

1 **Title:** Responses of native plants of the Patagonian steppe to reduced solar radiation caused by exotic coniferous
2 plantations: A nursery approach

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14

15 **Abstract**

16 In exotic coniferous plantations established in treeless environments, light availability is drastically reduced, limiting
17 the development of the native herb-shrub layer and consequently ecosystem functions and services. However, plants
18 exhibit different responses to deal with changes in the light environment. Aiming to contribute to management
19 guidelines favoring understory vegetation persistence in forest plantations, we evaluated, under nursery trial, the growth
20 of three representative species of the Patagonian steppe at 20, 60, and 100% irradiance. For each species, we compared,
21 among treatments, total biomass, biomass allocation, and specific leaf area several times during two growing seasons,
22 relative growth rate, net assimilation rate, and leaf area ratio at each time interval, and reproductive structures the
23 second growing season. *Berberis microphylla* and *Adesmia volckmannii* maintained their total biomass at 60%
24 irradiance, with *A. volckmannii* showing a tendency to increase it, whereas *Poa ligularis* tended to decrease total
25 biomass at irradiances below 60%. For the three species, changes in biomass allocation, generally higher leaf mass
26 fraction, and higher specific leaf area were detected at 20% and sometimes at 60% irradiance. Relative growth rate and
27 net assimilation rate, in general, tended to be higher at 60% and 100% irradiance, whereas leaf area ratio was higher at
28 20% and sometimes at 60% irradiance. *Adesmia volckmannii* and *P. ligularis* had fewer reproductive structures at 20%
29 irradiance. These results suggest that the analyzed species present a certain level of shade tolerance, at least up to 60%
30 irradiance, that may benefit their development in forest plantations with appropriate management.

31

32 **Keywords**

33 Light, Forest management, Herbs and shrubs productivity, Biomass allocation, Relative growth rate, Biodiversity
34 conservation

35

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40 content of this article.

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42 from the corresponding author on reasonable request.

43 **Code availability** Not applicable

44 **Author's contribution** Conceptualization: MMR, MFU, GED; Methodology: MMR, MFU; Formal Analysis: MMR;
45 Investigation: MMR; Resources: MFU, GED; Writing – original draft: MMR; Writing – review & editing: MMR, MFU,
46 GED; Visualization: MMR, MFU; Supervision: MFU; Funding acquisition: GED

47

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51

52 **Introduction**

53 Light is considered to be the main limiting factor for understory plants development, especially in forest plantations
54 established on treeless steppes (Barbier et al. 2008; Bremer and Farley 2010; Franzese et al. 2016). Such is the case in
55 ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson) plantations established in steppe areas in northern
56 Patagonia, Argentina, where plant richness and cover of the herb-shrub layer decrease linearly as available radiation
57 decreases (Rago et al. 2021). However, species respond differently to solar radiation, with some of them positively
58 related to radiation, although to a different extent (Fernandez et al. 2002, 2004; Rago et al. 2021). Besides, in treeless
59 environments invaded by exotic conifers, such as *Pinus contorta* Douglas ex Loudon in Chilean Patagonia, forest

60 canopy not only has an impact on plant richness and cover, but also drive plant community changes, affecting functional
61 vegetation traits associated with high radiation levels while promoting other traits associated with shade tolerance
62 (Bravo-Monasterio et al. 2016; Franzese et al. 2016).

63 The persistence of understory species in forest plantations promotes stability and ecosystem functions, and
64 furthermore, both biodiversity conservation and timber production (van Rensburg and Mill 2010; Cardinale et al. 2012).
65 To conserve a healthy understory in forest plantations, the implementation of appropriate forest management practices
66 (e.g., thinning, pruning) should be promoted, since light, water, and nutrient availability for understory vegetation may
67 depend on the intensities of these practices (Cummings and Reid 2008; Gyenge et al. 2011; Trentini et al. 2017; Rago et
68 al. 2021). However, plants have specific demands of essential resources, which may vary among species. Thus, forest
69 management guidelines should be based on the requirements of the species that are intended to be conserved.

70 Within the light availability gradient, plant species can be ordered in a range from higher to lower shade tolerance,
71 in which many species have intermediate light requirements (Wright et al. 2003; Valladares et al. 2004). In addition,
72 plant species exhibit different responses to changes in the light environment that could benefit their acclimatization to
73 different situations (Valladares and Niinemets 2008). A frequent response is a change in the allocation of resources to
74 leaves, stems, and roots (biomass allocation), which can be explained by the functional equilibrium theory (Brouwer
75 1962). This theory predicts that carbon allocation into leaves and stems increases when the availability of aboveground
76 resources, such as light and CO₂, is low, whereas carbon allocation to roots increases when the availability of
77 belowground resources, such as water and nutrients, is low. Thereby, plants maintain a greater capture of the most
78 limiting resource (Poorter and Nagel 2000). Morphological characters may also be modified when the light environment
79 changes, for example, specific leaf area (SLA), defined as the ratio of leaf area to leaf dry mass. This parameter usually
80 increases with radiation decrease, to maximize light capture (Liu et al. 2016). Changes may also occur in physiological
81 characters such as the respiratory rate and the light compensation point, which tend to decrease with radiation decrease
82 (Valladares et al. 2004), and in reproductive development characters, such as sex expression in monoecious plants and
83 phenology (Sultan 2000).

84 Plant growth analysis is a technique for estimating the fundamental parameters of the processes on which depend
85 plant persistence and growth. For that reason, this analysis is useful for assessing plant responses to changes in resource
86 availability (Di Benedetto and Tognetti 2016). Relative growth rate (RGR), defined as the biomass increase per unit
87 biomass and time, is the main measure of growth analysis. Relative growth rate can be decomposed into leaf area ratio
88 (LAR), which in turn can be decomposed into leaf mass fraction (LMF) and SLA, and net assimilation rate (NAR)
89 (Villar et al. 2004). Leaf area ratio is the ratio of leaf area to total plant biomass, and it constitutes the morphological

90 component of RGR. Net assimilation rate is the rate of increase of biomass per unit leaf area, and it constitutes the
91 physiological component of the RGR. Plant productivity is usually estimated by biomass production, which variation
92 among plants subjected to different irradiances is a good indicator of the capacity of species to tolerate shade (Liu et al.
93 2016). The reproductive response is also a good indicator of plant productivity in a period of time, as the number of
94 seeds or fruits decrease at lower irradiances, and even in some cases the plants stop reproducing (Liu et al. 2016;
95 Poorter et al. 2019).

96 In Patagonia, Argentina, ponderosa pine plantations have been established in steppe areas for timber production
97 since the '80 (Bava et al. 2015). This region is characterized by a Temperate-Mediterranean climate, with cold and rainy
98 winters and dry and warm summers (Köppen and Geiger, 1936). The soils are derived from volcanic ash with good
99 water retention and rich in nutrients (Etchevehere 1972). Thus, the water retained in depth during the winter becomes
100 available during the summer drought, allowing high growth rates of conifers (Gonda 1998; Irisarri and Mendia 1998).
101 Since the purpose of these plantations is timber production, the traditional and mostly used forest management in the
102 region maximizes the individual growth in diameter of the most valuable trees(Gonda 2001), without considering the
103 impacts on the natural ecosystem. However, there is an increasing interest in developing alternative schemes that
104 consider the maintenance of the biodiversity in these productive systems (Rusch et al. 2015, Bava et al. 2016).

105 The natural vegetation of the steppe is mainly composed of low shrubs and grasses, among which the shrubs
106 *Azorella prolifera* (Cav.) G.M. Plunkett & A.N. Nicolas, *Adesmia volckmannii* Phil., and *Berberis microphylla* G. Forst,
107 as well as many species of bunch grasses predominate (Soriano 1956; Oyarzabal et al. 2018). It has been found that, in
108 general, the richness and cover of this plant community decreases under the canopy of exotic conifer plantations, with
109 more abrupt changes in dense than in sparse canopies (Raffaele and Schlichter 2000; Fernández et al. 2002, 2006a;
110 Rusch et al. 2004, 2015; Lantschner et al. 2008; Orellana and Raffaele 2012; Dezzotti et al. 2019; Rago et al. 2020a,
111 2021). However, species may vary in their response to the level of canopy closure, with some of them not showing
112 changes in their cover or even increasing it up to certain canopy levels (Fernández et al. 2002, 2004; Rusch 2004; Rago
113 et al. 2021). This might be for different reasons, for example canopy reduces overheating and excessive transpiration
114 that steppe plants may experience (Fernández et al. 2004; Gyenge et al. 2010). Also, as this region has been subjected to
115 overgrazing since the introduction of domestic cattle at the end of the 19th century, a decrease in vegetation cover,
116 mainly palatable grasses has occurred (Bertiller and Bisigato 1998; Gaitán et al. 2017; Oliva et al. 2017). Thus,
117 plantations might benefit the increase of palatable grasses since their establishment is usually associated with livestock
118 reduction or exclusion (Gyenge et al. 2010). Regarding to light, in the open areas of arid and semi-arid ecosystems,
119 solar radiation is frequently not a limiting resource, on the contrary, it can sometimes be so high that photoinhibition

120 occurs (i.e. molecular processes in the face of excess light that lead to a reduction in the photosynthesis) (Valladares et
121 al. 2004). Thus, the shade generated by the plantation canopy could be contributing to reduce photoinhibition (Flores
122 and Jurado 2003). Besides, since the Patagonian steppe is close to the native forest, many species from the Patagonian
123 steppe also inhabit areas of the native forest, thus, they might be capable of acclimatizing to different light levels. In this
124 study, we proposed to evaluate the growth response of representative plant species of the Patagonian steppe to different
125 levels of irradiance, simulating different levels of the canopy cover of forest plantations. To reach this objective, we
126 established a nursery trial with three irradiance levels (treatments) that simulated situations of dense canopy, sparse
127 canopy, and open sky (20, 60, and 100% irradiance). Particularly for each evaluated species (*Berberis microphylla*,
128 *Adesmia volckmannii*, and *Poa ligularis* Nees ex Steud), we assessed the effect of irradiance on (1) total biomass (TB),
129 biomass allocation, and SLA at several times of the growing season during two growing seasons, (2) RGR, LAR, and
130 NAR at several time intervals during the two growing seasons, and (3) reproductive structures development during the
131 second growing season. We expected to find morphological and physiological modifications of the steppe plant species
132 at irradiances lower than 100%, such as higher SLA, LMF, and LAR, as well as lower NAR and RGR at the lowest
133 irradiances. We also expected that these modifications kept plant species productivity stable up to an irradiance
134 threshold, after which the productivity of the analyzed species decreased.

135

136 **Materials and methods**

137 *Selected species*

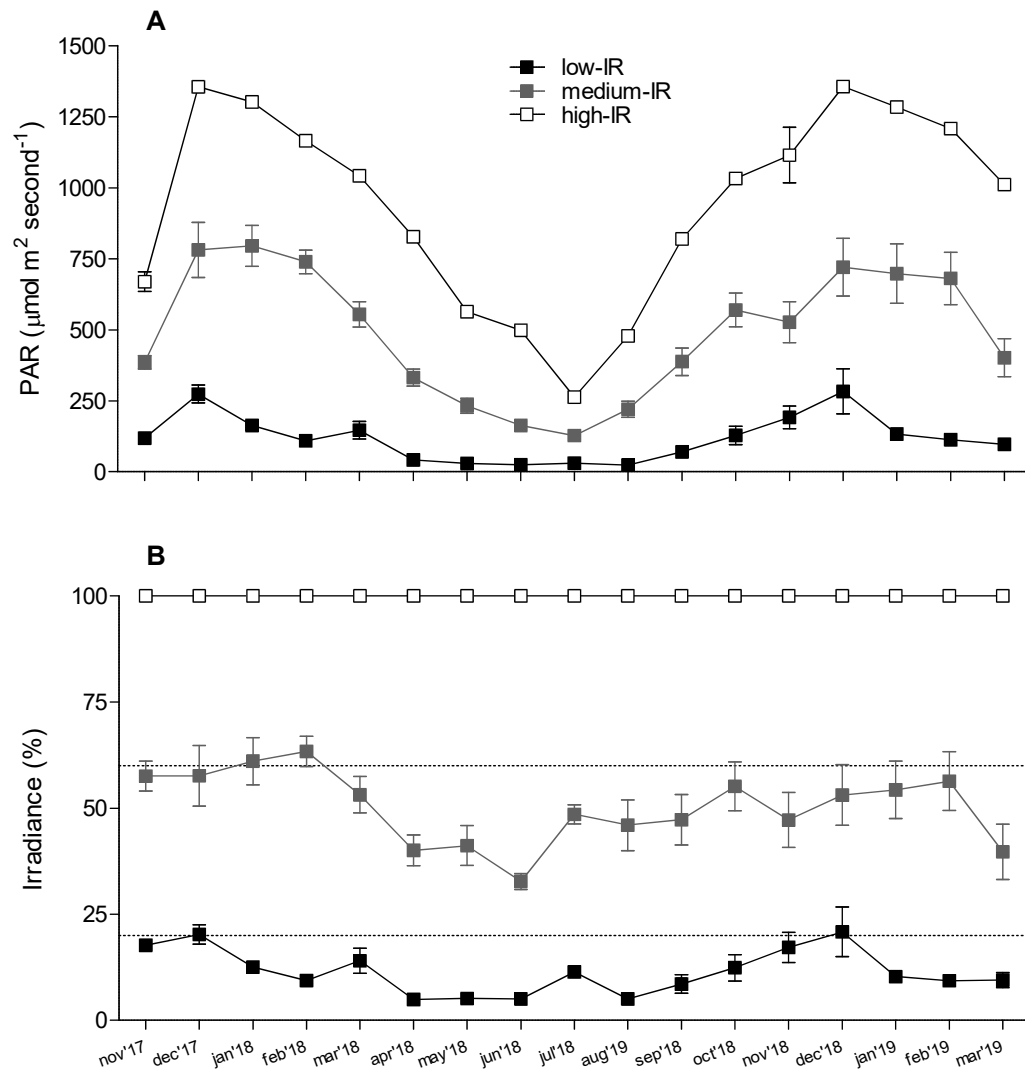
138 We selected three representative species of the Patagonian steppe where forest plantations are established: *Berberis*
139 *microphylla*, *Adesmia volckmannii*, and *Poa ligularis*. To choose them, we based on their predominance in the steppe
140 ecosystem and on the ecosystem services these species provide. Besides, on ponderosa pine plantations, these species
141 have shown different responses; whereas *Berberis microphylla* have presented a positive correlation between its cover
142 and diffuse radiation, neither *Adesmia volckmannii* nor *Poa ligularis* have shown a significant correlation (Rago et al.
143 2021). *Berberis microphylla* is an evergreen, spiny shrub, which can reach 3 m in height (Landrum 1999). It stands out
144 for the nutritional value of its berries, with a high content of carbohydrates, organic acids and phenolic compounds that
145 give it a high antioxidant capacity (Arena et al. 2012; Chamorro et al. 2019). This species is widely used by rural
146 communities, both as food as well as in medicines and other uses (Chamorro et al. 2019; Ochoa et al. 2019), and
147 constitutes a nutritional resource for wild animals. It inhabits in a great variety of conditions, from the native forest to
148 the steppe. *Adesmia volckmannii* is a deciduous shrub, spiny, which can reach 1.5 m in height (Ulibarri 1987). It is the

149 most conspicuous leguminous shrub of the Patagonian steppe, and it is estimated that it plays a central role in
150 atmospheric nitrogen fixation (Golluscio et al. 2006, 2014). Also, these two species are important fuel resources, due to
151 their fuel properties (Cardoso et al. 2015). *Poa ligularis* is a perennial bunchgrass, which constitutes a very important
152 forage resource for domestic cattle and presents a high tolerance to drought (Gittins et al. 2010). This species is very
153 frequent, and it was probably one of the most abundant grasses prior to overgrazing in the region (Defossé et al. 1990).
154 Due to all features and ecosystem services these species meet, it is important to conserve them in areas with forest
155 plantations in the Patagonian steppe.

156 ***Experimental design***

157 To evaluate the species growth at different levels of irradiance, we established a nursery trial under semi-controlled
158 conditions in the Patagonian Andean Forest Research and Extension Center (CIEFAP), Esquel, Argentina (42°55'50.3''
159 S, 71°21'51" W). For the choice of the lowest level of irradiance (20%), the lower limit of the canopy cover of a dense
160 stand was taken into account, defined as 80%, since higher covers are not recommended for the development of the
161 understory in the region (Rusch et al. 2015). For the choice of the next level of irradiance (60%), the intermediate value
162 between 20% and a situation without cover was considered, which also matches with stands where many native steppe
163 species may develop (Rago et al., 2021). The irradiance levels were achieved through the use of specially designed
164 cubicles of 0.8 m³ (120 cm long, 80 cm wide, and 80 cm high) covered by wood slats of 4 cm wide, arranged every 1
165 cm to obtain 20% irradiance, every 6 cm to obtain 60% irradiance and without slats to obtain 100% irradiance, thus
166 achieving low (low-IR), medium (medium-IR) and high (high-IR) irradiance treatments, respectively. The irradiance
167 percentages of the treatments were corroborated through the measurement of photosynthetically active radiation (PAR)
168 with a ceptometer (Cavadevises Ceptometer Model BARRAD100), that integrates the flow of photons in a linear meter
169 through 80 integrated sensors. A measurement was performed on each cubicle once a month at noon in completely
170 sunny days, obtaining the highest levels of irradiance (Fig. 1). For summer season, levels of 20% irradiance for low-IR
171 and 60% for medium-IR were corroborated. However, in the following months the levels were lower for both
172 treatments, reaching levels of 5% and 30%, respectively, in winter months. This is associated with the variation in the
173 angle with which the sun rays arrive at that time of the year, due to the latitude.

174



175 **Fig. 1** Photosynthetically active radiation (PAR) (A) and irradiance percentage (B) registered in a completely sunny
 176 noon at each irradiance treatments every month during the trial

177

178 *Berberis microphylla* and *A. volckmannii* were grown from seeds collected from a natural population in the vicinity
 179 of Esquel during the summer of 2016 and *P. ligularis* was obtained in the INTA station nursery of Trelew (43°19'20" S,
 180 65°21'40" W), also grown from seeds. Shrubs species were transferred to 3.5-liter pots and the bunchgrass to 5-liter
 181 pots. The substrate used was made up of two parts of black soil, one of volcanic sand and one of peat, to obtain a
 182 mixture rich in nutrients, and with an adequate aeration and moisture retention. Until the end of winter the plants were
 183 kept inside the CIEFAP nursery, and then they were placed in the open air, exposing them gradually to homogenize
 184 growing conditions before starting the trial, in October 2017. We distributed 190 plants of *B. microphylla*, 190 of *A.*
 185 *volckmannii* and 115 of *P. ligularis* in 6 cubicles (repetitions) per treatment. The plants within each cubicle were rotated
 186 weekly to ensure homogeneous treatment effect, until the end of the trial in April 2019. The humidity of all the pots was

187 kept between 60 and 80% of field capacity, simulating the natural rainfall they receive in the field as these species are
188 from semi-arid environments, so water was not a limiting factor or in excess.

189 *Samplings*

190 At the beginning of the trial, each species was morphologically characterized by processing a random sample of 10
191 individuals for *B. microphylla* and *A. volckmannii* and five for *P. ligularis*. We removed each plant from its pot and
192 washed their roots. After that, we divided them into leaves, stem and roots, and we selected four fully expanded leaves,
193 which were scanned and subsequently processed with the ImageJ software (Rueden et al. 2016) to obtain their leaf area.
194 Since *A. volckmannii* has small compound leaves, we selected four groups of two leaves each to improve the accuracy
195 of the measurement, and we considered both rachis and each leaflet as part of the leaf (Pérez-Harguindeguy et al. 2013).
196 The identified leaves and each fraction of the plants were oven-dried at 70° C for 48 hours and then weighed in a
197 0.0001g precision scale. We obtained TB (estimated as total dry weight), LMF, SMF, RMF (biomass allocation), and
198 SLA.

199 We carried out five destructive samplings at different times (mid and late) during two growing seasons. The
200 samplings of the first growing season were in February and April 2018, and those of the second were in December
201 2018, and in February and April 2019. In the mid-season samplings (February 2018 of the first season, and December
202 2019 and February 2019 of the second) six plants per species were randomly sampled by treatment. At the late-season
203 samplings (April 2018 of the first and April 2019 of the second) sampling efforts were doubled, selecting 12 plants per
204 species by treatment. At every time, we obtained TB, LMF, SMF, RMF, and SLA in the same way as indicated for
205 initial characterization. For *P. ligularis*, we distinguished that some plants had many dry leaves and tillers (stems). So,
206 from the sampling of February 2018, leaves and stems were classified as green and dry, and only the green ones were
207 considered in the estimates of TB and biomass allocation. Stems with at least one green leaf were selected and all their
208 leaves were cut, and only those with some part green were classified as green leaves. To estimate SLA, six plants per
209 species were sampled for each treatment at all times. Except the sampled plants, all plants remained alive in the three
210 treatments during the trial.

211 We made weekly observations of reproductive structures on 109 *A. volckmannii* plants and on 67 *P. ligularis* plants,
212 distributed in the different treatments during the second growing season. We did not register reproductive structures
213 during the first season because very few plants had developed them. For each species, we registered the proportion of
214 plants with reproductive structures, and we quantified reproductive structures as follows: for *P. ligularis*, we registered
215 the number of inflorescences, and for *A. volckmannii*, as flowers arise from spines, we registered the number of spines

216 with reproductive structures. In addition, in the sampling of April 2019 total spines per plant were quantified. *Berberis*
217 *microphylla* did not develop reproductive structures during the trial, thus there is no data for this species.

218 **Data analyses**

219 *Irradiance effect on total biomass, biomass allocation and specific leaf area*

220 We compared the effect of the irradiance treatments, independently for each species at each time, through linear mixed
221 models. The irradiance factor was modeled as a fixed effect with three levels (low-IR, medium-IR and high-IR). For
222 late season times (April 2018 and 2019) we added the subsamples (two plants per repetition) as a random effect.
223 Response variables were TB, LMF, SMF, RMF, and SLA. The assumptions of normality were corroborated by Shapiro-
224 Wilk test and homoscedasticity through residual analysis. When variance heterogeneity was detected, a second model
225 was performed, and the model with the lowest Akaike value was selected as the final model. When normality was not
226 corroborated, generalized linear mixed models with Poisson distribution were applied and the fit of the models was
227 estimated as the ratio of deviance to freedom degrees ($D^2 \text{ gl}^{-1}$). When differences for the irradiance factor were detected
228 ($p < 0.05$), LSD-Fisher contrast was applied. We carried out the analyses with the software InfoStat (Di Rienzo et al.
229 2018). InfoStat implements an interface with the R platform (R Core Team, 2018) for the estimation of linear mixed
230 models using the gls and lme functions of the Nonlinear library Mixed-Effects Models (Pinheiro & Bates 2004; Di
231 Rienzo et al. 2017) and for the estimation of generalized linear mixed models using the gml functions of the stats
232 library, and glmer from the lme4 library (Bates et al. 2015).

233 *Irradiance effect on relative growth rate, leaf area ratio, and net assimilation rate*

234 We compared the effect of the irradiance treatments, independently for each species at five time intervals between
235 successive sampling times: I (October 2017 – February 2018), II (February 2018 – April 2018), III (April 2018 –
236 December 2018), IV (December 2018 – February 2019) and V (February 2019 – April 2019). For each interval we
237 estimated RGR, LAR and NAR, by applying the following formulas:

$$238 \quad \text{RGR} = \left(\ln(TB_2) - \ln(TB_1) \right) / (t_2 - t_1) \quad [1]$$

$$239 \quad \text{LAR} = \left(\text{SLA}_1 * \text{LMF}_1 + \text{SLA}_2 * \text{LMF}_2 \right) / 2 \quad [2]$$

$$240 \quad \text{NAR} = \text{RGR} / \text{LAR} \quad [3]$$

241 Subscripts 1 and 2 correspond to start and end time of the interval under study, t_1 and t_2 , respectively.

242 RGR [1] was calculated for each pair of plants corresponding to the initial and final times of the interval under
243 study, grouped by treatment and repetition. For the late-season data, as there were two plants per repetition, we first
244 estimated the logarithm of TB for each plant and then the average of them, following Hoffmann and Poorter (2002)
245 recommendation, and then proceed with the calculations. For interval I, six out of the 10 plants of *B. microphylla* and *A.*
246 *volckmannii* from the initial characterization of October 2017 were randomly grouped with the six plants from the
247 sampling of February 2018. For *P. ligularis*, RGR for each treatment in each interval was always estimated from five
248 repetitions, since the characterization and sampling of February 2019 only had five plants per treatment. The time was
249 expressed in weeks.

250 To compare RGR and its components among treatments, we used linear models with the irradiance factor modeled
251 as a fixed effect with three levels (low-IR, medium-IR, and high-IR). The analyses and the assumption corroborations
252 were carried out the same way as it was detailed in the previous section.

253 *Irradiance effect on reproductive structures*

254 We compared the effect of the irradiance treatments, independently for *A. volckmannii* and *P. ligularis*, through
255 generalized linear mixed models. The irradiance factor was modeled as a fixed effect with three levels (low-IR,
256 medium-IR, and high-IR) and the factor subsample as a random effect with variable number of plants (6 to 7 and 3 to 4
257 plants by repetition for *A. volckmannii* and *P. ligularis*, respectively). The distribution used for the proportion of plants
258 with reproductive structures was binomial, and for the number of spines with reproductive structures was negative
259 binomial. To compare the total number of spines per plant in *A. volckmannii*, the irradiance factor was modeled as a
260 fixed effect with three levels (low-IR, medium-IR and high-IR) and the subsample factor as a random effect (with 2
261 plants per repetition) for April 2019 sampling. The distribution used was negative binomial. The fit of the models was
262 calculated as the ratio of deviance to freedom degrees ($D^2 \text{ gl}^{-1}$). These analyses were carried out with the InfoStat
263 software (Di Rienzo et al. 2018).

264

265 **Results**

266 *Berberis microphylla*

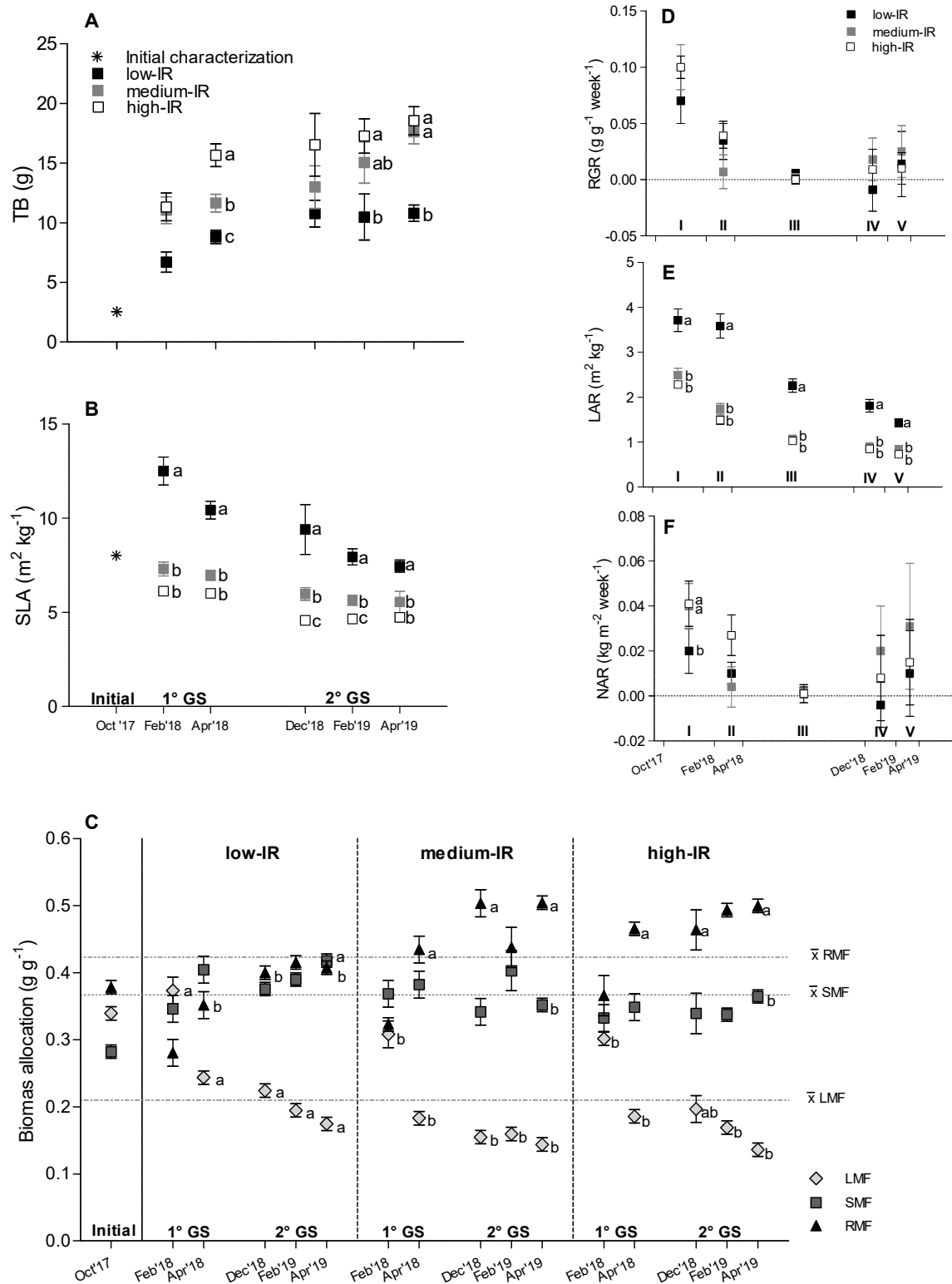
267 *Irradiance effect on total biomass, biomass allocation and specific leaf area*

268 For *B. microphylla* a pattern of greater TB was observed in high-IR compared to low-IR at all the evaluated times,
269 although differences were only significant in April 2018 ($p < 0.001$), February 2019 ($p = 0.039$) and April 2019 ($p <$
270 0.001). Total biomass in medium-IR showed a variable behavior, differing significantly from both high-IR and low-IR

271 in April 2018 and only from low-IR in April 2019 (Fig. 2A). Regarding biomass allocation, LMF was significantly
272 higher in low-IR than in medium-IR and high-IR at all the evaluated times, except in December 2018, when differences
273 were only significant between low-IR and medium-IR (p varied from 0.042 to < 0.001). Stem mass fraction only
274 differed significantly in April 2019 ($p = 0.002$), with the highest value in low-IR. Root mass fraction showed a pattern
275 of lower value in low-IR in all the evaluated times, although the differences were only significant in April 2018 ($p =$
276 0.001), December 2018 ($p = 0.01$) and April 2019 ($p < 0.001$) (Fig. 2C). Specific leaf area was significantly higher in
277 low-IR than in medium-IR and high-IR at all the evaluated times (p varied from 0.002 to < 0.001). In medium-IR, SLA
278 showed a variable behavior with respect to high-IR, with a value significantly higher than high-IR only in December
279 2018 and February 2019 (Fig. 2B).

280 *Irradiance effect on relative growth rate, leaf area ratio, and net assimilation rate*

281 Although RGR did not show significant differences for any of the evaluated intervals, a tendency to be lower in low-IR
282 and medium-IR was observed in intervals I and II, respectively. In interval I, all treatments presented the highest RGR
283 of the two growing seasons, which were reduced in interval II. During interval III, where the winter months were
284 included, the RGR were almost null, while for intervals IV and V, corresponding to the second growing season, they
285 remained lower than those of the first season (Fig. 2D). When decomposing RGR, LAR showed significant differences
286 in all intervals (p always < 0.001), always being higher in low-IR (Fig. 2E). On the other hand, NAR was significantly
287 different in interval I ($p = 0.027$), with higher NAR in high-IR and medium-IR, although it showed a pattern to be
288 higher in high-IR than in low-IR in all the evaluated intervals, except in interval III where it was almost null. In
289 addition, in the intervals of the second season, a tendency for NAR to be greater in medium-IR was observed (Fig. 2F).



290 **Fig. 2** *Berberis microphylla* total biomass (TB) (A), specific leaf area (SLA) (B), biomass allocation: leaf mass fraction
 291 (LMF), stem mass fraction (SMF), root mass fraction (RMF) (C), relative growth rate (RGR) (D), leaf area ratio (LAR)
 292 (E), and net assimilation rate (NAR) (F) for irradiance treatments. Different letters indicate significant differences for
 293 each variable among treatments at each analyzed time (A, B, C) or interval (D, E, F) during the 1° and 2° growing
 294 seasons (GS). For (C), discontinued horizontal lines indicate the corresponded mass fraction mean of every treatment
 295 and time

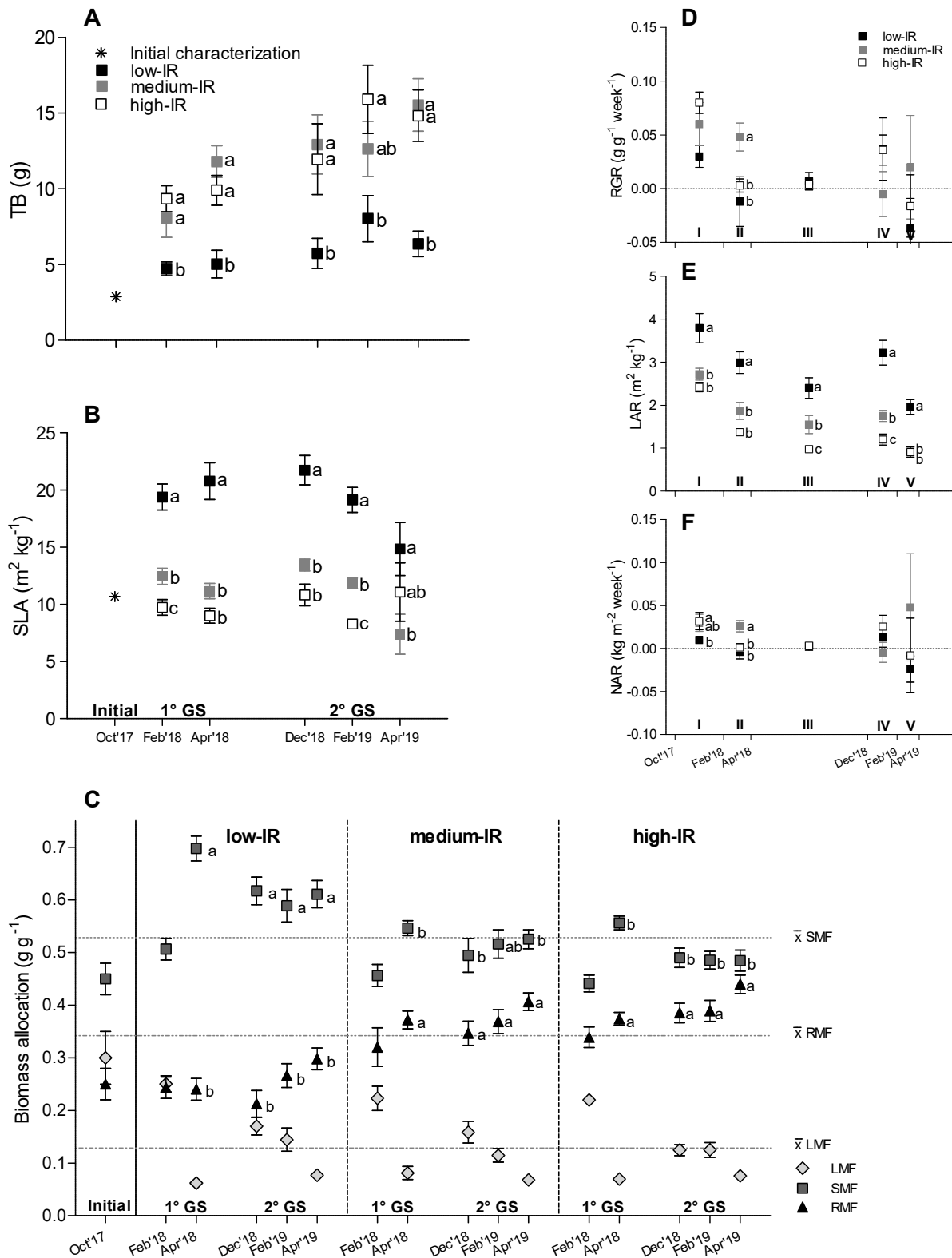
296 *Adesmia volckmannii*

297 *Irradiance effect on total biomass, biomass allocation and specific leaf area*

298 For *A. volckmannii* TB was higher in high-IR and medium-IR than in low-IR at all the evaluated times, except in
299 February 2019, which only presented significant differences between high-IR and low-IR (p varied from 0.032 to <
300 0.001). In addition, a trend towards higher TB in medium-IR was observed in April 2018, December 2018 and April
301 2019 (Fig. 3A). Regarding biomass allocation, LMF was variable during the two growing seasons and no significant
302 differences were detected between treatments for any of the evaluated times. Stem mass fraction was significantly
303 higher in low-IR at all the evaluated times from April 2018, except in February 2019, which only showed significant
304 differences between low-IR and high-IR (p varied from 0.033 to < 0.001). Root mass fraction was significantly higher
305 in high-IR at all the evaluated times from April 2018 (p varied from 0.003 to < 0.001) (Fig. 3C). Specific leaf area was
306 greater in low-IR than in the other treatments at all the analyzed times, except in April 2019, where it was only greater
307 than medium-IR (p varied from 0.041 to < 0.001). Medium-IR showed a pattern of higher SLA than high-IR, except in
308 April 2019, although differences between these treatments were significant only in February 2018 and February 2019
309 (Fig. 3B).

310 *Irradiance effect on relative growth rate, leaf area ratio, and net assimilation rate*

311 Relative growth rate showed a variable behavior, with significant differences only in interval II ($p = 0.018$). In this
312 interval, medium-IR presented the highest RGR, a trend that was repeated in interval V (Fig. 3D). When decomposing
313 RGR, LAR was significantly higher in low-IR at all the analyzed intervals (p always ≤ 0.001). A pattern of lower LAR
314 was observed in high-IR at all the intervals, differing significantly from medium-IR only in intervals III and IV (Fig.
315 3E). It is necessary to clarify that since *A. volckmannii* is a deciduous species, it loses its leaves in winter. Thus,
316 although it is not represented in the results, in a large part of interval III LAR was null. Net assimilation rate showed a
317 variable behavior, with significantly higher values in high-IR than in low-IR in interval I ($p = 0.049$) and in medium-IR
318 in interval II ($p = 0.012$) (Fig. 3F).



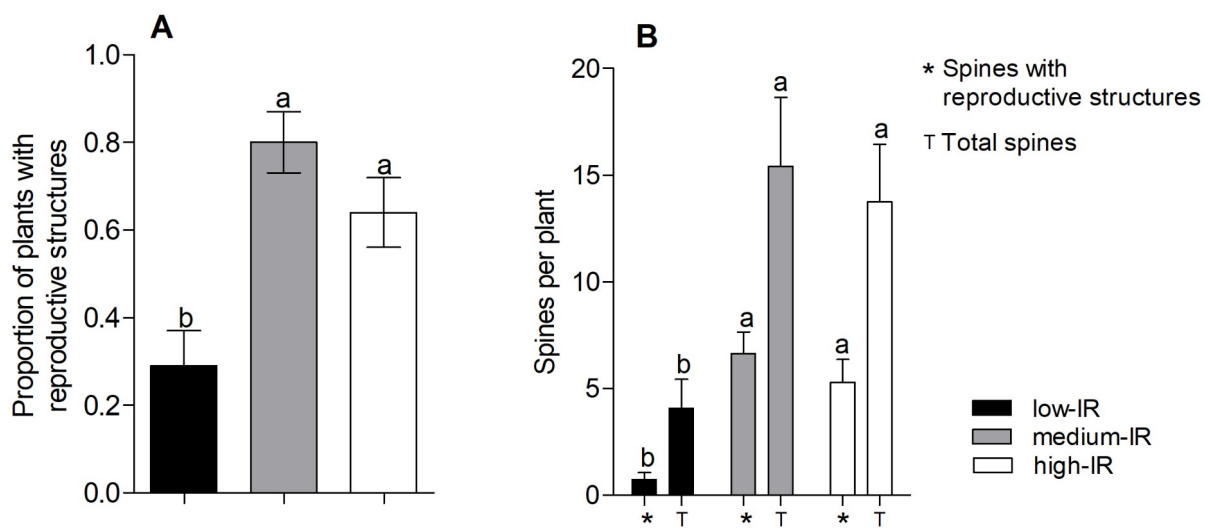
319 **Fig. 3** *Adesmia volckmannii* total biomass (TB) (A), specific leaf area (SLA) (B) biomass allocation: leaf mass fraction (LMF), stem mass fraction (SMF), root mass fraction (RMF) (C), relative growth rate (RGR) (D), leaf area ratio (LAR) (E), and net assimilation rate (NAR) (F) for irradiance treatments. Different letters indicate significant differences for each variable among treatments at each analyzed time (A, B, C) or interval (D, E, F) during the 1° and 2° growing seasons (GS). For (C), discontinued horizontal lines indicate the corresponded mass fraction mean of every treatment and time

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325 *Irradiance effect on reproductive structures*

326 From the second week of November 2018, *A. volckmannii* began to develop reproductive structures. This period lasted
 327 until the third week of January 2019, when many plants generated seeds, although others remained in the flower bud
 328 stage. The proportion of plants with reproductive structures was lower in low-IR than in medium-IR and high-IR ($p =$
 329 0.008 , $fit = 0.98$) (Fig. 4A). The number of spines with reproductive structures was also lower in low-IR than in
 330 medium-IR and high-IR ($p < 0.001$, $fit = 1$), and showed the same pattern as total spines ($p = 0.003$, $fit = 1.32$) (Fig.
 331 4B).

332



333 **Fig. 4** *Adesmia volckmannii* plants with reproductive structures (A) and spines (B) for irradiance treatments. Different
 334 letters indicate significant differences among treatments for the corresponded variable

335

336 *Poa ligularis*

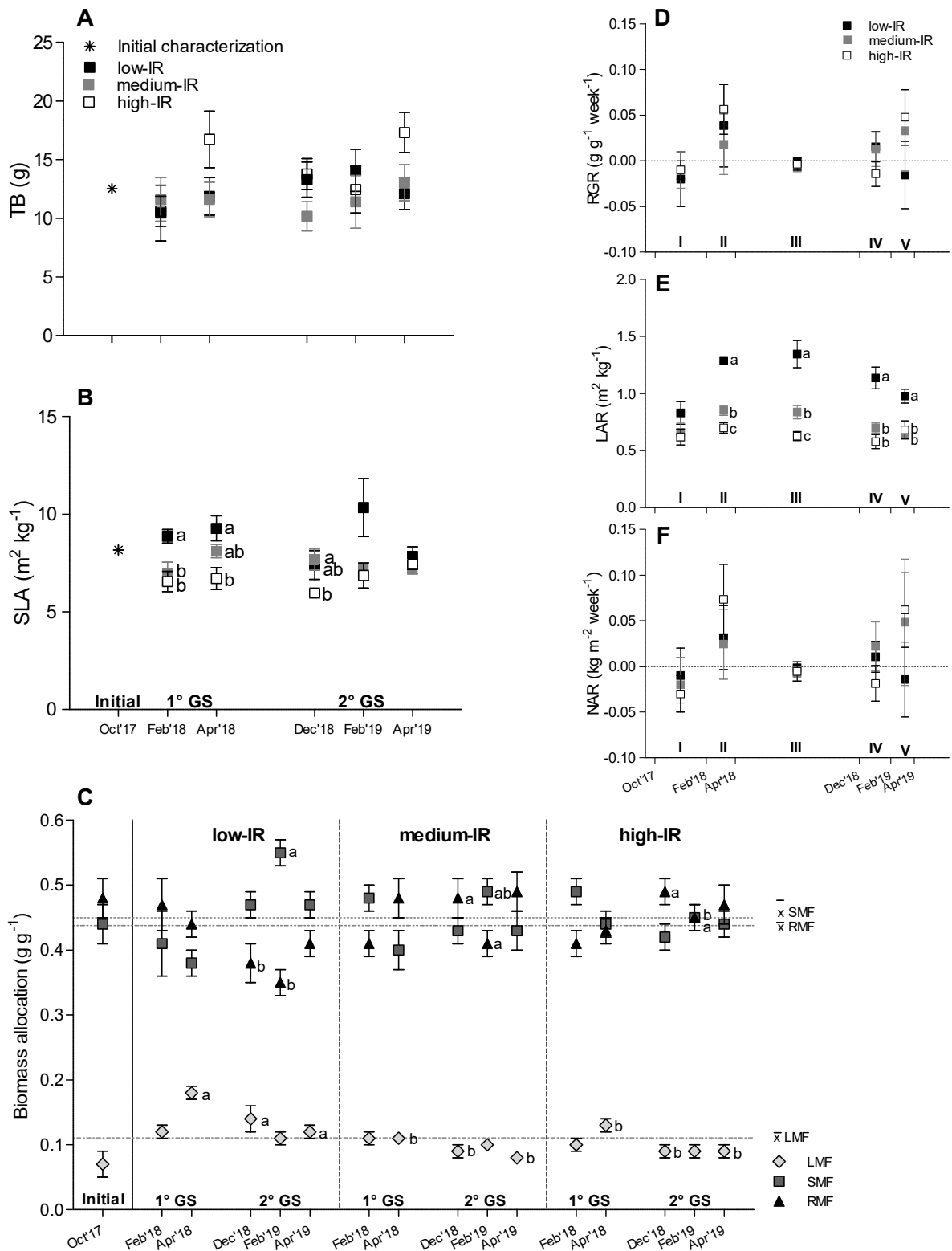
337 *Irradiance effect on total biomass, biomass allocation and specific leaf area*

338 *Poa ligularis* showed a tendency to present the highest TB in high-IR in April 2018 and April 2019, corresponding to
 339 the end of the growing season, although no significant differences were observed at any of the analyzed times (Fig. 5A).
 340 Regarding biomass allocation, LMF showed a pattern to be higher in low-IR than in medium-IR and high-IR at all the
 341 analyzed times, although differences were only significant in April 2018 ($p < 0.001$), December 2018 ($p = 0.005$) and
 342 April 2019 ($p < 0.001$). Stem mass fraction showed a variable behavior, with a significantly higher value in low-IR than
 343 in high-IR in February 2019 ($p = 0.021$). RMF also showed a variable behavior, with significantly lower values in low-
 344 IR in December 2018 ($p = 0.009$) and February 2019 ($p = 0.006$) (Fig. 5C). Specific leaf area showed a variable

345 behavior at all the analyzed times. In February 2018 ($p = 0.011$) and April 2018 ($p = 0.013$), SLA was significantly
346 higher in low-IR, although in April 2018 medium-IR did not differ from the other treatments. In December 2018 ($p =$
347 0.018), SLA was significantly higher in medium-IR than in high-IR (Fig. 5B).

348 *Irradiance effect on relative growth rate, leaf area ratio, and net assimilation rate*

349 Relative growth rate presented a variable behavior, with no significant differences in any of the evaluated intervals (Fig.
350 5D). When decomposing RGR, LAR was significantly higher in low-IR in all intervals (p varied from 0.004 to < 0.001)
351 except in interval I, where no significant differences were detected. High-IR showed a tendency to be the treatment with
352 the lowest LAR, although differences with medium-IR were only significant in intervals II and III (Fig. 5E). Net
353 assimilation rate showed a variable behavior, similar to the pattern observed in RGR, although no significant differences
354 were detected in any of the evaluated intervals (Fig. 5F).

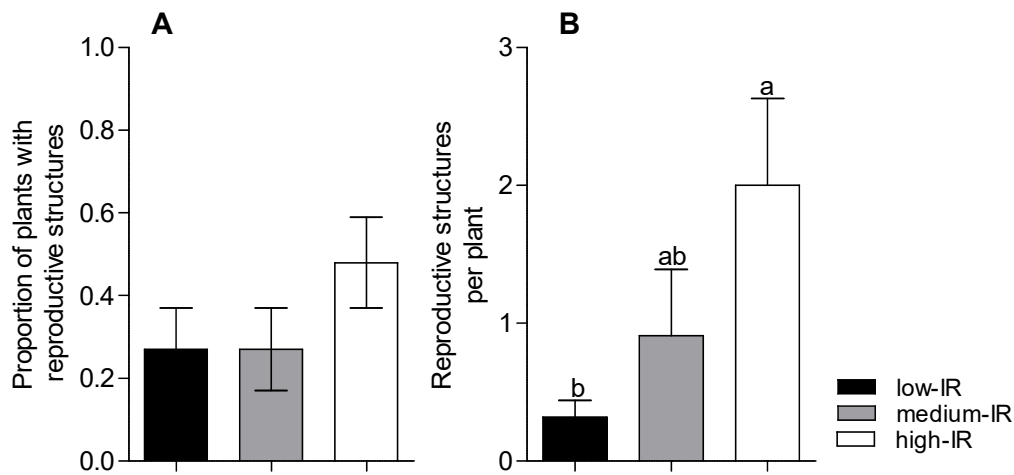


355 **Fig. 5** *Poa ligularis* total biomass (TB) (A), specific leaf area (SLA) (B) biomass allocation: leaf mass fraction (LMF),
 356 stem mass fraction (SMF), root mass fraction (RMF) (C), relative growth rate (RGR) (D), leaf area ratio (LAR) (E),
 357 and net assimilation rate (NAR) (F) for irradiance treatments. Different letters indicate significant differences for each
 358 variable among treatments at each analyzed time (A, B, C) or interval (D, E, F) during the 1° and 2° growing seasons
 359 (GS). For (C), discontinued horizontal lines indicate the corresponded mass fraction mean of every treatment and time

360 *Irradiance effect on reproductive structures*

361 *P. ligularis* began to develop reproductive structures in the first week of October 2018, a period that lasted until the first
 362 week of December 2018. The proportion of plants with reproductive structures did not show significant differences
 363 between irradiance treatments, although there was a tendency to be higher in high-IR (Fig. 6A). The number of
 364 reproductive structures was significantly different between treatments ($p < 0.025$, fit = 0.77), with the highest value in
 365 high-IR, differing from low-IR (Fig. 6B).

366



367 **Fig. 6** *Poa ligularis* plants with reproductive structures (A) and reproductive structures per plant (B) for irradiance
 368 treatments. Different letters indicate significant differences among treatments

369

370 Discussion

371 The three analyzed species showed different responses to the evaluated levels of irradiance, and in general terms their
 372 productivity was similar between 60 and 100% irradiance, suggesting the ability of these species to acclimatize and
 373 maintain their productivity at irradiance levels lower than 100%, up to a certain value of decrease in irradiance.

374 Faced with a decrease in irradiance, plants increase their SLA and retain more photosynthates in their leaves to
 375 ensure maximum capture in low light (Brouwer 1962; Poorter et al. 2019). Thus, as expected, an increase in SLA was
 376 detected for *B. microphylla* in plants subjected to 20% irradiance, which was maintained throughout the trial and
 377 corresponded with a higher LAR. However, NAR decreased at 20% irradiance in the first interval, which may be caused
 378 by a reduction in photosynthesis since PAR values recorded for the first interval at that irradiance level were lower than
 379 $250 \mu\text{mol m}^{-2} \text{seconds}^{-1}$, whereas the saturation point for this species was established at approximately $1500 \mu\text{mol m}^{-2}$
 380 second^{-1} , and it decreases by 95% at $100 \mu\text{mol m}^{-2} \text{second}^{-1}$ PAR (Peri et al. 2011). However, another study registered
 381 that the saturation point of this species is approximately at $500 \mu\text{mol m}^{-2} \text{second}^{-1}$ (Iogna 2017), which could also

382 explain the reduction in TB at irradiances of 60% detected at the end of the first growing season, since between March
383 and April the recorded PAR at 60% irradiance was lower than $500 \mu\text{mol m}^{-2} \text{second}^{-1}$. The increase in biomass at 60%
384 irradiance to levels similar to that of plants growing at 100% irradiance at the end of the second season could be due to
385 the fact that plants growing at 60% irradiance had a greater SLA and a tendency to increase NAR than those growing at
386 100% irradiance, which could favor carbon gain (Evans and Poorter 2001).

387 In *A. volckmannii*, although a higher proportion of aerial biomass was detected at 20% irradiance, this increase was
388 recorded for the stem, but not for the leaves. Although this behavior is unusual, it has been detected in some species
389 such as *Geum urbanum* L. (Pons 1977; Poorter and Nagel 2000). Besides, the increase in SLA detected for this species
390 when the irradiance was 20% would not be enough to match the level of photosynthesis of the plants subjected to higher
391 irradiances. The increase in RGR and NAR of the plants subjected to 60% irradiance during the second interval could
392 be indicating that in the early stages of its development, the intermediate irradiances favor this species, a fact that is also
393 evident in the tendency towards a greater TB at 60% irradiance at the end of both seasons. Also, the reproductive
394 response showed this tendency; a lower proportion of plants with reproductive structures was detected at 20%
395 irradiance, but a trend to be greater at 60% than at 100% irradiance, which could be associated with the lower
396 production of spines, from which flowers emerge in this species (Ulibarri 1987).

397 Contrary to the evaluated shrub species, *P. ligularis* did not vary its TB with the different levels of irradiance.
398 However, it showed a tendency to accumulate a higher TB at the end of the first and, more markedly, at the end of the
399 second growing season at 100% irradiance. Besides, it presented a greater number of reproductive structures at 100%
400 irradiance. These results suggest a reduction in its productivity at lower irradiances that could be explained, in part, by
401 the similar SLA between plants subjected to different levels of irradiance towards the end of the second growing season.
402 Regarding biomass allocation, the highest LMF and the lowest RMF at 20% irradiance at the times when differences
403 were detected, following what is to be expected by the functional equilibrium theory (Brouwer 1962). In Patagonia, the
404 response of some perennial grasses to different irradiances in ponderosa pine plantations has been studied in order to
405 assess the potential development of silvopastoral systems. *Festuca pallescens* also changes its biomass allocation, with
406 a higher aerial proportion at low irradiances (Fernández et al. 2004) and a tendency to lower growth under canopy cover
407 above 80% (Fernández et al. 2006a). On the other hand, *Pappostipa speciosa* does not show relative growth increases
408 under canopy covers greater than 70% (Fernandez et al. 2002). The tolerance of *F. pallescens* to low levels of irradiance
409 could be due to changes in its architecture, such as the tendency to present greater angles at low irradiances, achieving a
410 more effective interception of direct radiation in the midday hours, when radiation levels are higher (Fernández et al.
411 2004). *Festuca pallescens* also shows a slight increase in the maximum assimilation rate and efficiency of light use in

412 leaves growing in the shade (Fernández et al. 2006b). Evaluating these characters in *P. ligularis* could help explain the
413 responses observed in this study. Likewise, the curve of photosynthetic response to radiation does not present
414 differences neither in *F. pallescens* nor in *P. speciosa* (Fernandez et al. 2002, 2006b), which indicates that these species
415 could make use of the radiation pulses that arrive through openings in the canopy, but that this lack of plasticity does
416 not allow them to tolerate high canopy covers (Fernández et al. 2006b). This might also occur in *P. ligularis*.

417 Irradiance reduction usually drives a strong RGR decrease due to a drop in NAR (Di Benedetto and Tognetti 2016).
418 In this study, an abrupt decrease in RGR was not detected in the analyzed species, probably because the immediate
419 response of the three species to solar radiation decrease was an increase in SLA and LAR, together with a higher LMF
420 in most cases, which could have contributed to maximizing light capture (Poorter et al. 2019). However, RGR, in
421 general, tended to be higher in plants growing at irradiances of 60 and 100%, and showed a similar pattern to that of
422 NAR, as it has been also observed in other studies (Di Benedetto et al. 2015; Iralu and Upadhaya 2018). These results
423 suggest that the assessed species show certain levels of shade tolerance that may benefit their development under the
424 canopy of forest plantations with a proper light management. Considering also that richness and cover of the Patagonian
425 steppe plant community decrease in ponderosa pine plantations with basal areas between 10 and 20 m² ha⁻¹, which
426 correspond to approximately 50 to 70% diffuse radiation (Rago et al. 2021), we suggest that ponderosa pine plantations
427 with irradiances higher than 60% would be appropriate to maintain a rich and abundant herb-shrub layer. In this sense, it
428 is important to also consider other limiting resources, such as soil water (Fernández et al. 2008), as well as the complex
429 interactions in the field. Besides, analyzing the response of these species to other levels of irradiance, as well as that of
430 other species relevant from the Patagonian steppe, would provide useful information to more precisely define the levels
431 of solar radiation needed in forest plantations in northwestern Patagonia to allow the persistence of species from the
432 steppe community.

433

434 **Conclusions**

435 Plant species contribute differently to ecosystem functions (e.g., constituting food or shelter for other species,
436 contributing to processes such as nutrient cycling, etc.); therefore, the persistence and development of different species
437 under the canopy of forest plantations is relevant. This study showed that three representative plant species of the
438 Patagonian steppe responded to the reduction of solar radiation, managing to maintain their productivity up to certain
439 levels of irradiance. The results suggest that the three species have a certain level of shade tolerance that would favor
440 them to develop under different levels of forest plantation canopy. Therefore, forest management should focus on light
441 management, achieving certain light heterogeneity to allow the development of the different species. These could be

442 possible through appropriate plantation densities, pruning and thinning. The management of forest residues generated
443 by these silvicultural interventions, and the litter that falls from the trees, must also be considered in management
444 programs, since they can shade the vegetation if they are deposited on it (Rago et al. 2020b). Keeping these species
445 under the tree canopy is very important since they represent key elements of the natural community, either because of
446 their predominance in cover as well as the ecological functions they fulfill. In addition, maintaining the appropriate
447 conditions for the development of these species would contribute to the persistence of other plant species with similar
448 requirements and of other taxa that benefit from the vegetation by using it as food and shelter.

449

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