

Assessing native grassland species potential to compete with the invasive grass *Eragrostis plana*

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Abstract

Ecological restoration of degraded areas can be important to prevent or slow down invasions of alien species. The objective of this study is to evaluate the potential of native species in applying the seeding technique and to compete with the invader *Eragrostis plana*, aiming ecological restoration at *Campos Sulinos* grasslands (South Brazil). Seeds of six native species (*Anthaenantia lanata*, *Aristida laevis*, *Aristida jubata*, *Chamaecrista repens*, *Panicum olyroides* and *Paspalum plicatulum*) and of *E. plana* were sown in isolated and competition (one native species plus the invader) pots. Germination rate, survival rate, germination rate index (GRI), above and belowground biomass were analyzed using ANOVAs and GLMs, and the impact of native species' attributes at the invader biomass were analyzed using linear regressions. We found that *Aristida laevis* and *A. jubata* had the highest germination and GRI, although had low survival. *Anthaenantia lanata* and *Paspalum plicatulum* had medium germination rate and GRI, but *P. plicatulum* had high survival and was the only native species to achieve a great biomass development. The invader proved to be a great competitor, with a high GRI, germination and survival rate and biomass production. High germination speed didn't inhibit the early growth of the invader, although our results show that a high production of native biomass can slow down the development of *E. plana*. The only native species that was as predominant as the invader at the competition pots was *P. plicatulum*, and further studies can be important to understand the dynamic between those two species.

Introduction

Subtropical and tropical grasslands around the world are strongly impacted by habitat conversion and by invasive species (MEA 2005; Gibson 2009). These ecosystems have low resilience to habitat conversion (Buisson et al. 2019), thus actively restoring degraded areas in former grasslands is important to ensure biodiversity conservation, ecosystem functioning, and associated services (Clewel and Aronson 2006; Funk et al. 2008; Gibson 2009). Biological invasions are closely related with habitat degradation, and the high pressure of invasive species propagules is one of the major challenges for ecological restoration, being its control a common priority (D'Antonio and Meyerson 2002; Funk et al. 2008).

An important concern in invasive species control is the releasing of local resources by removing invasive species individuals, which often allows a re-invasion (Davis et al. 2000; D'Antonio and Meyerson 2002; Levine et al. 2004). Moreover, invasive species often have rapid germination, a relevant side for the invasion process (Gioria and Pyšek 2017). Thus, to prevent invasive dominance, it is crucial to introduce native species able to fast germinate, establish, and compete, while controlling invasive species through time. Early establishment of native grasses can reduce the germination and competitive effect of invasive grasses (ex. Levine et al. 2004; Medeiros and Focht 2007; Stevens and Fehmi 2011). However, knowledge gaps on basic seed biology of grassland species limit our capacity to use seed-based restoration strategies (Buisson et al. 2021). Assessing the potential of germination and establishment from seeds of native species is uppermost relevant to applicability of direct seeding for large-scale grassy ecosystems restoration, a likely cost-effective technique to reintroduce functionally diverse grassland communities (Saatkamp et al. 2019; Buisson et al. 2021).

South Brazilian grasslands (*Campos Sulinos* grasslands) are heterogeneous ecosystems in terms of physiognomy and species composition (Andrade et al. 2019) with high ecological, economic, and cultural importance. However, circa 60% of their original cover was converted (Vélez-Martin et al. 2015) and many areas have been invaded by the African grass *Eragrostis plana* Nees (Guido and Guadagnin 2015). *E. plana* establishment and spread is highly successful because it is a fast-growth cespitose C4 species, with high seeds production and germination rate, that tolerate cold, frost and drought events. In addition, its leaves are unpalatable to cattle whereas its panicles (and seeds) are, which in turn facilitate its propagation and expansion in invaded grasslands (Medeiros and Focht 2007). Invaded areas show species losses (Baggio et al. 2018; Dresseno et al. 2018) and economical losses in livestock production (Medeiros et al. 2009; Vélez-Martin et al. 2015). Many studies have pointed the competitive advantage of *E. plana* on native species, even in greenhouse experiments (Medeiros and Focht 2007; Guido et al. 2019). However, restoration ecology of *Campos Sulinos* ecosystems is a recent issue of high priority and techniques are under development (e.g., Thomas et al. 2019). There is still a lack of information about germination and initial establishment of native species (ex. Guarino et al. 2018), and about the potential of species in compete with *E. plana* (Guido et al. 2019).

This study aimed to evaluate the potential of native species in applying the seeding technique for ecological restoration of *Campos Sulinos* grasslands and in compete with the invader *Eragrostis plana* on the phase of germination and initial establishment. Our specific objectives were (i) evaluate the germination and the survival rates, and (ii) the germination velocity of native grassland species, and (iii) evaluate their potential to compete with *E. plana* at early stages of development. Our main hypothesis was that species with faster germination and higher germination rate would have a higher potential to establish in the early stage and compete with *E. plana* (Gioria and Pyšek 2017).

Methods

Selected species and seeds collection

Six common native species on Campos Sulinos were used in this study: the cespitose grasses *Anthraenantia lanata* (Kunth) Benth, *Aristida jubata* (Arechav.) Herter, *Aristida laevis* (Nees) Kunth, *Panicum olyroides* Kunth, and *Paspalum plicatulum* Michx, and the prostrate legume *Chamaecrista repens* (Voge) H.S.Irwin & Barneby. Those species were selected based on their abundance and facility of obtaining seeds, an important characteristic for the utilization on ecological restoration projects.

Seeds were collected between December 2020 and February 2021 in two protected areas: Parque Natural Municipal Saint-Hilaire, in Viamão (30°05'S, 51°07'W; *A. laevis*, *A. jubata*, *A. lanata* and *C. repens*), and Parque Nacional da Lagoa do Peixe, in Mostardas (31°15'S, 50°58'W; *P. plicatulum*), considering natural patches of plant populations distributed in the grasslands of both protected areas. The *E. plana* seeds were collected in several invaded grasslands and roadsides across the region. Visually healthy seeds were selected and stored in plastic pots and kept in a dry place at natural temperature until the beginning

of the experiment. Seed of *C. repens* were submitted to a mechanic scarification with a sand paper, as legumes often present dormancy that can be overcome by scarification.

Experimental design

In a greenhouse, each species was sown separately in garden pots, with 20 seeds each and five replicates, totalizing 100 seeds per species, to evaluate the first two objectives. To answer the third objective, *E. plana* was sown with each one of the six native species, where we put 10 seeds of *E. plana* and 10 seeds of the native species in each vase, also with five replicates each.

Garden pots (16 cm x 16 cm x 13 cm) were filled with gravel at the bottom 2 cm and then with a 50:50 mixture of sterile substrate and Carolina Soil® (vermiculite and peat compost). The experiment was settled at the greenhouse of the Botanical Garden, in Porto Alegre, Brazil, at the beginning of the Autumn of 2021 and kept under natural conditions of temperature, but with frequent irrigation, per 93 days. The garden pots were distributed in a workbench and moved frequently to avoid small differences in irrigation and luminosity inside the greenhouse.

Data collection

Species germination in each garden pot was monitored at an interval of two or three days in the first two months and weekly in the third month. Germination criteria was the exposition of the seedling shoot above the soil surface. At the end of the 93 days of experiment, germination rate (ratio between the number of germinated individuals and the total of seeds) and survival rate (ratio between the number of living individuals at the end of the experiment and the number of germinated individuals) were obtained for each species, in each replicate. Moreover, we calculated the germination rate index (GRI; Maguire 1962), which is an indicative of the germination velocity of a species, using the formula:

$$GRI(\% d) = \sum_{i=2}^{93} \left[\frac{G_i - G_{i-1}}{i} \right]$$

Where i is the day of the germination counting, varying between day 2 to 93, G_i is the germination rate at the day i and G_{i-1} is the germination rate at the day before day i .

At the end of the 93 days, all the individuals were harvested, separated between the aerial and radicular parts, dried at 60° C per 72 hours and then weighted (i.e., above and belowground biomass). The above and belowground biomass of each species per replicate was divided by the number of living individuals, to obtain an average biomass value per individual. To get to this value, although, we excluded the individuals that have germinated at the last two weeks to avoid underestimation per individual, once they were too small to contribute with the final value of the biomass.

Data analyses

Germination rate and survival rate of each species when sown isolated were compared between all species, inclusive *E. plana*, using Generalized Linear Models (GLMs). The GRI values, above and belowground biomass per individual for each species were compared using Analysis of Variance (ANOVA). To infer about the potential of competition of native species with *E. plana*, linear regressions to assess the effect of GRI and aerial biomass of native species over the *E. plana* biomass (above and belowground) were performed. Survival rate of native species was highly correlated with GRI (0.728), whereas belowground biomass was correlated with aboveground biomass of native species (0.963), and these two variables were thus not used in the models. GRI and biomass data were square root transformed to reach the analyses assumptions. For the significant results we made post-hoc comparisons using TukeyHSD to ANOVAs and emmeans to GLMs (emmeans package, Lenth 2021). The normality and heteroscedasticity assumptions were observed for all the analyses, and overdispersion to the GLMs. All the analyses were made using the software R (R Foundation for Statistical Computing, Vienna, Austria).

Results

Germination rate differed between some species (Fig. 1a). The highest value was for *A. laevis* (0.90 ± 0.09), but it was similar to *A. jubata*, *A. lanata*, *P. plicatulum*, and *E. plana*. All these species differed from *P. olyroides* and *C. repens*, which in turn were similar in terms of germination rate. Detailed results are available at the Supplementary Information Table 1.

Germination rate index (GRI) also showed differences between species. The two species of the genus *Aristida* and the invasive *E. plana* germinated faster than any other native species, reaching more than 50% of the seeds germinated at the end of the first week (GRI final values of 13.36 ± 2.42 , 11.46 ± 1.92 , and 9.01 ± 4.54 , respectively to *A. jubata*, *A. laevis* and *E. plana*; Fig. 2). *A. lanata*, *P. plicatulum* and *C. repens* had a median GRI (5.39 ± 1.63 , 3.93 ± 1.12 , and 3.11 ± 1.65 , respectively), while *P. olyroides* had the lowest value (0.58 ± 0.52).

Survival rate also differed between species (Fig. 1b). The species *P. plicatulum*, *P. olyroides* and the invasive *E. plana* were similar and had the highest survival rates. The two species that had the highest germination, *A. laevis* and *A. jubata*, had high mortality. No individuals of *C. repens* survived; two pots were attacked by ants, killing the seedlings, but even on those non-attacked no individual have survived (Fig. 1b). Hence, we excluded *C. repens* from analysis of aboveground and radicular biomass.

Both above and belowground biomass of *E. plana* were higher than the biomass of native species (Fig. 1c and d). The only native species that had a great production was *P. plicatulum*, whose biomass per individual (aboveground: $0.082 \text{ g} \pm 0.008$, belowground: $0.026 \text{ g} \pm 0.003$) differed from all the other native species. The below ground biomass of *P. plicatulum* did not differ from *E. plana*, but the aboveground biomass was lower than *E. plana*. All other native species had low biomass values and almost did not differ from each other (only *P. olyroides* had even lower belowground biomass in comparison with the others).

Results of the competition experiment were summarized by linear regression models, considering the effect of the variables GRI and aboveground biomass of native species on the biomass of *E. plana*, tested either for the above and belowground biomass of the invader (p-value: 0.0019 and 0.0181, respectively; Supplementary Information Tables 2 and 3). We observed that as high as the native species' GRI is (which was correlated with the germination rate), higher was the biomass of the invader (Fig. 3a and c). However, for the model of *E. plana* aboveground biomass, we had a significative interaction between GRI and aboveground biomass of native species, thus the GRI result alone must be interpreted with caution. There is a negative relationship between the aboveground biomass of native species and the aboveground biomass of *E. plana* (Fig. 3b). Thus, considering both isolated patterns (GRI and aerial biomass) and the interaction, our results are showing that a species with fast germination (high GRI) lead to a better performance of the invader only if it does not accumulate enough biomass in the early growth phase (here, three months). This was the case of *A. jubata*, with high GRI but very low biomass. On the other hand, *P. plicatulum*, with medium GRI, became the stronger competitor of *E. plana* because of its high biomass accumulation along the studied growth phase. This can be visually observed at Fig. 4, which shows the aerial part of *P. plicatulum* and *E. plana* when planted alone and together. In the pot together, the native was predominant.

Discussion

Our study evaluated the potential of six native species for using in direct seeding technique for ecological restoration in *Campos Sulinos* grasslands and in competing with the invader *E. plana* during germination and initial establishment (three months). Results showed significant differences between native species in terms of germination velocity and biomass accumulation. However, contrary to the initial hypothesis (Verdú and Traveset 2005; Gioria and Pyšek 2017), faster germination did not reflect in better establishment and growth, both considering the species growing alone in the pots or together with the invader. Results have clearly shown that the relation between germination velocity and establishment and/or competition with the invader are not direct. The growth ability, accumulating biomass in early development stages, seems to be more important than germination velocity to effectively compete with the invader *E. plana* in restoration areas subject to invasion.

The two species of the genus *Aristida* (*A. jubata* and *A. laevis*) presented the highest germination rate and GRI, but the survival rate was low and they did not accumulate much biomass over the experiment period. Previous studies, in Petri dishes experiments, had already demonstrated high germination rates for *A. laevis*: 83.3% (Guido et al. 2017) and 98% (Overbeck et al. 2006), although another study carried out on a greenhouse registered low germination for those two species: 4.0% for *A. jubata* and 11.0% for *A. laevis* (Silva et al. 2020). In this last experiment, however, those individuals that germinated presented a higher survival rate (*A. jubata* 75.0% and *A. laevis* 74.2%). Germination and survival rates of *Aristida* species may thus vary a lot and further studies are necessary to better conclude about their potential use in ecological restoration. By now, we would recommend a large number of seeds to guarantee success on germination and establishment of these species in degraded field conditions. However, the two *Aristida* species had a low performance when competing with *E. plana*, and there was even an increase trend of

the invader biomass per individual when compared with the pots where *E. plana* was alone, indicating potential facilitation (data not shown). Guido et al. (2019) already considered *A. laevis* as a species with low potential to prevent the establishment of *E. plana*.

Another species whose germination rate was high was *A. lanata*, with an average of 77%, equal to the result of Overbeck et al. (2006) in Petri dishes, but very different from the 8.0% observed by (Silva et al. 2020), that also cultivated in pots in a greenhouse. There were no previous studies for *P. plicatum* and *P. olyroides*, therefore future experiments are necessary to evaluate better their potential use for restoration. By our results, *P. olyroides* was the species with lowest germination (17%), indicating a low potential for application in direct seeding in degraded areas. Similarly, *C. repens* presented a low germination rate (24%), slightly higher than the observed in a previous study (15%, Fidelis et al. 2016), but no individual survived, thus indicating a low potential for direct seeding. On the other hand, *P. plicatum* was the only species that achieved high germination (67%) and survival (91%) rates, indicating its potential to be used on this type of technique for ecological restoration of grasslands.

In terms of competition and inhibition of the invader performance when cultivated with native species, we observed that a high GRI itself does not inhibit the growth and establishment of *E. plana*. Our study results are showing the opposite - where species with higher GRI increased the invader biomass. We are confident that this happened because among the species we tested none had both high GRI and development in terms of biomass, and those with higher GRI had very low biomass. Among the native species, *P. plicatum* was the only one that had a great early development (Fig. 1c and d), even though it germinated more slowly (Fig. 2). Its higher biomass led to a lower individual performance of the invader (Figs. 3 and 4). Another study has already registered its potential of due to an increase of ground coverage in invaded areas by *E. plana* and other alien species (Ferreira 2007). Because of its high germination and survival rates, and especially its high biomass production in early development stages, we indicate that *P. plicatum* has great potential to be used in ecological restoration of degraded areas subjected to invasion by *E. plana*. Other native species with similar characteristics should be tested to increase the possibilities to recover grassland communities under *E. plana* invasion.

In our experiment, we observed that *E. plana* did not have the highest germination rate nor the highest GRI, but had the highest biomass production. Nevertheless, the native species with the higher biomass production could delay the early growth of the invader, suggesting the potential of at least slow down the invasion process, acting as 'biotic containment' (Levine et al. 2004). Guido et al. (2017) have already demonstrated that some native species could delay the germination and development of *E. plana*. Furthermore, our results demonstrate the difficulty to find species that can compete with the invasive and highlights that restoration studies must go beyond the germination and early establishment steps.

Restoration of degraded grasslands that are highly fragmented and/or that do not have large seed and bud banks can be very slow or unsuccessful (Foster et al. 2007; Vieira et al. 2015), as grasslands do not have the regeneration dynamic relied in nuclei to attract animal dispersers that greatly accelerate the process and is commonly observed in forests (Overbeck et al. 2013). Direct seeding can be an efficient

(Foster et al. 2007; Török et al. 2011; Pellizzaro et al. 2017) and cheap (Török et al. 2011; Palma and Laurance 2015) technique to reintroduce species in a degraded area. However, as our results have shown and is commonly observed when direct seeding is used to restore grasslands, germination and establishment rates vary across sowed species (ex.: (Pellizzaro et al. 2017; Seahra et al. 2019)). An alternative can be create monospecific patches (Seahra et al. 2019), and this could work in the case of *Campos Sulinos*, where there is a lack of native seeds for restoration (Overbeck et al. 2013).

Seen the lack of studies about ecological restoration in grassy ecosystems (Guerra et al. 2020) and the difficulty of increasing species richness in degraded areas of grasslands (Thomas et al. 2019b; Thomas et al. 2019a), our results are important contributions to further develop and apply the technique of direct seeding in ecological restoration projects in the *Campos Sulinos* region. By the results here found, the species that stood the most was *P. plicatum*, which had high germination, survival, and biomass production, even being a species with low GRI (the plateau was reached only after 20 days, Fig. 3). We also highlight that *A. lanata* presented high germination and survival rates, demonstrating potential for use in direct seeding. On the other hand, *A. laevis* and *A. jubata*, despite the high germination rate and velocity, had low survival and biomass production, indicating that a greater number of propagules may be necessary to reach good establishment results of those species in degraded areas. This last point, however, is relevant since many of native grassland species seems present low rates of germination and/or establishment or even highly variable but that should be considered at any way to restore biodiversity of high diverse grasslands.

Moreover, it had been demonstrated that *E. plana* is an invader with strong competitor characteristics, being a species presenting high performance in all measured attributes: germination rate, survival rate, speed of germination, and biomass per individual. Grassland restoration on invaded areas (or highly subjected to invasion) depends on improved methods for invasive grass control (Sampaio et al. 2019). Long-term studies on plant development may bring additional contributions to understanding the dynamic between *P. plicatum* and *E. plana*, and eventually with other native species with similar characteristics as the observed for *P. plicatum*, once the competitive response of the invader could be more important in later stages, as in persistence and expansion of invaded areas (Guido et al. 2019).

Statements & Declarations

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Figures

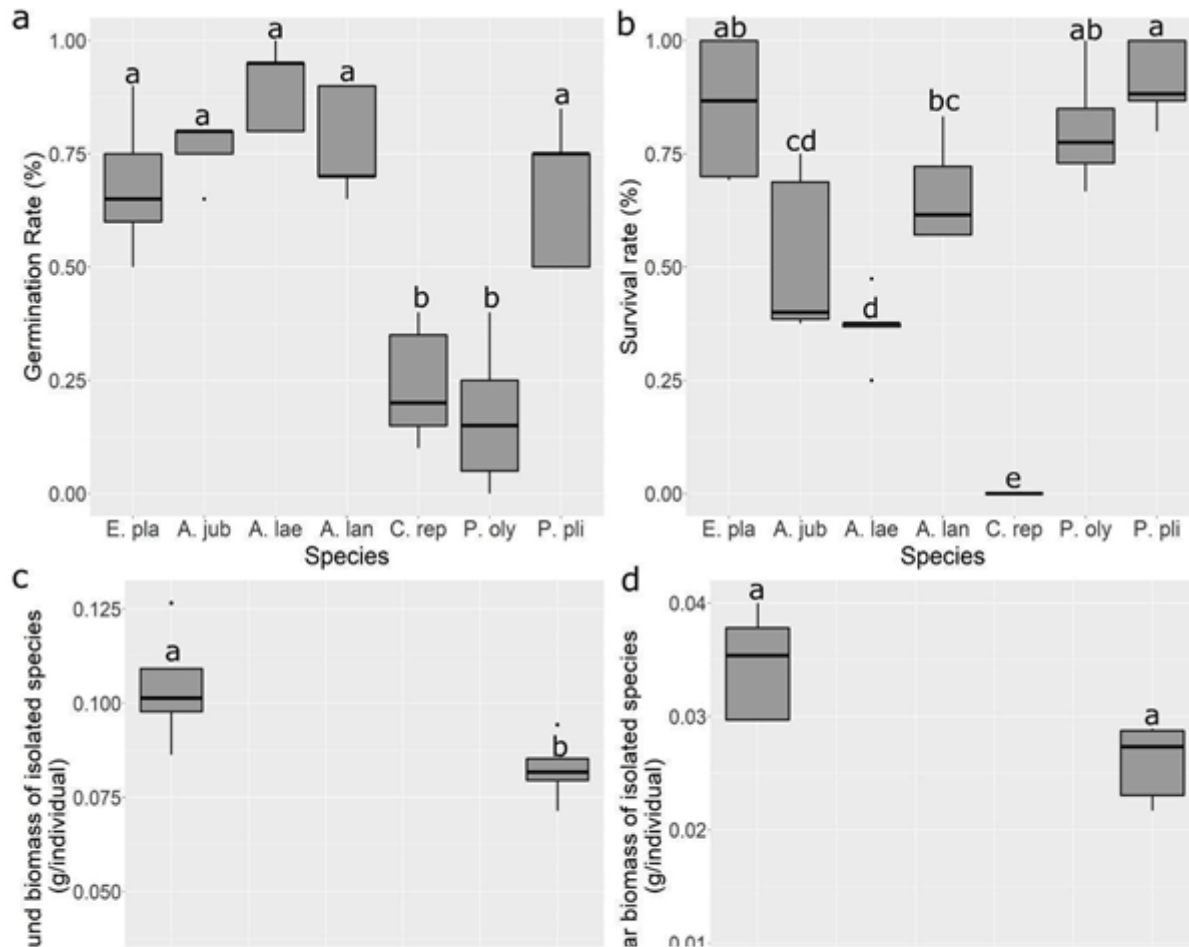


Figure 1

Boxplots with the values of (a) germination rate, (b) survival rate, (c) above and (d) belowground biomass per individual for the six native species: *A. jubata* (*A. jub*), *A. laevis* (*A. lae*), *A. lanata* (*A. lan*), *C. repens* (*C. rep*), *P. olyroides* (*P. oly*) and *P. plicatulum* (*P. pli*) and the invasive *E. plana* (*E. pla*) of isolated culture.

Different letters indicate significant differences between species ($p < 0.05$). Outliers are represented by black dots.

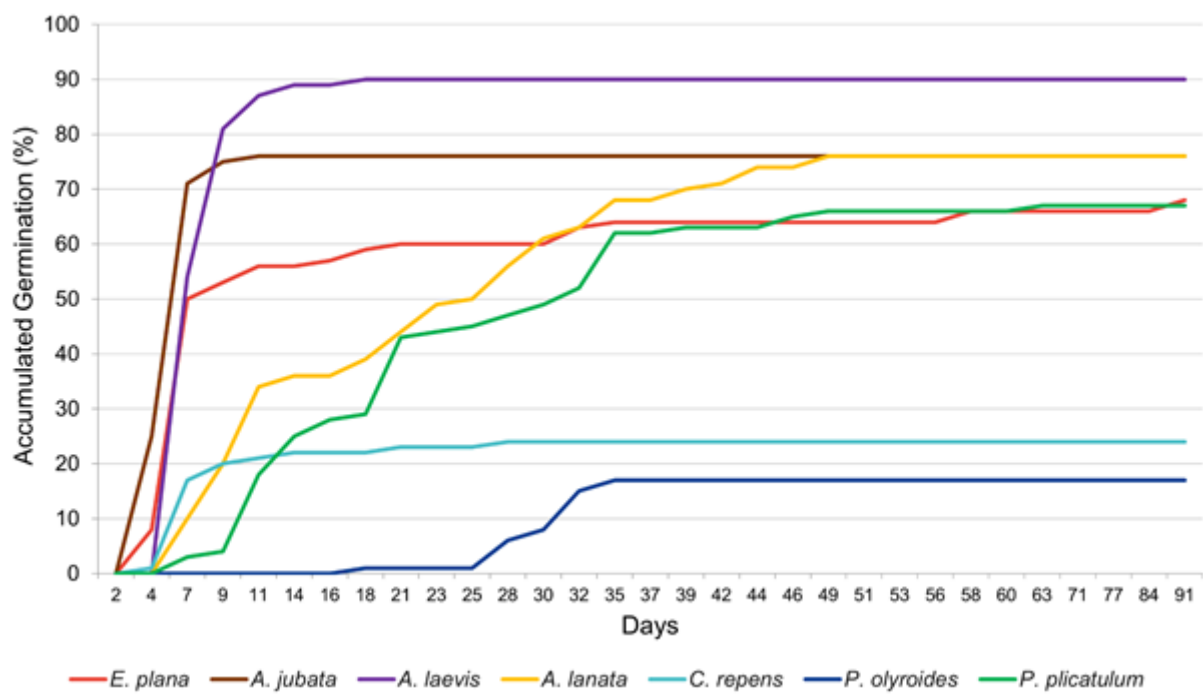


Figure 2

Average percentage of accumulated germinations per species per day, cultivated as isolated species in garden pots, in a greenhouse environment, under regular irrigation.

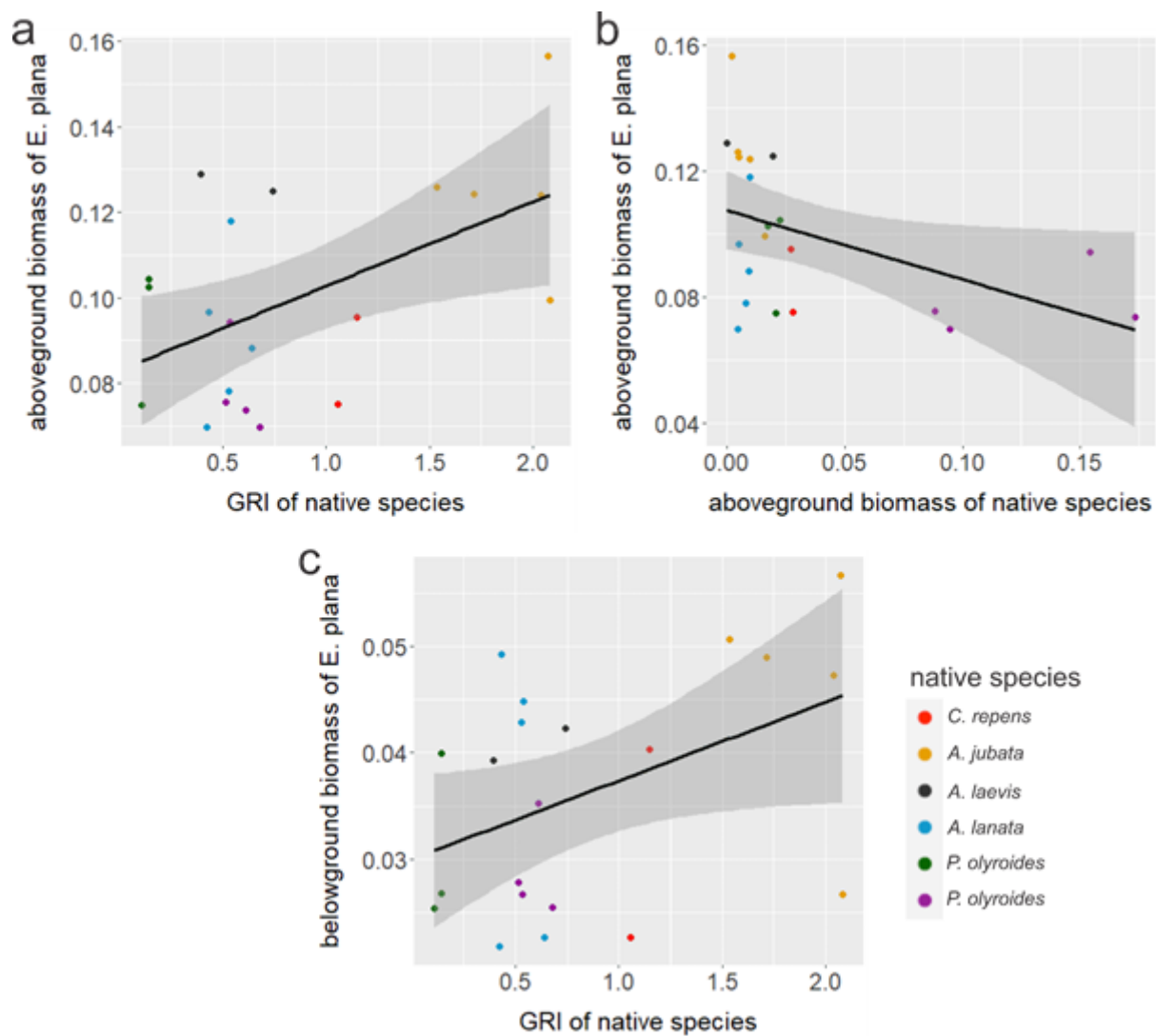


Figure 3

Linear regressions showing the relationships between variables of native species that were significant in determining the biomass of *E. plana*: GRI (a) and aboveground biomass (b) of the native species related to the aboveground biomass of *E. plana* and the GRI of the native species related to the belowground biomass of *E. plana* (c).



Figure 4

Pots of *P. plicatulum* (left), *P. plicatulum* and *E. plana* together (middle) and *E. plana* alone (right) at the end of the experiment, at day 93.

Supplementary Files

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