LIGHT EFFECTS ON THE GERMINATION AND GROWTH OF THE INVASIVE ALIEN GRASS *Eragrostis plana*

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Abstract: Changes in light conditions may affect invasiveness as they can constrain different stages of plant development during the invasion process. This is particularly true in grazed grasslands, as livestock selectively removes above-ground biomass, promoting light heterogeneity. We assessed how light intensity and quality affect the germination and growth of *Eragrostis plana*, one of the most invasive alien grasses of the Río de la Plata grasslands (southern Brazil, Uruguay, and eastern Argentina). We performed two experiments under laboratory conditions, one assessing germination responses and another evaluating its growth. The germination experiment compared the percentage of germination and the mean germination time between four treatments, resulting from combining of two levels of light intensity and quality. The growth experiment was performed for two initial stages of *E. plana*'s growth (3-month and 5-month-old plants) under contrasting light intensity levels. We found that lower light intensity reduced the number of germinated seeds and increased the mean germination time of *E. plana*. Moreover, it affected its growth by reducing the number of leaves and height of 3-month-old plants. Reducing light intensity can be a valuable tool to prevent the colonization of *E. plana* in new areas (by affecting its germination) and limit its spread in invaded grasslands (by reducing its early growth).

Keywords: Capín Annoni; invasion, light intensity; light quality; lovegrass; Río de la Plata grasslands.

INTRODUCTION

Biological invasions have generated important impacts worldwide, altering diversity and ecosystem functioning (Pyšek *et al.* 2012, IPBES 2023). Although it is a complex phenomenon driven by several interacting factors, biological invasion can be summarized as a function of (i) propagule pressure, (ii) environmental abiotic characteristics, (iii) and biotic features of both the invader and the recipient community (Catford *et al.* 2009). Thus, the success of an invasive alien species can vary spatially and

temporally, along with environmental conditions and community characteristics which can be modified by human activities (Davis *et al.* 2000, Thomsen & D'Antonio 2007). Research on this topic has primarily focused on understanding why and how some species can colonize, persist, and expand their ranges into new ecosystems (Lonsdale 1999, Richardson *et al.* 2000). In this context, resource availability has been the focus of several hypotheses related to species invasiveness and community invasibility, constituting an essential framework on biological invasion ecology research and the role of human activities in the invasion process (Catford *et al.* 2009, Blackburn *et al.* 2011).

Light intensity (*e.g.,* μmol photons.m^{-2}.s^{-1}) and quality (*e.g.,* red to far red ratio, R: FR) are two important factors for plant germination and growth (Lee *et al.* 1996, Casal & Sánchez 1998, Lazzarini *et al.* 2018). Several studies have focused on light intensity's role in determining invasion success (Milbau *et al.* 2005, Flory *et al.* 2007). For instance, some invasive alien plants that colonize open ecosystems, such as C$_4$ grasses in grasslands (*i.e.* shade-intolerant species), can take advantage of high-light conditions and grow rapidly in response to natural or human-induced canopy gaps (D'Antonio *et al.* 2001, Dobarro *et al.* 2010). However, when light availability decreases, these species' growth might diminish, and the invasion can thus be constrained (Dobarro *et al.* 2010, McDaniel & Ostertag 2010). The quality of light also influences plant germination and growth, exerting significant effects across different stages of development (Smith 2000, Courbier & Pierik 2019). Nonetheless, fewer studies evaluated the effects of light quality on the invasion success. Some of them evaluated, for instance, how the quality of light affected the height, leaf number, and biomass of *Celastrus* species, and these effects were higher in the invasive *Celastrus orbiculatus* than in the native congener *C. scandens* (Leicht & Silander 2006). Hence, the manipulation of light conditions could be a strategy to decrease the success of a target invasive species when promoting abiotic resistance to invasion, affecting its germination or growth (McDaniel & Ostertag 2010, Batlla & Benech-Arnold 2014).

In this study, our focus was *Eragrostis plana* Nees, one of the most problematic invasive alien plants in South America's Río de la Plata grasslands (Medeiros & Focht 2007, Guido & Quiñones 2021). It is a perennial tussock grass introduced from South Africa to southern Brazil, where it became invasive, being also invasive in Uruguay (Guido & Quiñones 2021) and possessing a high potential for spreading further throughout South America (Barbosa *et al.* 2013). The most significant consequences of *E. plana* invasion are associated with the reduction of native species richness and cover (Guido & Pillar 2017, Dresseno *et al.* 2018) and the decrease of forage palatability and nutritional value for livestock (Guido *et al.* 2021). Hence, its invasion not only negatively impacts grasslands biodiversity and conservation but also contributes to socio-economic problems that are difficult to reverse (Zabala-Pardo & Lamego 2024). The invasiveness of *E. plana* is associated with its superior competitive ability (Guido *et al.* 2019), mainly because of its great production of seeds that germinate faster than native species (Guido *et al.* 2017). Both characteristics were also observed under abiotic stress, as seeds of *E. plana* still germinate at a wide range of conditions of light, temperature, and osmotic potential (Maldaner *et al.* 2019), while the competitive ability of adult plants is high even under water stress (Soares de Lima *et al.* 2022). However, questions still remain about which environmental conditions may negatively affect its invasiveness at different stages of development (*i.e.,* from germination to later growth stages), and thus provide abiotic resistance to further spread.

As grazing is a historically economic activity in the Río de la Plata grasslands (Paruelo *et al.* 2022), changes in light availability are continually promoted by livestock. Grazers remove aboveground biomass selectively, creating spatial heterogeneity of plant biomass (Lezama & Paruelo 2016) and light conditions (Bakker *et al.* 2003). Grazer-induced defoliation not only alters the intensity of light reaching the soil but can also has the potential to modify its quality by changing the R: FR ratio (Dobarro *et al.* 2010). These different conditions between the intensity and the quality of light could affect the germination or growth of *E. plana*, as it is a C4 grass of open ecosystems that prefer high-light environments (Osborne & Freckleton 2009). In this study, we aimed to evaluate the effect of the intensity and quality of light on the germination and growth of *E. plana*. For that, we performed two laboratory experiments in which light conditions were manipulated at three different stages of plant development: germination, seedlings

(3-month-old plants with one tiller), and young plants (5-month-old plants with ca. 10 tillers). We expect that reducing light intensity and quality will hinder *E. plana*'s germination and growth, a fact to be considered in management strategies to prevent and control its invasion.

MATERIAL AND METHODS

Eragrostis plana's germination

On February 18th, 2021, we collected seeds of *E. plana* on an invaded roadside verge of a highly transited route (Cerro Largo Department, Uruguay). From February 24th to May 27th, 2021, in a plant growth chamber at the Instituto Nacional de Investigación Agropecuaria (Treinta y Tres Department, Uruguay), we performed a germination experiment in which light conditions were manipulated. The experiment consisted of two factors, intensity (I) and quality (Q) of light, with two levels each, low (-) and high

(+), resulting in four treatments: I-Q-, I+Q-, I-Q+ and I+Q+ (Figure 1A). The levels of light intensity consisted of 100 µmol photons.m^{-2}.s^{-1} (I +), and 50 µmol photons.m^{-2}.s^{-1} (I -). The quality of light was manipulated by the R: FR ratio, which was 1.5 (Q +) and 0.75 (Q -). To set up these different combinations of light conditions, we used a commercial LED growth light, Elixia LX602C (Heliospectra AB, Gothenburg, Sweden) equipped with four tunable wavelengths. Treatments were customized at the shelf height, and to define the Elixia configurations we used an AccuPAR LP80 Ceptometer (Decagon Devices Inc., Pullman, USA) and a R: RF light meter FieldScout (Spectrum Technologies Inc., Illinois, USA).

Each experimental unit consisted of a Petri dish (100 mm in diameter) with two layers of filter paper, moistened with 4 mL of distilled water, where we placed 25 seeds of *E. plana*, forming a grid of five rows by five columns. We included four replicates per treatment, thus obtaining 16 Petri dishes. Petri dishes were externally sealed with paper tape to
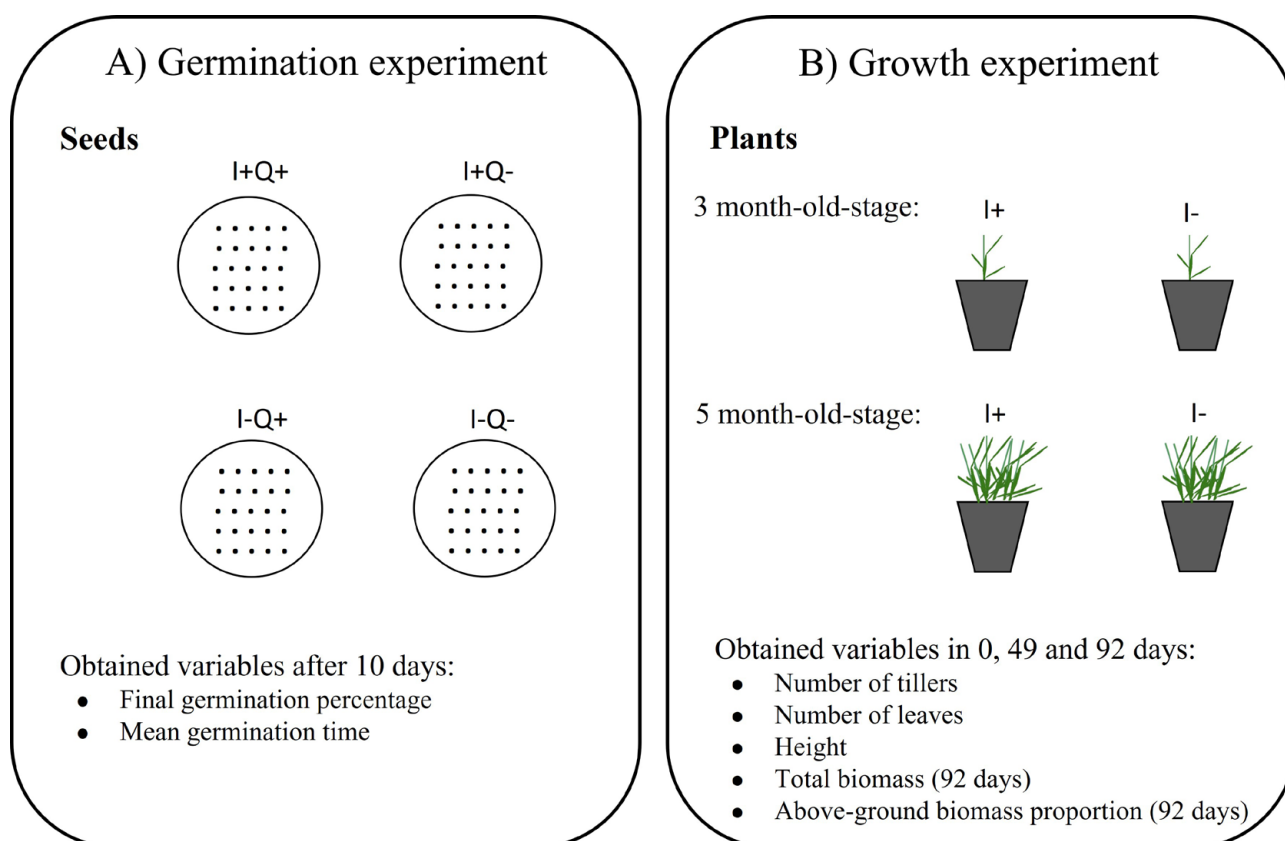

Figure 1. Schematic representation of the experimental design. A) *Eragrostis plana*'s germination experiment in which light intensity (I-: low; I+: high) and light quality (Q-: low; Q+: high) were manipulated. B) *Eragrostis plana*'s growth experiment in which light intensity I-: low; I+: high) was manipulated for two stages of plant growth: seedlings (3-month-old-plants) and young plants (5-month-old plants).

minimize water evaporation during the experiment, but we occasionally added water as needed. All treatments had a 12 h-photoperiod and a fixed temperature of 25 °C. Each treatment lasted ten days and was executed separately (one at a time), since only one Elixia light was available to program each condition. We evaluated the germinated seeds daily in the stereoscope with the help of a green safety light to prevent the stimuli that white light has on germination (Taylor *et al.* 2004). For each treatment, we obtained the final percentage of germination ((germinated seeds/total seeds) * 100) and the mean germination time according to the following formula:

$$Mean\ germination\ time\ (day) = \sum (Ni * i)/N$$

where Ni is the number of seeds germinated on the ith day, i is the day number (from 1 to 10) and N is the total number of seeds germinated at the end of the experiment.

Eragrostis plana´s growth: 3 and 5-month-old stages

In a plant growth chamber at Facultad de Ciencias (Montevideo Department, Uruguay), we evaluated the effect of light intensity on two stages of *E. plana´s* growth: 3 and 5-month-old stages. For that, we used seeds collected for previous studies (April 2018 – a highly invaded roadside verge in Artigas Department, Uruguay) and checked for their germination potential. To represent both stages of growth, we sowed seeds of *E. plana* at two different times: August 26th, 2021 (5-month-old stage) and November 3rd, 2021 (3-month-old stage). On each date, *E. plana* seeds were placed to germinate in eight pots of ca. 1600 cm³ (13 cm diameter and 12 cm deep). At the bottom of each pot, a layer of approximately 2 cm of stones was placed to facilitate drainage in case of water excess and completed with a substrate mixture of organic soil and sand (2:1). Until the beginning of the experiment, the plants (*i.e.*, one individual per pot) were maintained at similar light (12h-photoperiod; 4 LED tubes), temperature (fixed at 25 °C) and water (on demand) conditions.

On February 2nd, 2022, the above-ground portion of all plants was cut at a height of 20 cm, to avoid differences in self-shading that may mask later light effects. The roots of the 5-month-old stage were also homogenized to a size of 10 cm to prevent the size of the pot from impeding its response. All plants were transplanted into pots of the same size (1600 cm³) with renewed substrate at the same organic soil and sand proportions (2:1). After one week of acclimatization, on February 9th, 2022, the growth experiment began, and light intensity was manipulated. At this time (T_0), the 3-month-old stage consisted of plants with only one tiller, while the 5-month-old stage had, on average, 10 tillers. The treatments were as follows: high light intensity (I +; provided by 4 LED tubes, 9W, 720 Lm each), and low light intensity (I -; provided by 1 LED tube, 9W, 720 Lm). Thus, the growth experiment consisted of four treatments (n=4) resulting from the combination of two factors with two levels each: stage of development (3- and 5-month-old stages) and light intensity (high and low; Figure 1B). In this experiment, light quality was not evaluated since we could not transport the equipment to Facultad de Ciencias due to mobility restrictions.

On three dates (T_0; T_1: 49 days later; and T_2: 92 days later) the following variables were measured: number of tillers, total number of leaves (both live and senescent), and maximum height. After the last measurement, the plants were harvested and fractionated into above- and below-ground biomass. These fractions were dried for 48 h at 70 °C in an oven and weighed on a precision scale to obtain total dry biomass and above-biomass fractions.

Data analysis

The data analysis was conducted separately for each experiment. For the germination experiment, we compared two response variables: the final germination percentage (*i.e.*, percentage of germination at the end of the experiment) and the mean germination time (*i.e.*, average time required for germination of a seed lot) between treatments. When differences between treatments were detected (p-value <0.05), *a posteriori* pair-wise contrasts were performed. Regarding the growth experiment, for each stage of development (*i.e.*, 3 and 5-month-old stages), we evaluated the effect of light intensity (*i.e.*, comparing between the levels of low and high intensity) on the following variables: number of tillers, total number of leaves, height, total biomass

and the proportion of above-ground biomass. For all cases, we used an analysis of variances with permutation tests (10 000 permutations), which does not rely on assumptions about the underlying distribution of the data (Manly 2007). All analyses were performed in MULTIV *software* (Pillar 1997; available at http://ecoqua.ecologia.ufrgs.br).

RESULTS

Eragrostis plana´s germination

Light intensity and the interaction between intensity and quality of light significantly affected both the final germination percentage and the mean germination time of *E. plana* (Figure 2; Table 1A; Appendix 1). The highest final germination percentage (≥90 %) was observed at high light intensity, irrespective of light quality, and it was reached in only three days (Figure 2A). At low light intensity and high quality (I-Q+), the final germination percentage of *E. plana* was 52 ± 7 %, representing the lowest value for the experiment (Figure 2A). Moreover, high light intensity reduced mean germination time compared to low light intensity (Figure 2B). At high levels of light intensity, reduced light quality decreased the mean germination time (1.86 ± 0.17 and 1.54 ± 0.10 days for high and low quality, respectively; Figure 2B; Table 1A). However, at low intensities of light, the quality did not significantly affect the mean germination time (Figure 2B).

Eragrostis plana´s growth: 3 and 5-month-old stages

On average, in the 3-month-old plants, treatments with low light intensity presented a smaller total number of leaves (Figure 3C), shorter plant height (Figure 3E), and lower total biomass of 58%, 51%, and 95%, respectively (Table 2A), when compared to plants with high light intensity (Table 1B). However, the proportion of above-ground biomass did not vary between treatments (Tables 1B and 2A). In contrast, none of these growth variables were significantly affected by light intensity for the 5-month-old stage, although there was a marginal effect (P=0.0578) on the number of tillers, which was, on average, 55% lower when light intensity was reduced (Figure 3B; Table 1C).

DISCUSSION

Light conditions vary spatially and temporally and exhibit quantitative and qualitative heterogeneity in natural ecosystems. This phenomenon is particularly noticeable in grazed grasslands, where livestock selectively remove above-ground biomass, creating light heterogeneity due to differences in the height of remaining vegetation (Bakker *et al.* 2003). Changes in light conditions determine differences in the invasiveness of shade-intolerant alien species (McDaniel & Ostertag 2010, Funk 2013), as they could affect plant germination and growth during the different steps of the invasion process (Theoharides & Dukes 2007). This study evaluates light conditions as a possible abiotic constraint for *E. plana´s* invasion in the Río de la Plata grasslands. We found that light, and particularly its intensity, affects *E. plana´s* germination and early growth. Our results show that the earlier stages of development, *i.e.*, germination and the 3-month-old stage, were more affected by light conditions than later stages (*i.e.*, 5-month-old stage). These responses are essential to understanding how environmental variables influence *E. plana* invasion and to designing timely prevention or containment strategies that complement conventional herbicide applications. Reducing light intensity can be useful to prevent the colonization of *E. plana* in new areas (by affecting its germination) and constraint the spread in already invaded grasslands (by reducing its early growth).

Studying germination dynamics and its environmental constraints is essential to understanding how a target invasive alien species colonizes gaps and spreads in the recipient community. At higher light intensities, the germination percentage was not significantly affected by reduced light quality, as 96% and 90% of the seeds germinated at high and low quality, respectively. This result has considerable implications, as many studies have suggested that germination success is positively associated with the establishment or spread of invasive alien species (Gioria & Pysek 2017). Although we expected that a reduction in light intensity and quality would affect *E. plana*'s germination, these conditions did not significantly reduce the number of germinated seeds (I-Q-: 75% of germination).

Changes in light quality could be associated with the presence of neighboring plants since plant
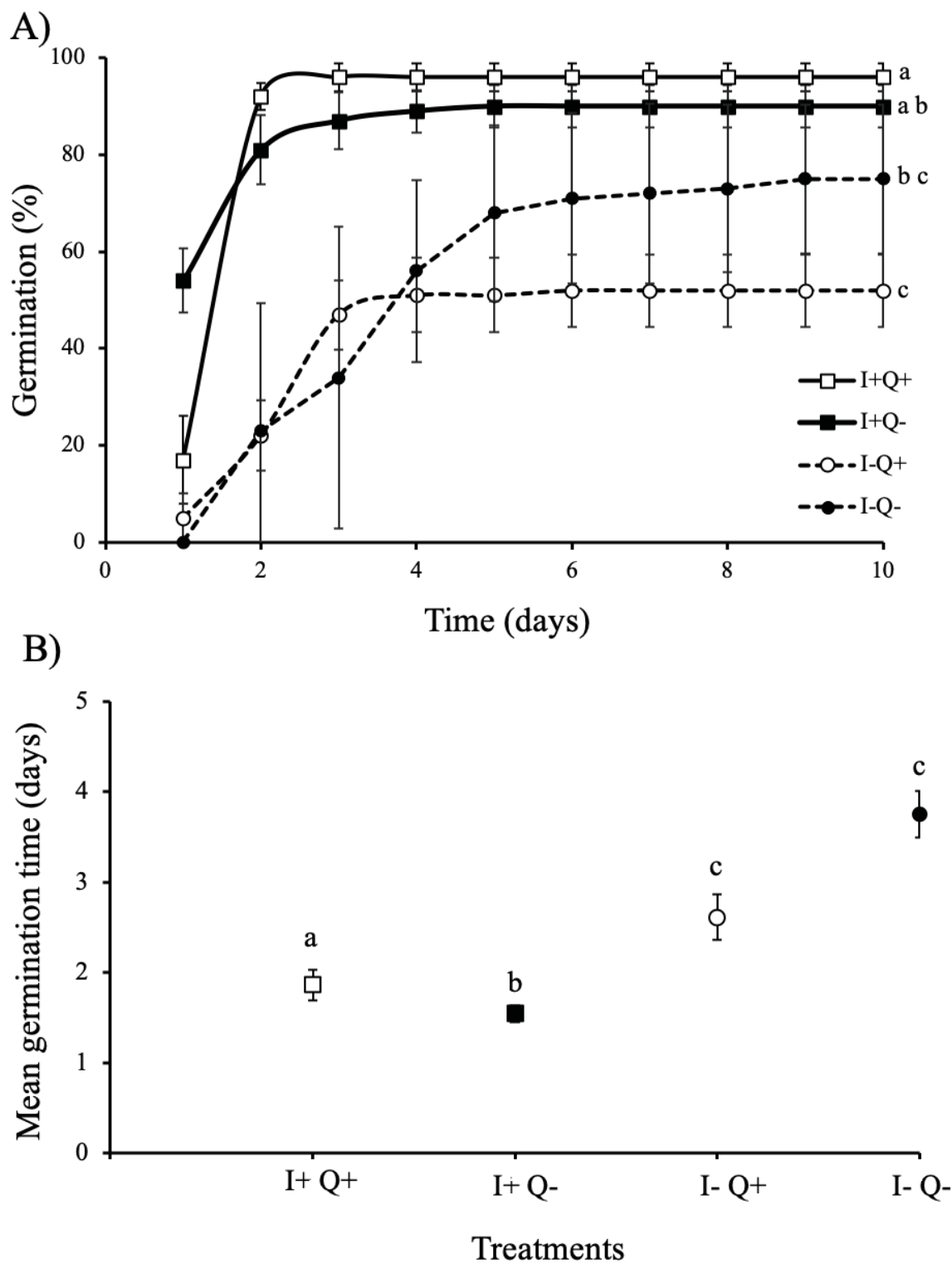
Figure 2. Germination responses of *Eragrostis plana* to different light treatments (mean ± SD; n=4) A) Cumulative percentage of germination (%) per day, where germination at day 10 corresponds to the final percentage of germination. B) Mean germination time (days). The treatments resulted from the combination of light intensity (I-: low; I+: high) and the quality of the incident light (Q-: low; Q+: high). Different letters indicate differences between treatments (significant for P≤0.05 or marginally significant when 0.059≥P>0.050). See Table 1 and Appendix 1 for statistical details.

Table 1. The sum of squares (SS) and P-values (P) resulting from the ANOVAs with permutation test for evaluating the effects of light (intensity: I, quality: Q, and its interaction) on response variables according to the different stages of *Eragrostis plana*'s development: A) germination; B) 3-month-old stage; C) 5-month-old stage.

Stage of growth	Response variable	Factor	SS	P
A) Germination	Final germination percentage	I	3481	0.0042
		Q	289	0.2771
		I*Q	841	0.0163
	Mean germination time	I	8.74	0.0003
		Q	0.67	0.1724
		I*Q	2.13	0.0185
B) 3-month-old stage	Number of tillers	I	2	1
	Total number of leaves	I	406	0.0306
	Height	I	3003	0.0290
	Total biomass	I	4	0.0282
	Above-ground biomass proportion	I	126	0.3470
C) 5-month-old stage	Number of tillers	I	136	0.0578
	Total number of leaves	I	4095	0.2947
	Height	I	200	0.1129
	Total biomass	I	42	0.0868
	Above-ground biomass proportion	I	184	0.0848

tissue differentially absorbs more photons in the red region than in the far red one (Smith 2000). It has been shown that some seeds can detect and respond to changes in the R: FR ratio by modifying their germination characteristics (Batlla *et al.* 2000, Batlla & Benech-Arnold 2014). Regarding mean germination time, we found that *E. plana* germinated faster when the light intensity was high and the quality was low (I+Q-), and it germinated slower when both conditions were reduced (I-Q-). It is possible to interpret an environment with high light intensity and a reduction in light quality as a gap in the recipient community with nearby neighbors, where fast germination could be an advantage for *E. plana* colonization. On the other hand, an environment with a reduction in both conditions means a closed canopy, where slower germination could be a bet for remaining in 'safe' pre-germination phases when the probability of seedling establishment is low. It would be interesting to elucidate which native species can generate light conditions that limit *E. plana*'s germination. Moreover, comparative studies between the responses of *E. plana* and other native grasses should also be performed to better
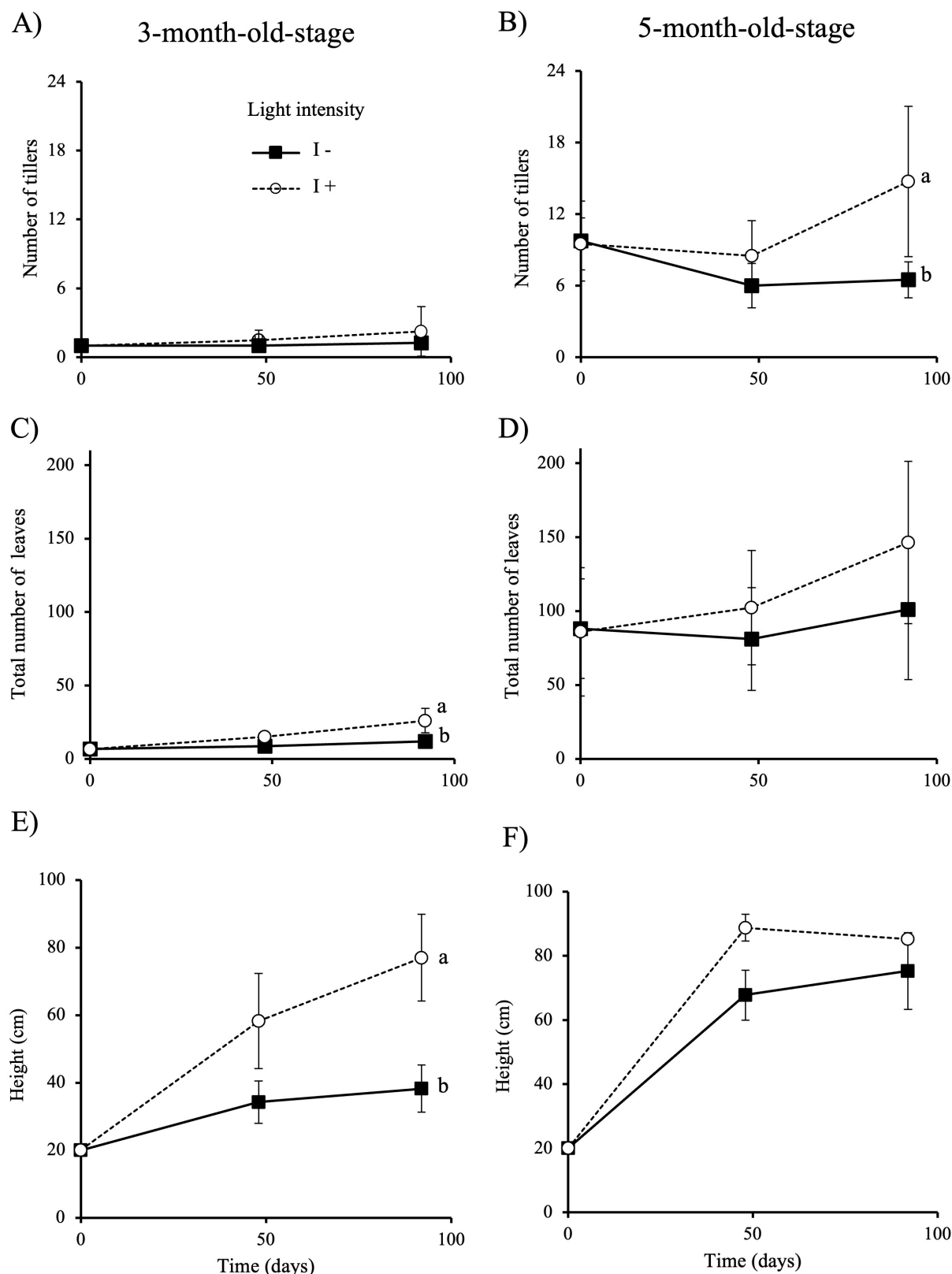
Figure 3. Mean (n=4) ± SD for the number of tillers, total number of leaves and height (cm) for low (I-) and high (I+) intensity of light during the experiment (92 days) for two stages of development of *Eragrostis plana* (3 and 5-month-old stages). Different letters indicate differences between levels of light intensity at the end of the experiment between treatments (significant for P≤0.05 or marginally significant when 0.059≥P>0.050). See Table 2 for statistical details.

Table 2. Mean (n=4) ± SD for the total biomass (g) and the proportion of above-ground biomass of *Eragrostis plana* for low (I-) and high (I+) intensity of light. A) 3-month-old stage. B) 5-month-old stage. Different letters indicate significant differences (P≤0.05) between light treatments for each variable within each stage of development.

Stage of growth	Response variables		
	Light intensity	Total biomass (g)	Above-ground biomass proportion
A) 3-month-old stage	I-	0.080 ± 0.03 a	0.85 ± 0.10
	I+	1.535 ± 0.39 b	0.77 ± 0.06
B) 5-month-old stage	I-	3.562 ± 2.20	0.91 ± 0.06
	I+	8.140 ± 3.02	0.82 ± 0.02

understand the complexity of neighbor interactions during the invasion process. For example, a previous study in Río de la Plata grasslands found that the germination of two native C4 grasses was not affected by the reduction of light intensity (López-Mársico *et al.* 2019); nevertheless, the R: FR ratio was not evaluated.

A lower light intensity, albeit still at high quality (I-Q+), negatively affected *E. plana*´s germination by reducing at 52% the final percentage of germinated seeds. However, this value remains relatively high compared to the native species of the recipient community in the study region (*e.g.,* Guido *et al.* 2017). Considering the biological invasion framework, our results are consistent with many studies that have experimentally shown higher and faster germination of invasive alien species as key traits to enhance invasion success (Gioria & Pysek 2017). Seeds germinating copiously and fast, without pretreatment, and in a wide range of conditions, are more likely to establish and spread (Gioria & Osborne 2014, Gioria & Pysek 2017). Notably, Maldaner *et al.* (2019) observed that darkness inhibited the germination of *E. plana*; however, despite extended periods of darkness, it could not fully prevent its germination (72% germinated during the most prolonged period of darkness). Other experiments have demonstrated that *E. plana* still germinates at different temperatures and osmotic potentials, which makes the species successful in a wide range of abiotic conditions (Bittencourt *et al.* 2017, Maldaner *et al.* 2019). These responses to different conditions are expected to convey fitness benefits and could be a crucial strategy that increases invasiveness and allows alien species to succeed in multiple environments (Godoy *et al.* 2012, Funk 2013).

Lower levels of light intensity decreased the growth of *E. plana*, but this reduction differed depending on the development stage. For the 3-month-old stage, the total number of leaves, plant height, and total biomass decreased significantly when the light intensity was reduced by 75%. For the 5-month-old stage plants, where the tillering phase had already started, only the number of tillers was marginally affected by the light intensity reduction. This difference in *E. plana*'s response suggests that reduced light intensity would affect the growth variables in which the species invest more. For instance, in the 3-month-old stage, plants primarily invest in leaf production and elongation (Moore *et al.* 1991) and, consequently, reduced light availability would mainly affect these processes. In later stages, the individuals produce new tillers to enhance lateral colonization, and hence, reduced light availability would negatively affect tillering (Deinum *et al.* 1996). Previous studies indicate that, without light restrictions, *E. plana* is a better competitor than some native C4 grasses (Guido *et al.* 2019, Soares de Lima *et al.* 2022). However, a reduction in light intensity can favor the growth of other native species with lower light requirements (Fernández *et al.* 2014, 2019), which can change competition outcomes between *E. plana* and native species and its invasion success.

Although our experiments were performed under laboratory conditions, and we are aware of their limitations, we believe light restrictions in the field could decrease *E. plana*´s success. The

early stages of plant development are critical, so decreasing light intensity can reduce germination percentages, thus increasing germination time, negatively affecting plant growth and limiting its success. Changes in light conditions can be promoted by grazing management, as grazers can modify light availability for some plants by shaping the structure of vegetation, such as vegetation height and species composition (Fahnestock & Knapp 1994, Augustine *et al.* 2012). By avoiding heavy grazing and promoting a moderate grazing regime, vegetation height and biomass increase, preventing bare soil and reducing light availability, both characteristics that may constrain an *E. plana* invasion. Baggio *et al.* (2018) experimentally demonstrated that heavy grazing plus soil disturbance increased the *E. plana* invasion, suggesting that grasslands under moderate grazing may be more resistant. Since grazing exclusion is not recommended to conserve the biodiversity of the Río de la Plata grasslands (Paruelo *et al.* 2022), an adequate grazing intensity would promote a vegetation structure that limits invasion while ensuring subsequent native recruitment. This point is crucial since once *E. plana* is well established, livestock strongly avoids its consumption and prefers native species, promoting a positive feedback loop of invasion and creating the need of other control strategies (Zabala-Pardo & Lamego 2024). As many studies have demonstrated, proper grassland management ensures biodiversity conservation, making it more resistant to invasion and providing the socio-economic services (Guido *et al.* 2023). This reinforces the significance of human activities on grasslands as key determinants of biological invasions. However, further experiments, particularly under field conditions, are necessary to deeply understand the invasion process as it involves several interactive factors and many underlying mechanisms.

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