growth rates between aliens and natives. Classically, RGR can be broken down into the product of ULR \times LAR, and LAR can be further broken down into LMR \times SLA (Hunt, 1982). To assess these parameters, a growth analysis of congeneric species from the genus Senecio present in Spain was conducted under optimal growth-chamber conditions. Two of these species (the aliens Senecio inaequidens and S. pterophorus) can be classified as “novel, invasive colonizers” in Europe, with invaded areas of distinct size. The other two (the natives S. malacitanus and S. jacobaea) can be classified as “successional colonizers” (Davis & Thompson, 2000), although the latter is a “novel, invasive colonizer” type of invader in Australia and New Zealand (Parsons & Cuthbertson, 1992; Wilson et al., 1992). In previous studies comparing S. inaequidens, S. pterophorus, and S. malacitanus, we have found that there were no differences in the ability to emerge and establish between the native S. malacitanus and the alien S. inaequidens, whereas S. pterophorus had a lower emergence but a proportionally higher establishment (García-Serrano, Escarré & Sans, 2004). Furthermore, the competitive abilities of the two aliens were higher than those of the natives when resources were not limiting (H. García-Serrano, unpubl. data).

### Methods

#### PLANT MATERIAL

**Senecio inaequidens** and **S. pterophorus** are dwarf shrubs of south-African origin. The former was introduced accidentally in Europe at the end of the nineteenth century (Ernst, 1998). Today, it is widespread throughout Western Europe, where it forms dense populations in recently abandoned fields and in road margins. It also colonizes heavily grazed grasslands. First recorded in 1995 near Barcelona (Pino et al., 2000), **S. pterophorus** was recently introduced in Europe, and its geographical distribution is still small. It also forms very dense populations, mainly in disturbed riverbeds, and plants can grow up to 2 m high. According to Davis and Thompson (2000), these two species can be classified as “novel, invasive colonizers”, although **S. inaequidens** is far more widespread than **S. pterophorus**.

**Senecio malacitanus** (also named **S. linifolius**) is a dwarf shrub native to southern Europe that forms sparse populations in temporarily flooded rivers and other disturbed sites nearby. Its geographical distribution is limited to the southeast of the Iberian Peninsula and the Maghreb, in semi-arid climates (under 350 mm·y⁻¹). **Senecio jacobaea** is a biennial or short-lived perennial native to Europe and is widespread throughout the entire continent. It can form dense stands in damp pastures with a certain degree of disturbance, and sometimes coexists with **S. inaequidens** (Ernst, 1998). Both species are “successional colonizers” (sensu Davis & Thompson, 2000) in Europe, although **S. jacobaea** is an aggressive invader in Australia and New Zealand (Parsons & Cuthbertson, 1992; Wilson et al., 1992).

Seeds from all four species were collected from populations growing in the Iberian Peninsula. Seeds from

### Table I. Abbreviations, name, and units of growth and morphological parameters.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Name</th>
<th>Units</th>
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<tr>
<td>RGRDM</td>
<td>Relative growth rate (dry mass)</td>
<td>g·g⁻¹ plant·d⁻¹</td>
</tr>
<tr>
<td>RGRA</td>
<td>Relative growth rate (area)</td>
<td>m²·m⁻² total·d⁻¹</td>
</tr>
<tr>
<td>ULRDG</td>
<td>Unit leaf rate (dry mass)</td>
<td>g·g⁻¹ leaf·d⁻¹</td>
</tr>
<tr>
<td>ULRA</td>
<td>Unit leaf rate (area)</td>
<td>g·m⁻²·d⁻¹</td>
</tr>
<tr>
<td>LAR</td>
<td>Leaf area ratio</td>
<td>m²·kg⁻¹ plant</td>
</tr>
<tr>
<td>LMR</td>
<td>Leaf mass ratio</td>
<td>g leaf·g⁻¹ plant</td>
</tr>
<tr>
<td>SMR</td>
<td>Stem mass ratio</td>
<td>g stem·g⁻¹ plant</td>
</tr>
<tr>
<td>RMR</td>
<td>Root mass ratio</td>
<td>g root·g⁻¹ plant</td>
</tr>
<tr>
<td>SLA</td>
<td>Specific leaf area</td>
<td>m²·kg⁻¹ leaf</td>
</tr>
<tr>
<td>LDMC</td>
<td>Leaf dry matter content</td>
<td>g dry mass·g⁻¹ fresh mass</td>
</tr>
</tbody>
</table>
S. inaequidens were collected from a recently abandoned field in Cantallos, northern Catalonia, near the Spanish-French border, while those from S. pterophorus were collected from a population growing on the riverside of the Ripoll river, near Barcelona. Seeds from S. malacitanus came from Rambla del Rambutjar, a seasonal Mediterranean river near Alacant, and those from S. jacobaea were collected in a population growing in a disturbed site near Burgos. The mass of five replicates of 10 seeds of each species was determined and tested for differences by an analysis of variance and LSD test.

We selected these four species because 1) they differ in origin and extent of distribution area; 2) they are of the same genus, thereby reducing phylogenetic biases in the comparison; 3) they colonize similar habitats, disturbed and nutrient-rich sites (disturbed riverbeds and riversides of temporary watercourses, roadsides, recently abandoned fields, and waste ground); 4) they are all perennials; three of them are dwarf shrubs (S. malacitanus, S. inaequidens and S. pterophorus) and one is a hemicyryptophyte (S. jacobaea), which does not usually flower during the first growing season (Bolòs & Vigo, 1995); and 5) their current distribution areas nearly overlap in Europe. Senecio malacitanus can easily be mistaken for S. inaequidens, to the point that the first authors to find S. inaequidens in Europe identified it as S. linifolius (a synonym of S. malacitanus). Both exotic species are extending their respective ranges towards the south of the Iberian Peninsula and may, in the future, interact competitively with the native S. malacitanus. Although the growth form of S. jacobaea is not the same as that of the other three species, it was included in this study because it already coexists with S. inaequidens in Central Europe and is also invasive in other regions of the world.

Growth Technique

Seeds were germinated on moist filter paper placed vertically in plastic folders, with a 12:12 h photoperiod and temperatures of 22 °C (day) and 19 °C (night). All seeds were germinated in deionized water. Twenty-five plants were transplanted into a water culture system when their cotyledons were fully expanded and before the formation of any true leaves, when their size was between 2 and 5 cm length, including the radicle (day 0). Plants were grown hydroponically in a growth room, as described in Garnier (1992), with the nutritive solution described by Koch et al. (1987), and artificial light was provided by four metal halide lamps (Osram HQI-T 400 W, Berlin, Germany). The photoperiod was set at 16:8 h (day:night), the air temperature was 22:18 °C and relative humidity was maintained above 60%. The mean (± SE) photosynthetically active radiation (PAR) at seedling height was 515 ± 8 μmol·m⁻²·s⁻¹ (n = 100).

Harvests and Growth Analysis

Four to five plants per species were harvested at days 10, 15, 18, 22, and 25 after transplantation into the culture system. Each plant was divided into roots, stems, and leaves. Cotyledons and the hypocotyl were included in the leaf and in the stem, respectively. The leaf area of each plant was determined with a Delta-T area meter (MK2, Cambridge, United Kingdom). Fresh mass was measured for each organ, and dry mass was measured after drying at 60 °C for 48 h.

Relative growth rates expressed on a total dry mass (RGRₐ: unit of dry mass increment per day and per unit of total dry mass of plant) and on a leaf area basis (RGRₐ: unit of leaf area increment per day and per unit of leaf area) and unit leaf rates (ULRₐ: plant dry mass increment per day per unit leaf area or ULRₐ: per unit leaf dry mass) were calculated following the functional approach described by Hunt (1982), using a Fortran version of the HPCurves program written by Hunt and Parsons (1974). Differences in RGR between species were tested with an ANCOVA on the natural logarithm of total dry mass or leaf area, with number of days after transplanting into the culture system as covariate, and were considered significantly different when the interaction species × time was significant. As only one value for each species and harvest is obtained for ULR from Hunt’s program, it is not possible to perform an analysis of variance and multiple comparisons of means for this parameter.

As some growth parameters are size dependent, these were calculated for one harvest for each species such that the mean total dry mass of the four species ranged between 0.165 g and 0.242 g (Table II) and did not differ significantly between them (F₃,₁₄ = 1.00, F > 0.05). This corresponded to harvests on day 15 for S. inaequidens and S. pterophorus and on day 18 for S. malacitanus and S. jacobaea. All comparisons for growth parameters were performed on data from these harvests, except RGR (see above paragraph). Specific leaf area (SLA: unit of leaf area per unit of leaf dry mass), leaf area ratio (LAR: unit leaf area per unit total mass), leaf, stem, and root mass ratios (LMR, SMR, RMR: unit organ mass per unit total mass), and leaf dry matter content (LDMC: leaf dry mass per unit of leaf fresh mass) were calculated and compared among species by means of a one-way ANOVA. When differences were found, a least significant difference test (LSD) was performed to check for differences between specific means. Analyses were performed with SAS Version 8 (SAS Institute, Cary, North Carolina, USA).

Results

Seed Size

Seed mass was significantly different among species (Table II), with the two aliens having smaller seeds than the two natives. The species with the smallest seed mass was S. pterophorus, followed by S. inaequidens, S. malacitanus, and S. jacobaea.

Dry Matter Allocation

The proportion of dry matter allocated to leaves, stems, and roots differed significantly among species (Table II) and remained almost constant over time (Figure 1). Senecio jacobaea was the species that allocated the highest proportion of biomass to roots (RMR), whereas it devoted the least to stems (SMR). Senecio pterophorus allocated significantly more biomass to leaves (LMR) and was the species that directed the least to roots (RMR).
Table II. Mean (± SE) growth parameters calculated at comparable total masses of the four species (day 18 for Senecio inaequidens and S. pterophorus and day 22 for S. malacitanus and S. jacobaea). Different letters indicate significant differences among species for each variable (protected LSD tests). Numbers in parentheses apply to growth analysis parameters.

<table>
<thead>
<tr>
<th>Species</th>
<th>Senecio inaequidens</th>
<th>Senecio pterophorus</th>
<th>Senecio malacitanus</th>
<th>Senecio jacobaea</th>
<th>F&lt;sub&gt;S, 14&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass of 10 seeds (mg)</td>
<td>6.88 ± 0.19&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.98 ± 0.22&lt;sup&gt;b&lt;/sup&gt;</td>
<td>8.50 ± 0.05&lt;sup&gt;b&lt;/sup&gt;</td>
<td>9.94 ± 0.59&lt;sup&gt;a&lt;/sup&gt;</td>
<td>147.64***</td>
</tr>
<tr>
<td>Total mass (g)</td>
<td>0.242 ± 0.035&lt;sup&gt;ns&lt;/sup&gt;</td>
<td>0.165 ± 0.016&lt;sup&gt;ns&lt;/sup&gt;</td>
<td>0.182 ± 0.033&lt;sup/ns&lt;/sup&gt;</td>
<td>0.235 ± 0.039&lt;sup&gt;ns&lt;/sup&gt;</td>
<td>1.57 ns</td>
</tr>
<tr>
<td>Proportion of mass</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Root mass ratio (RMR)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.247 ± 0.019&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.192 ± 0.009&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.244 ± 0.014&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.308 ± 0.035&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>7.14 **</td>
</tr>
<tr>
<td>Stem mass ratio (SMR)</td>
<td>0.113 ± 0.006&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.109 ± 0.004&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.176 ± 0.006&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.079 ± 0.009&lt;sup&gt;b&lt;/sup&gt;</td>
<td>47.89***</td>
</tr>
<tr>
<td>Leaf mass ratio (LMR)</td>
<td>0.640 ± 0.019&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.699 ± 0.007&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.580 ± 0.010&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.613 ± 0.033&lt;sup&gt;b&lt;/sup&gt;</td>
<td>8.94***</td>
</tr>
<tr>
<td>Leaf area (cm&lt;sup&gt;2&lt;/sup&gt;)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>31.6 ± 4.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>25.2 ± 2.7&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>18.9 ± 2.6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>32.9 ± 6.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.50 *</td>
</tr>
<tr>
<td>Leaf area ratio (LAR)</td>
<td>13.0 ± 0.2&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>15.3 ± 0.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10.9 ± 1.0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>13.8 ± 0.6&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>6.04 **</td>
</tr>
<tr>
<td>Specific leaf area (SLA)</td>
<td>20.3 ± 0.4&lt;sup&gt;ns&lt;/sup&gt;</td>
<td>22.0 ± 1.5&lt;sup&gt;ns&lt;/sup&gt;</td>
<td>18.6 ± 1.4&lt;sup&gt;ns&lt;/sup&gt;</td>
<td>22.6 ± 0.7&lt;sup&gt;ns&lt;/sup&gt;</td>
<td>2.37 ns</td>
</tr>
<tr>
<td>Leaf dry matter content (LDMC)</td>
<td>0.130 ± 0.015&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.223 ± 0.018&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.128 ± 0.013&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.111 ± 0.019&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10.10***</td>
</tr>
<tr>
<td>Unit leaf rate (ULR)&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ULR area</td>
<td>25.3 ± 1.6</td>
<td>25.2 ± 2.0</td>
<td>25.8 ± 1.7</td>
<td>20.2 ± 1.3</td>
<td></td>
</tr>
<tr>
<td>ULR dry mass</td>
<td>0.537 ± 0.030</td>
<td>0.542 ± 0.029</td>
<td>0.527 ± 0.030</td>
<td>0.449 ± 0.03</td>
<td></td>
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</table>

A ANOVA performed on data transformed with natural logarithms.
* P < 0.05; ** P < 0.01; *** P < 0.001; ** P > 0.05.

GROWTH PARAMETERS

RGR differed significantly among species, expressed both on dry mass and leaf area, as shown by results of analysis of covariance (RGR<sub>DM</sub>: F<sub>3, 89</sub> = 5.65, P < 0.01 and RGR<sub>A</sub>: F<sub>3, 89</sub> = 4.25, P < 0.001). The two aliens showed a significantly higher RGR than the natives (Table III).

RGR<sub>DM</sub> was analyzed from the product of ULR<sub>A</sub> × LAR (Hunt, 1982), and LAR was further broken down into LMR × SLA. Taking the values from harvests of equal sizes for the four species (Table II), significant differences in LAR were detected due to the lower value in S. malacitanus. The values of SLA were not significantly different among them, whereas LMR was significantly smaller in S. malacitanus. Finally, LDMC was significantly higher in S. pterophorus.

Senecio jacobaea showed the lowest ULR values, while the three other species had comparable values for this parameter (differences in ULR cannot be formally tested: see Methods section).

TRENDS OF GROWTH PARAMETERS OVER TIME

LAR decreased over time in all species; given a constant RGR, this produced an increase in ULR<sub>A</sub> over time (Figures 2a and 2b). As stated above, ULR<sub>A</sub> was lower in S. jacobaea than in the other species, which explains its lower RGR given its high LAR (Table II). Moreover, LAR and ULR<sub>A</sub> in this species were nearly constant over time. In contrast, ULR<sub>A</sub> in S. malacitanus was similar to that of the two aliens, but its LAR was significantly lower because of its significantly smaller LMR, which explains its lower RGR.

Discussion

GROWTH PARAMETERS AND DRY MATTER ALLOCATION

The RGRs of the four species are among the highest values found in studies performed on European herbaceous species (Grime & Hunt, 1975; Poorter & Remkes, 1990; Ryser & Wahl, 2001). In the same growth system, Garnier (1992) found a mean value of 0.21 g·g<sup>-1</sup>plant·d<sup>-1</sup> for annual and perennial grasses, and Meerts and Garnier (1996) found values between 0.381 and 0.432 g·g<sup>-1</sup>plant·d<sup>-1</sup> in several ecotypes of Polygonum aviculare. Marañón and Grubb (1993) found values of RGR between 0.239 and 0.333 g·g<sup>-1</sup>·d<sup>-1</sup> for seven annual Asteraceae. High values of RGR are usually related to high values of LAR, and this is usually related to high values of SLA (Poorter & van der Werf, 1998; Poorter & Garnier, 1999). However, the LAR values in our study were small compared to those obtained for other species with similar RGRs (Poorter & Remkes, 1990). The fastest growing species, S. pterophorus, had a high value of LAR compared to S. malacitanus, but it did not differ from that of S. jacobaea, which showed a lower RGR. Analyzing the components of LAR we found that the four species had smaller SLAs and similar LMRs compared to the values reported by Poorter and Remkes (1990) and to the values for seven annual Asteraceae reported by Marañón and Grubb (1993). However, a comparison of the four species shows that SLA did not differ among them, whereas LMR was the only parameter that was higher in the fast-growing S. pterophorus and smaller in the slow-growing S. malacitanus. Nevertheless, our observations do not explain the differences in the RGR of S. inaequidens and S. jacobaea, whose RGRs differed but whose values of LAR and its components were similar. Thinner leaves should compensate the higher value of LDMC in S. pterophorus, because SLA (1/[LDMC × leaf thickness]) did not differ between species.

The values of ULR calculated for the four Senecio species were higher than those reported for several perennial plants by Poorter and Remkes (1990) and for seven annual Asteraceae by Marañón and Grubb (1993), indicating that the high RGRs in the Senecio species are not related to LAR and its components but to ULR. Comparison of ULR values among the four species showed that the lower RGR of S. jacobaea was related to its lower ULR. In fact, the growth form of this species differs considerably from that of the other three, as it
forms a rosette of leaves, which may cause more leaf overlapping and shading. A comparison of the ULR between *S. pterophorus*, *S. malacitanus*, and *S. inaequidens*, which have the same growth form, showed that the species with the higher RGR, *S. pterophorus*, had a slightly lower ULR, whereas the more slowly growing *S. malacitanus* had a slightly higher ULR. Although a negative relation between RGR and ULR is not usually detected in interspecific studies, other studies that compared genotypes within a species or closely related species also reported this negative trend (Gottlieb, 1978; Meerts & Garnier, 1996). The lack of clear relationships between RGR and its parameters across the species studied can be explained by the fact that we analyzed only four species and all four are within a narrow range of RGR values.

*Senecio jacobaea* is a biennial or short-lived perennial, and it forms a basal rosette of leaves and a taproot during its first growing season in order to store energy to elongate the reproductive stem in the second year. This is consistent with its higher RMR. In contrast, *S. malaci-

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**TABLE III.** Relative growth rates (mean ± SE) and classification of the four *Senecio* species. Different letters indicate significant differences among species for each variable (protected LSD tests).

<table>
<thead>
<tr>
<th>Colonizer type</th>
<th>Status</th>
<th>RGR&lt;sub&gt;DM&lt;/sub&gt; (g·g&lt;sup&gt;-1&lt;/sup&gt; plant·d&lt;sup&gt;-1&lt;/sup&gt;)</th>
<th>RGR&lt;sub&gt;A&lt;/sub&gt; (m&lt;sup&gt;2&lt;/sup&gt;·m&lt;sup&gt;-2&lt;/sup&gt; total·d&lt;sup&gt;-1&lt;/sup&gt;)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. inaequidens</em> novel, invasive</td>
<td>alien/widespread</td>
<td>0.343 ± 0.019&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.317 ± 0.019&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>S. pterophorus</em> novel, invasive</td>
<td>alien/restricted</td>
<td>0.365 ± 0.019&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.349 ± 0.019&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>S. malacitanus</em> successional colonizer</td>
<td>native/restricted/arid</td>
<td>0.298 ± 0.018&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.279 ± 0.016&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>S. jacobaea</em> successional colonizer</td>
<td>native/widespread/humid</td>
<td>0.274 ± 0.014&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.268 ± 0.015&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

RGR<sub>DM</sub>: Relative growth rate calculated from dry matter increase.
RGR<sub>A</sub>: Relative growth rate calculated from leaf area increase.
tanus allocated significantly less biomass to leaves, and this may be due to an adaptation to the dry habitats that it inhabits in southern Spain. This hypothesis is supported by a lower LAR value.

**RGR and Invasive Ability**

It has been hypothesized that alien invaders are more competitive than natives (Baker, 1965; Noble, 1989; Bakker & Wilson, 2001). Competitive ability can be related to size, and the size of a seedling depends on its RGR and on the size of the seed (Marañón & Grubb, 1993). Moreover, seedling size can be critical for resisting environmental constraints (Solbrig & Solbrig, 1984). Our results show that although there are differences in seed mass among species, differences in the final seedling size of the four species studied are related to RGR and not to seed size. The growth potential of the two alien species is higher than that of the two natives. Other studies have reported that alien species are able to exploit resources better than natives (Burke & Grime, 1996; Baruch & Goldstein, 1999; Milberg, Lamont & Perez-Fernandez, 1999; Alpert, Bone & Holzapfel, 2000; Blicker, Olson & Engel, 2002; Kolb et al., 2002; Morris, Walck & Hidayati, 2002; Gerlach & Rice, 2003; Leger & Rice, 2003). For example, the growth of *S. madagascarensis*, a South African invader in Australia that is the diploid form of *S. inaequidens* (Lafuma et al., 2003), was enhanced by nitrogen and phosphorus addition in Australian pastures more than coexisting native grassland species (Sindel & Michael, 1996). Moreover, *S. madagascarensis* was found to grow faster than its native Australian congener *S. lautus* (Radford & Cousens, 2000).

As stated previously, our results show that there is no clear relation between RGR and LAR, and even less between RGR and SLA. Although some explanation for the higher values of the RGR of aliens can be found in LMR, ULR also plays an important role in explaining differences among the four species. Grotkopf, Rejmanek, and Rost (2002) compared the RGR of 29 invasive and non-invasive *Pinus* species and found that the RGR of invader pines was higher than that of non-invaders, and that this was strictly related to differences in SLA. Garnier et al. (1989) compared the growth of two *Bromus* species, one invader and one non-invader, but found no differences in RGR or its components. Patterson, Goldstein, and Ares (1998) compared the growth and biomass allocation of four native and five alien species in Hawaii grown under a range of irradiance. Only one pair of congenic species, from the genus *Bidens*, were compared in their study; they reported that the higher RGR of the invader was mainly due to a higher LAR, especially under shade conditions. On the basis of those studies, it is surprising that differences in the invasive behaviour of the species included in our study were not clearly related to these parameters.

**How Do Our RGR Results Help to Improve Knowledge of the Invasive Ability of the Species Studied?**

The two alien species analyzed in this study, *S. inaequidens* and *S. pterophorus*, displayed the highest RGR of all four species. A high RGR can be a valuable trait in a colonization event, as plants with this trait can grow fast after germination, thereby avoiding competition from other plants. However, our experiment was performed under optimal nutrient conditions, and results may differ depending on the availability of soil resources.

In field conditions, *S. pterophorus*, which had the highest RGR in our experiment, grows preferentially in areas with abundant resources and seems to be sensitive to water stress. Well-established populations of this species are restricted to places with high resource avail-
ability, where it can grow to its high RGR potential. *Senecio inaequidens* populations are more widespread, colonizing old fields and road margins. Both species might benefit from the availability of sufficient resources to reach their highest RGR potential in order to establish and compete with pioneer species. A high initial growth rate and a perennial life-history make a good life-history trait combination that favours establishment after a disturbance and allows the maintenance of a stock of adult plants when establishment is difficult because of a scarcity of suitable sites.

On the other hand, field and controlled experiments with the two aliens *S. inaequidens* and *S. pterophorus* and the native *S. malacitanus* (Sans, Garcia-Serrano & Añín, 2004; H. Garcia-Serrano, F. X. Sans & J. Escarré, unpubl. data) have shown that the two aliens are more competitive than the native *S. malacitanus*, especially *S. inaequidens*, which out competes the other two species even under water stress. In addition, the two alien species start flowering very early in their life, particularly *S. inaequidens*. An early flowering can confer a high invasive potential on these species, as they can establish populations that are a crucial source of seeds for the colonization of nearby sites.

The two natives also displayed high RGRs, which is to be expected since they colonize disturbed and nutrient-rich environments. However, their maximum potential RGR is lower than that of the aliens, and this may explain their lower invasive potential. Nevertheless, the case of *S. jacobaea* differs, since it is an alien invader in other parts of the world. Because of its distinct growth form (an initial basal rosette) and life cycle (hemicyryptophyte), our results for this species are not strictly comparable with the other three species analyzed. The strategy of growing a rosette of leaves and storing nutrients in a root might reduce RGR because of shading among leaves in the rosette, but it may be a good strategy for pre-empting the space available. However, flowering does not occur until the next growing season, and compared to the two alien species, this may reduce its invasive potential.

Finally, *S. malacitanus* showed the lowest RGR among the species analyzed, although it is rather high compared to other species; this high RGR may be an adaptation for colonizing disturbed habitats. The distribution area of this species is located in zones with considerable periodic water restrictions, and this may explain its lower LAR and, therefore, its lower RGR. A lower LAR, related to a low LMR, may be an adaptive response to prevent water loss in arid environments. Moreover, this species starts flowering later than the two aliens (H. Garcia-Serrano, unpubl. data), thus reducing its invasive ability.

A high RGR appears to be a favourable trait for a colonizing species, as shown by the high values found in the four species analyzed, although in this case different combinations of RGR components yielded similar RGRs. The alien species in our study showed higher RGRs than the natives, and this, combined with other ecological and life-history traits, such as enhanced competitive abilities, early flowering, and a high reproductive output, can enhance their ability to invade new habitats.

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Literature cited


