

# Relative growth rates of three woody legumes: implications in the process of ecological invasion

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*Acacia longifolia*, an Australian leguminous tree, is one of the main invasive plant species in the coast of Portugal and a major threat to the native vegetation in the Reserva Natural das Dunas de São Jacinto. With the establishment of this exotic species, other native woody leguminous species such as *Cytisus grandiflorus* and *Ulex europaeus* have been displaced from their original areas. Several factors are involved in the process of biological invasion by exotic species. Plant physiology and development, characteristic of each species, can give certain advantages in the establishment and colonization of new areas. We tested if there are differences in the Relative Growth Rate (RGR) of the exotic and native species because this could be relevant in the first stages of the invasion process. Our results showed that *A. longifolia* was the species with lowest RGR. Therefore, other factors apart from RGR might explain the invasion of coastal dunes by this species. We propose that *A. longifolia* might be a better competitor than the two native legumes and that this process might be mediated by the interaction with soil organisms.

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Biological invasions have a great impact on ecosystem structure and functioning (Cronk and Fuller 1995) and are considered the second major threat to biodiversity (Vitousek 1997). Several hypotheses that examine either the characteristics of the invasive species, the invaded community, or the interactions between the invasive species and other organisms, have been proposed to explain the success of exotic species in colonizing new areas. Areas with high levels of disturbance, high resource availability or reduced diversity tend to be more easily colonized by exotic species (Shea and Chesson 2002). Exotic plant species could also be successful invaders because they lack the specific natural enemies which regulate their populations in native areas (Crawley 1997, Keane and Crawley 2002), or because they evolve an increased competitive ability in the new invaded areas (Blossey 1995). Plants with specific

physiological or morphological attributes that make them good colonizers are likely to become invasive in new areas (Blumenthal 2005). Accordingly, a high relative growth rate (RGR) could be an important factor determining the success of exotic species and the displacement of native vegetation.

The invasion of *A. longifolia*, a species introduced in Portugal for dune stabilization, represents a major threat to the preservation of the local plant community in the Reserva Natural de São Jacinto and in many coastal areas in Portugal (Marchante 2003). The main areas affected by the invasion of this exotic species are in the secondary dune, therefore displacing other native woody species. *Ulex europaeus* and *Cytisus grandiflorus* are the most abundant native woody legumes in this habitat and they are highly affected by the expansion of *A. longifolia*.

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In order to elucidate the mechanisms that lead to the invasion success of this exotic species, we performed an experiment to estimate the RGR of *A. longifolia*, *U. europaeus* and *C. grandiflorus*. Since *A. longifolia* is displacing the other two native species, our hypothesis was that *A. longifolia* has a higher RGR than the two native species *U. europaeus* and *C. grandiflorus*.

## Material and methods

### Seeds

Seeds from the three plant species were randomly collected from plants in the Reserva Natural das Dunas de São Jacinto (Portugal) during summer 2005. Seed mass for each species was estimated by repeated measures of different groups of ten seeds in the case of *A. longifolia* and 50 seeds for the two other species. Seeds were dried at 40°C for 24 h and weighted in a laboratory weighing scale to estimate average seed mass.

### Plants

Thirty seeds of each plant species were surface disinfected in 96% ethanol for 30 s and 4% bleach for two min, and then washed with autoclaved water previous to scarification. Seeds were scarified using a scalpel and placed in sterilized Petri dishes with autoclaved wet filter paper at 25°C for germination. After radicle emergence, seedlings were transplanted individually into one l pots, containing 700 g of sterilized quartz sand (eight h at 150°C for three times with intervals of eight h). Pots were watered with 100 ml of full strength Hoagland's solution on the first week, and then on every four days, with 30 ml of distilled water alternated with 30 ml of full strength Hoagland's solution. Plants were grown in a 700 EDTU Aralab Fitotron with a cycle of 16 h of light at 25°C, and eight h of darkness at 18°C.

### Harvest and data analyses

Ten plants for each species were harvested at four, eight and twelve weeks. The fresh weight of shoot and root were

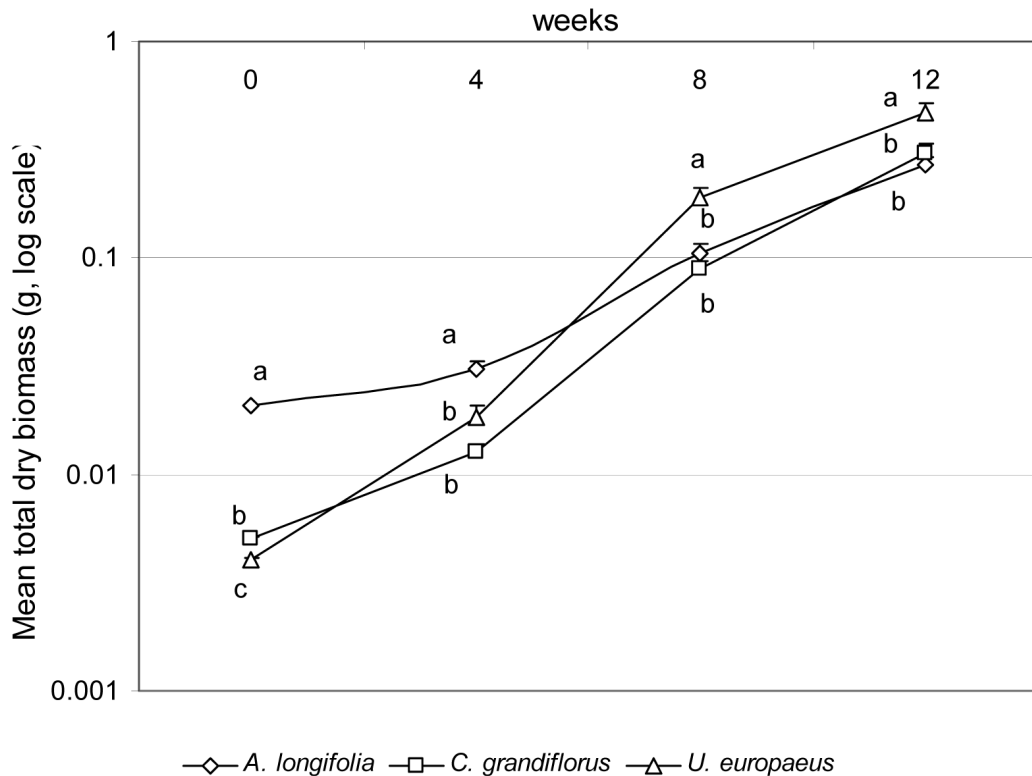


Fig. 1. Total dry biomass (mean  $\pm$  SE) for each harvest. The data for week 0 correspond to the seed weights. Different letters mean significant differences ( $p < 0.05$ ) between species in each harvest after one way ANOVA and Tukey's test. Note the log scale.

recorded for each plant. Shoots and leaves were scanned with a HP scanjet 5370c at 300 dpi, and the leaf area was determined with the software ImageJ-Image Processing and Analysis in Java (available at <http://rsb.info.nih.gov/ij/index.html>).

Plants were subsequently dried at 65°C for 48 h to measure the dry weight of shoot and root for each plant.

From these data, the following indices were calculated using Hunt's (2002) software:

RGR (mean Relative Growth Rate) – Rate of dry mass increase per dry mass unit ( $d^{-1}$ ). RGR can be decomposed as  $ULR \cdot LAR$ .

ULR (mean Unit Leaf Rate) – Rate of dry mass production per leaf area unit ( $mg\ cm^{-2}\ d^{-1}$ ).

LAR (mean Leaf Area Ratio) – Ratio between total leaf area per plant and total dry weight per plant ( $cm^2\ mg^{-1}$ ).

ANOVA and Tukey's test were used to compare biomass, RGR, ULR and LAR among the three species.

## Results and discussion

Significant differences were found between the seed weight of the three species (Fig. 1). The biggest seeds were those of *A. longifolia* and the smallest the seeds produced by *U. europaeus*. This difference affected the early growth of the three plant species. After four weeks, the *A. longifolia* seed-

lings were significantly bigger than the seedlings of the other two species (Fig. 1). However, in the following harvests, at eight and 12 weeks, the highest values of biomass were found for the seedlings of *U. europaeus*. This value was significantly different from the biomass of the other two species.

We found significant differences in the RGR values between *A. longifolia* and the other two species over the entire studied period. The greatest value was found for *U. europaeus* (Fig. 2a). This species was also the one that showed the highest ULR (Fig. 2b), i.e. the highest growth rate per unit of leaf area. Since this is a measure of the plant physiological activity (Hunt et al. 1993), *U. europaeus* could be the species with the greatest photosynthetic efficiency, which is calculated as the ratio between the amount of total solar energy available and the chemical energy produced during photosynthesis. Since ULR also accounts for dark respiration rates, which were not measured in this work, we were not able to determine if the differences were due just to the photosynthetic efficiency or to a combination of both photosynthetic and respiration rates.

Significant differences in LAR values were also found between *U. europaeus* and the other two species. *A. longifolia* was the species with highest LAR values (Fig. 2c), i.e. the highest leaf area per unit of total dry mass of the three plant species. This might be an advantage in the coloniza-

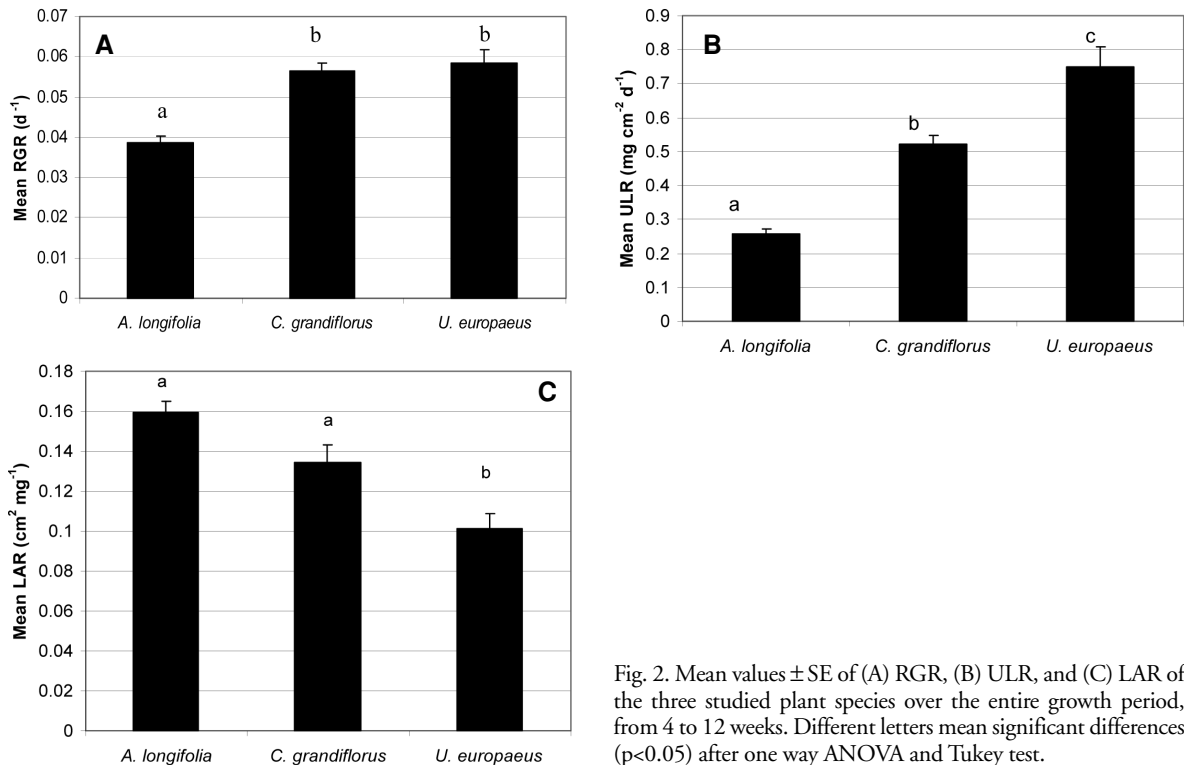


Fig. 2. Mean values  $\pm$  SE of (A) RGR, (B) ULR, and (C) LAR of the three studied plant species over the entire growth period, from 4 to 12 weeks. Different letters mean significant differences ( $p < 0.05$ ) after one way ANOVA and Tukey test.

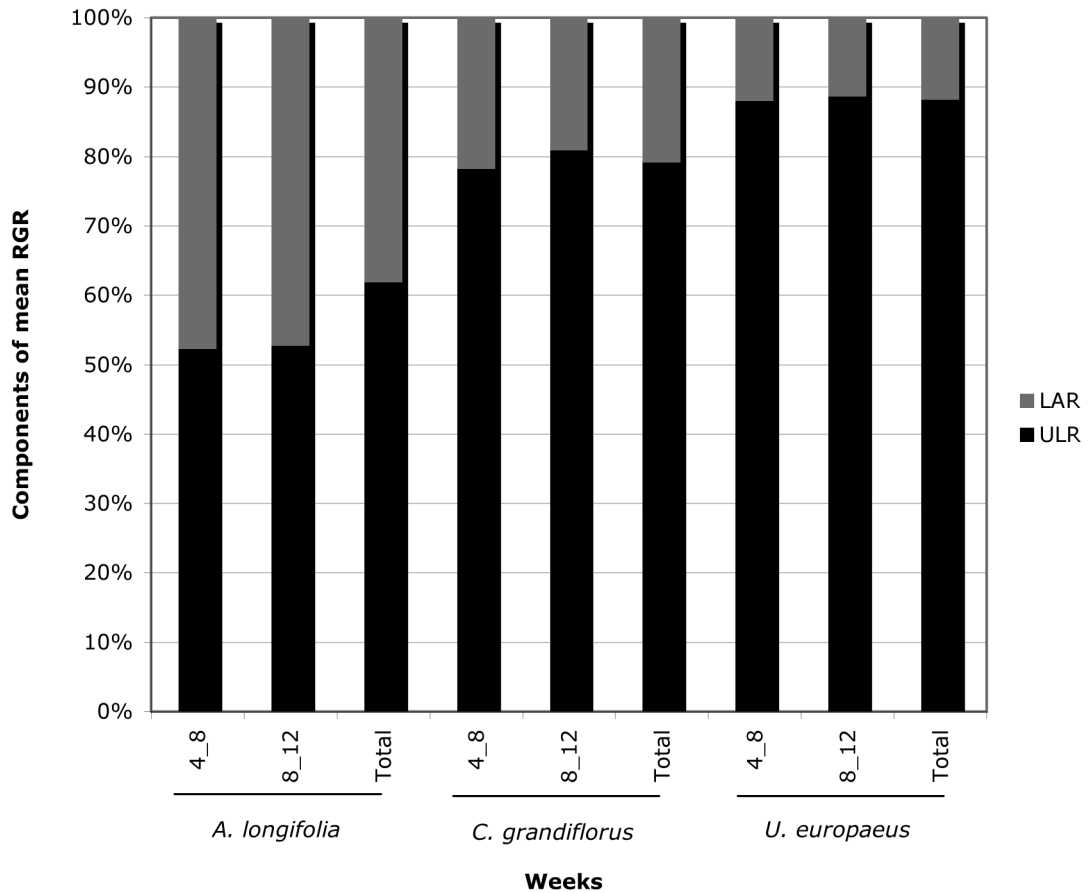


Fig. 3. Contribution (in percentage) of ULR and LAR to the value of RGR in the three plant species. Data refer to the growth period between four to eight weeks; eight to twelve weeks; and for the entire period (total).

tion process, because a higher leaf area can decrease the light available to seedlings of other species which are in the proximity of *A. longifolia* plants (Walters et al. 2000).

The analysis of the two components of the RGR hinted to ULR as the factor that most contributed to RGR (Fig. 3). This indicates that all species had a greater part of their RGR explained by the photosynthetic efficiency (Hunt et al. 1993). The relative contribution of ULR and LAR to RGR showed very little variation from one period to the other. Other previous studies have shown a temporal variation in the relative contribution of ULR to RGR because of the natural variation of the photoperiod (Antúnez 2001). In our experimental conditions, the photoperiod was constant so this could partially explain the even contribution of ULR and LAR to RGR through time.

The values of RGR were higher in the first monitored growth period (four–eight weeks) than in the second period (eight–twelve weeks) in all species. The greatest decrease in RGR was found for *U. europaeus* (Table 1). Al-

though LAR had a greater decrease in all species from the first period to the second period, differences in RGR were also due to a decrease in ULR. This happens because ULR is the major component of RGR; therefore, little variation will have a significant effect in the values of RGR. These data highlight the rapid growth of *U. europaeus* between four and eight weeks.

To conclude, the species with the greatest RGR was *U. europaeus* followed by *C. grandiflorus* and then by *A. longifolia*. Thus, the high success of *A. longifolia* in the invasion process cannot be explained by the specific RGR of the three studied species. These results were obtained in controlled conditions with no nutrient shortage and the absence of other biotic interactions. The successful displacement of the native species in the field might be related to other factors such as differences in the competitive ability of each species (Blossey 1995) or interactions with other organisms that could change both the growth rate and the competitive outcome among the plant species (Klironomos 2002, Callaway 2004).

Table 1. Values of relative growth rate (RGR,  $d^{-1}$ ), unit leaf rate (ULR,  $mg\ cm^{-2}\ d^{-1}$ ) and leaf area ratio (LAR,  $cm^2\ mg^{-1}$ ) for the two monitored periods, 1: from four to eight weeks, 2: from eight to twelve weeks. Differences between the two periods are expressed as percentages.

	RGR1	RGR2	RGR2-RGR1	ULR1	ULR2	ULR2-ULR1	LAR1	LAR2	LAR2-LAR1
<i>A. longifolia</i>	0.041925	0.035042	-16.42%	0.217392	0.210371	-3.23%	0.198471	0.188714	-4.92%
<i>C. grandiflorus</i>	0.069174	0.043565	-37.02%	0.528359	0.439395	-16.84%	0.14719	0.103844	-29.45%
<i>U. europaeus</i>	0.083256	0.033561	-59.69%	0.8281	0.593167	-28.37%	0.113129	0.075676	-33.11%

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