



Competition effect exerted by two nonnative invasive plant species on a native under contrasting conditions of resource availability

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Abstract Competition between native and nonnative invasive species is a key interaction determining community composition. The identity and number of interacting species plus the level of resource availability can affect the competition outcome. In this study, we performed a greenhouse experiment with seedlings to analyze the intraspecific competition experienced by the native species *Lithraea molleoides* and the interspecific competition exerted by two nonnative invasive species (*Ligustrum lucidum* and *Pyracantha angustifolia*) separately and together, under two contrasting water and light availability conditions. The selected species coexist in the Chaco Serrano mountains in central Argentina. In particular, we found that interspecific competition by the nonnative invasive *L. lucidum* had a higher negative effect on the performance of the native species than intraspecific competition as well as than interspecific competition by both nonnatives. The negative effect of *L. lucidum* on the native species showed a tendency to be stronger under higher resource availability. Additionally, a joint effect of both nonnatives on the native species was observed, consisting of a lower root biomass under low water availability. Our results highlight the importance of controlling one of the most

important woody invaders in Argentina, but also draw attention on the relevance of measuring numerous traits and different resource conditions to fully evaluate the possible joint effects of nonnatives on native species.

Resumen La competencia entre especies nativas y exóticas invasoras es clave en la determinación de la composición de las comunidades. La identidad y el número de especies que interactúan, así como los niveles de disponibilidad de recursos pueden afectar el resultado de la competencia. En este estudio analizamos la competencia intra-específica en la especie nativa *Lithraea molleoides* y la competencia inter-específica que experimenta esta especie cuando interactúa con dos exóticas invasoras (*Ligustrum lucidum* y *Pyracantha angustifolia*) en niveles contrastantes de disponibilidad de recursos. Las especies seleccionadas coexisten en las montañas pertenecientes al Chaco Serrano en el centro de Argentina. Realizamos un experimento de invernadero en el que las plántulas de la especie nativa crecieron en competencia intra- o inter-específica (i.e., con ambas exóticas juntas o con cada una de ellas por separado), en dos niveles contrastantes de luz y agua. Encontramos que la competencia inter-específica por *L. lucidum* mostró un efecto negativo mayor sobre el desempeño de la especie nativa que la competencia intra-específica o la inter-específica por dos exóticas juntas. Este efecto negativo de *L. lucidum* sobre la nativa tuvo una tendencia a ser mayor cuando la disponibilidad de recursos era mayor. Además, se

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observó un efecto conjunto de ambas exóticas, que consistió en una menor biomasa radical de la especie nativa en condiciones de baja disponibilidad de agua. Nuestros resultados destacan la importancia de controlar una de las leñosas invasoras más importantes de Argentina, pero además, resaltan la importancia de incluir muchos caracteres y distintas condiciones de disponibilidad de recursos para evaluar el efecto conjunto de las exóticas sobre las nativas.

Keywords Intraspecific competition · Interspecific competition · Exotic species seedlings · Woody species

Introduction

Competition among native and nonnative invasive species is a key interaction determining community composition (Kuebbing and Nuñez 2016). Moreover, there is a particular need to study the effects of this interaction at the seedling stage. This stage is one of the main filters of plant life cycle because of the occurrence of high mortality (Fenner and Thompson 2005; Leck et al. 2008). Thus, competition at the seedling stage must influence community composition because it plays a role in shaping recruitment (Leck et al. 2008; Gioria and Osborne 2014). In fact, a higher competitive ability of nonnative invasive species than of native ones at the seedling stage could be a triggering attribute of invasion processes (Davis et al. 2000; Shea and Chesson 2002; Fargione et al. 2003; Brooker 2006; Kuebbing and Nuñez 2016; Ferenc et al. 2021).

It is widely accepted that the effects of intraspecific competition are stronger than those of interspecific competition due to the similar resource acquisition strategies of individuals of the same species (Aarssen 1983; Goldberg and Barton 1992). However, there is increasing evidence that the effects of interspecific competition from nonnative invasive species on natives are stronger than those of intraspecific competition among individuals of a native species (Vilà and Weiner 2004; Skálová et al. 2013; Gioria and Osborne 2014; Kuebbing and Nuñez 2016; Guido et al. 2019). This higher competitive ability of nonnative invasive species could be a result of a different or a more efficient use of the available resources than that of natives (Davis et al. 2000; Shea and Chesson

2002; Leishman et al. 2007). In this sense, most of the studies that tested the competitive abilities of invasive species performed experiments in pairs (Mangla et al. 2011; Bottollier-Curtet et al. 2013; Skálová et al. 2013; Tabassum and Leishman 2016). However, in nature, most natives tend to interact with more than one nonnative (Kuebbing et al. 2013), which could have a more negative effect on native species performance than the interaction with each nonnative species separately (Kuebbing and Nuñez 2016; Ferenc et al. 2021).

The outcome of interactions among species could change with variations in resource availability in space or time (Brooker et al. 2006). Both resource availability and competition can modulate seedling survival, functional trait expression, and biomass allocation (Čuda et al. 2015). In resource-poor environments, resource availability is considered the most limiting factor, whereas competition is more important in resource-rich environments (Grime 1977; Esch et al. 2018). However, some invasive species showed a better performance than natives, independently of resource availability (Richards et al. 2006; Zou et al. 2009; Molina-Montenegro et al. 2012; Čuda et al. 2015). All in all, the outcome of competition between native and nonnative invasive species in variable resource environments deserves further studies (Mangla et al. 2011; Skálová et al. 2013; Leal et al. 2022).

The tree *Ligustrum lucidum* W.T. Aiton (Oleaceae) and the shrub *Pyracantha angustifolia* (Franch) C.K. Schneid (Rosaceae) are important nonnative invasive species worldwide (Rejmánek and Richardson 2013) and two of the most abundant in the Chaco Serrano of central Argentina (Giorgis and Tecco 2014; Tecco et al. 2006; Giorgis et al. 2021). *L. lucidum* and *P. angustifolia* coexist with the native dominant *Lithraea molleoides* (Vell.) Engl. (Anacardiaceae) (Tecco et al. 2006; Zeballos et al. 2014). Both nonnative invasive species produce a great amount of seeds (Ferrerías et al. 2008; Vergara-Tabares et al. 2016) and the three species are dispersed mainly by birds (Ferrerías et al. 2008; Vergara-Tabares et al. 2016; 2018b). Moreover, the seedlings of these two nonnative invasives can establish and survive at higher elevations, where levels of invasions are lower, than their current distribution (Tecco et al. 2016); this fact highlights its role as species commonly found at the invasion front (Hoyos et al.

2010; Gavier-Pizarro et al. 2012; Zeballos et al. 2014). In addition, previous studies in this lowland area observed that *P. angustifolia* facilitated *L. lucidum* invasion through a nurse effect on its seedlings (Tecco et al. 2006). The seedling density of *L. lucidum* was four times higher under *P. angustifolia* canopy than under a native shrub species (Tecco et al. 2006). Thus, these two nonnative invasive species can be considered the main competitive threat from woody species to seedlings of the native dominant *L. molleoides*.

The Chaco Serrano has few remaining forest fragments (Cabido et al. 2018) and is threatened mainly by invasion of nonnative species (Hoyos et al. 2010; Giorgis et al. 2017). This area presents a marked seasonality, interannual variation in precipitation and diversity of physiognomies (De Fina 1992; Zeballos et al. 2014; Giorgis et al. 2017); all of these factors determine a wide array of microclimatic conditions for seedlings, mainly due to variations in light and water availability (Ferrerías et al. 2019; Whitworth-Hulse et al. 2020). Therefore, in this study we performed a greenhouse experiment in which we analyzed intraspecific competition in the native species *L. molleoides* and the interspecific competition exerted by two nonnative invasive species under two contrasting levels of light and water availability. We hypothesized that the performance of the native species would be determined by the identity of the competitive species and the level of available resources. Therefore, we predict that: (1) the interspecific competition by the nonnative invasive species will have a stronger negative effect on the performance of the native species than the intraspecific competition; (2) two different nonnative invasive species will have a stronger negative effect on the performance of the native species than each of the nonnative invasive species separately; and (3) in both previous predictions the effect on the native species will be stronger under higher resource availability. Our results are important to understand the mechanisms that modulate the invasion of nonnative invasive plants in the Chaco Serrano of Córdoba.

Materials and methods

Experimental design

The study was carried out in the greenhouse of the Instituto Multidisciplinario de Biología Vegetal (IMBIV) in Córdoba, central Argentina. Seeds were collected between the end of 2018 and the beginning of 2019, coinciding with the end of the dispersal period of each species (Tecco et al. 2006), in areas where the three species coexist. Fruits of at least 10 individuals were collected and stored in paper bags at room temperature until the start of the experiment. To obtain the desired number of seedlings, seeds were set to germinate in trays containing sand in the greenhouse. Once the seedlings reached the cotyledon stage, they were transplanted to 0.5-L pots filled with soil and sand in a 2:1 ratio. The soil was collected from areas with the presence of these species in the Chaco Serrano. Only the sand was sifted, while the soil was not sterilized or sifted in order to maintain the microorganisms and soil structure.

To assess the effects of competition and resource availability on the native species, *L. molleoides*, seedlings were grown simultaneously under three different treatments: (1) neighbors; (2) light availability; and (3) water availability. The neighbors treatment comprised five levels: (a) control group: native *L. molleoides* growing alone, without competition (N); (b) intraspecific competition: three individuals of *L. molleoides* (NNN); (c) interspecific competition with *L. lucidum*: *L. molleoides* with two individuals of *L. lucidum* (NLL); (d) interspecific competition with *P. angustifolia*: *L. molleoides* with two individuals of *P. angustifolia* (NPP); and (e) interspecific competition with both nonnative invasive species: *L. molleoides* with one individual of *L. lucidum* and one of *P. angustifolia* (NLP).

For the light availability treatment, two contrasting levels were applied. The pots were distributed in two different benches: one was exposed to natural light (high light availability) and the other was under shade (low light availability). The low light availability treatment was obtained using several layers of half shade cloth supported by metal frames (Sánchez-Gómez et al. 2006). Throughout the experiment, photosynthetically active radiation was measured above the pots in each of the treatments using a LI-COR LI sensor (LI-COR Environmental, Lincoln, NE, USA).

A mean (\pm standard error) of $118.22 \pm 6.83 \mu\text{mol}/\text{m}^2/\text{s}$ and of $21.24 \pm 0.85 \mu\text{mol}/\text{m}^2/\text{s}$ were recorded in the high and low light availability treatments, respectively. The water availability treatment consisted of two contrasting levels: high water availability (pots irrigated with 40 ml of water) and low water availability (pots irrigated with 10 ml of water). Water was supplied to each pot twice a week. A pilot experiment was performed to obtain the desired water volumes and irrigation frequency. During the experiment, soil moisture was measured with a TDR-MPM160 sensor (Moisture Probe Meter) in five pots per water treatment. Moisture was measured in pots without seedlings to avoid damage to seedlings. Consistent differences were observed between water availability treatments. At high water availability, a mean of $33.01 \pm 1.00\%$ in soil moisture content was recorded, whereas in the low water availability, a mean of $14.04 \pm 0.34\%$. Finally, temperature for each of the conditions (means of $19.92 \pm 0.12 \text{ }^\circ\text{C}$ for high light availability and $19.89 \pm 0.13 \text{ }^\circ\text{C}$ for low light availability) and relative humidity in the greenhouse (mean of $68.06 \pm 0.45\%$ humidity) were measured with sensors (Thermochron iButton DS1921G) every 3 h.

To reduce possible heterogeneity in the different portions of each bench, the pots were distributed in 12 blocks under each light availability condition, so that all treatments were represented in the different portions of the benches (Poorter et al. 2012). Each combination of factor levels had 12 replicates, totaling 240 pots (5 levels of the neighbors treatment \times 2 levels of light availability \times 2 levels of water availability \times 12 replicates) containing 624 seedlings.

Seedling measurements

Seedling measurements were performed only in the native species *L. molleoides*. Thus, in the intraspecific competition treatment, one of the three individuals of *L. molleoides* per pot was randomly selected and marked at the beginning of the experiment as the focal plant to be measured. Seedlings were allowed to grow for 126 days until harvest. This growth period was chosen to focus our study on the seedling stage (plants with cotyledons or with a short time elapsed since they dropped off), which is the most sensitive stage -i.e., highest mortality- of a woody plant's life cycle (Fenner and Thompson 2005; Leck et al. 2008). In each seedling, we measured survival, biomass-related

variables and several performance indicators and functional traits. Seedling biomass was separated into leaves, stems and roots, and dried in an oven at $60 \text{ }^\circ\text{C}$ for 48 h to constant dry weight. We measured the following biomass variables: total biomass, relative growth rate based on total biomass and biomass allocation. To calculate the relative growth rate based on biomass data, at the beginning of the experiment we harvested 12 seedlings of *L. molleoides*, which we dried to constant weight, and weighed. The average biomass of these seedlings was used as initial biomass; relative growth rate was calculated as the difference between the final biomass values and the average initial biomass divided by the length of the growth period (Sánchez-Gomes et al. 2006). Biomass allocation to leaf, stem and root was calculated as the biomass of each compartment divided by the total biomass (named leaf, stem and root mass fraction). In addition, we calculated the root to shoot mass ratio. We measured the following performance indicators: seedling height, number of leaves, and basal stem diameter. We also measured the following functional traits: leaf greenness as an estimator of chlorophyll concentration in leaves (SPAD), specific leaf area and main root length. For the SPAD measurement, we extracted a leaf at an intermediate height from each seedling and estimated the amount of chlorophyll using the SPAD502 meter. The same leaf was scanned to obtain leaf area using the ImageJ program (Version 1.50). Leaf dry weight was then obtained and the specific leaf area was calculated by dividing the leaf area by the leaf dry biomass. Standard protocols were followed in the measurement of all these traits (Cornelissen et al. 2003; Perez-Harguindeguy et al. 2016; Klimešová et al. 2019).

Data analysis

We assessed the effect of neighbors and resource availability on biomass-related variables, performance indicators and functional traits of *L. molleoides* seedlings using general linear mixed-effects models (GLMMs; except for leaf number, see below). The fixed effects were water availability (two levels) and neighbors (five levels), while the random effect was the blocks that were arranged on each bench. The light availability treatment was not included as a factor to avoid pseudo-replication, since only one bench exposed to light and one under shade were available

(Mazia et al. 2001). Thus, separate analyses were performed for high and low light availability. Furthermore, in the low light availability condition only three levels were considered for the factor neighbors (i.e., N, NNN, NLL) due to high mortality of *P. angustifolia* seedlings (only 38.9% of the individuals survived under this light condition). The number of leaves was analyzed using generalized linear mixed models with Poisson error distribution with the same fixed and random factors as those previously described.

The structure of the final models was obtained by applying the likelihood ratio test (Zuur et al. 2007), using the `anova()` function (Ferenc et al. 2021). First, the significance of the random term was tested by comparing a model with and without random effects. We used general linear models (GLMs) instead of GLMMs when the model including the random term did not differ significantly from the model not including that term. Then, a systematic model simplification was applied (i.e., top-down model simplification beginning with a model including all the desired variables) based on the AIC values. In all cases, the assumptions of normal distribution of residuals and homogeneity of variance (homoscedasticity) were tested. The response variables that did not meet the assumptions were transformed to Log_{10} . Once the most parsimonious model was selected, the `lsmeans()` function of the `emmeans` package was used to evaluate the significant differences among factor levels through the Tukey's a posteriori test. All analyses and graphs were performed with the R statistical program Version 3.6.1.

Results

Survival and biomass variables

Almost all the seedlings of *L. molleoides* survived until the end of the experiment in all the treatments applied (average of 99.7%). Water availability and neighbors -i.e., competition, in particular from *L. lucidum*- did influence the general response of *L. molleoides* seedlings through changes in its total biomass and in the allocation of biomass in different fractions. Only in the root mass fraction was a joint effect of both nonnatives observed.

Under both light availability conditions, water availability did not mediate competition outcome on

relative growth rate or total biomass (Table 1). Under high light availability conditions, these variables showed lower values under low water availability. In addition, *L. molleoides* showed a significant reduction of 41 and 37% in total biomass and 18 and 37% in relative growth rate, in high and low light availability respectively, when it grew in interspecific competition with *L. lucidum* seedlings in relation to the control treatment (N) (Fig. 1).

Under both light conditions, the aboveground biomass (leaf and stem mass fractions) showed higher values under the high water availability level (Fig. 2a, b, e, f), whereas root mass fraction and the root/shoot mass ratio showed higher values under the low water availability level (Fig. 2c, d, g, h). Under the high light condition, water availability influenced competition outcome on leaf mass fraction, root mass fraction and root/shoot mass (i.e., significant interaction of water availability and neighbors; Table 1). Under the high light condition and in the low water availability level, leaf mass fraction of *L. molleoides* did not change with neighbor identity (Table 1), whereas in the high water availability level, *L. molleoides* growing in interspecific competition with *L. lucidum* showed a 9% reduction in leaf mass fraction with respect to control (Fig. 2a). By contrast, root mass fraction and root/shoot mass ratio of *L. molleoides* did not exhibit a competition effect in the high water availability level. However, in the low water availability level, a reduction of 19 and 31% was observed in root mass fraction and root/shoot mass ratio, respectively, when *L. molleoides* grew with both nonnatives (NLP) in relation to the control (N) (Table 1; Fig. 2c, d). Conversely, under low light availability conditions, water availability did not mediate competition outcomes (Table 1). Under that light condition, *L. molleoides* growing in intraspecific competition (NNN) showed a 23% reduction in root mass fraction with respect to the control treatment (N) (Fig. 2g). When growing in interspecific competition with *L. lucidum* (NLL), *L. molleoides* showed a 6% increase in stem mass fraction values with respect to the control (N) (Fig. 2f).

Performance indicators and functional traits

Water availability and neighbors -i.e., competition-, in particular by *L. lucidum*, influenced the general response of *L. molleoides* seedlings through changes in most performance indicators (height and basal

Table 1 Statistics and p values for the response variables analyzed in seedlings of the native species *Lithraea molleoides* growing with neighbors in different combinations and two contrasting conditions of water availability

Measured traits	Light conditions	Neighbors (N)	Water availability (W)	N*W
Total biomass	High	F=6.87; $p < 0.01^*$	F=241.32; $p < 0.01$	NIM
	Low	F=9.05; $p < 0.01^*$	NIM	NIM
Relative growth rate	High	F=8.48; $p < 0.01^*$	F=332.73; $p < 0.01^*$	NIM
	Low	F=9.78; $p < 0.01^*$	NIM	NIM
Leaf mass fraction	High	F=4.16; $p < 0.01^*$	F=137.22; $p < 0.01^*$	F=2.77, $p = 0.03^*$
	Low	NIM	F=4.27; $p = 0.04^*$	NIM
Stem mass fraction	High	F=2.7; $p = 0.03^*$	F=4.8; $p = 0.03^*$	NIM
	Low	F=3.56; $p = 0.03^*$	NIM	NIM
Root mass fraction	High	F=2.25; $p = 0.07$	F=116.2; $p < 0.01^*$	F=3.52; $p < 0.01^*$
	Low	F=3.37; $p = 0.04^*$	F=18.67; $p < 0.01^*$	NIM
Root to shoot mass ratio	High	F=1.64; $p = 0.17$	F=98.76; $p < 0.01^*$	F=2.79; $p = 0.03^*$
	Low	NIM	F=15.37; $p < 0.01^*$	NIM
Height	High	F=14.73; $p < 0.01^*$	F=331.72; $p < 0.01^*$	NIM
	Low	F=8.7; $p < 0.01^*$	NIM	NIM
Number of leaves	High	NIM	$\chi^2 = 119.8$; $p < 0.01^*$	NIM
	Low	NIM	NIM	NIM
Basal stem diameter	High	F=8.38; $p < 0.01^*$	F=388.1; $p < 0.01^*$	NIM
	Low	F=11.58; $p < 0.01^*$	F=6.25; $p < 0.01^*$	NIM
SPAD	High	NIM	F=76.07; $p < 0.01^*$	NIM
	Low	NIM	F=163.52; $p < 0.01^*$	NIM
Root length	High	NIM	F=150.78; $p < 0.01$	NIM
	Low	NIM	F=9.17; $p < 0.01$	NIM
Specific leaf area	High	F=4.15; $p = 0.39$	F=116.15; $p < 0.01^*$	F=14.99; $p < 0.01^*$
	Low	F=4.84; $p < 0.01^*$	F=13.52; $p < 0.01^*$	NIM

For each variable, only the factors that were kept in the final model are shown. The values are provided for the two light availability conditions included in the experiment (see methods). NIM= Term not included in the final model

Statistical significance is denoted with * when p-values are lower than 0.05 ($p < 0.05$)

stem diameter) and all functional traits. Under the high light condition, most of the performance indicators (except for the number of leaves) and functional traits (except for SPAD) analyzed showed higher values under high water availability level (Table 1; Fig. 3). Height and basal stem diameter also exhibited a significant reduction (27 and 17.5%, respectively), in interspecific competition with *L. lucidum* (NLL) with respect to the control (N) (Fig. 3a, c). The maximum value of specific leaf area was recorded in the control (N) in high water availability, whereas the lowest value was recorded in the control (N) in low water availability. However, no differences in the competition outcome were recorded within each water condition (Table 1; Fig. 3f).

Under the low light condition, water availability did not mediate competition outcomes for any of the

performance indicators or functional traits evaluated (i.e., no interaction effect of water availability and neighbors; Table 1). The basal stem diameter and specific leaf area showed higher values under high water availability (Fig. 4c, f), whereas SPAD and root length showed higher values under low water availability (Fig. 4d, e). In addition, *L. molleoides* seedlings showed a reduction of 18 and 16% in height and basal stem diameter, respectively, and an 8% increase in specific leaf area when growing in interspecific competition with *L. lucidum* (NLL) with respect to the control (N) (Fig. 4a, c, f). The number of leaves was not affected by any of the treatments (Fig. 4b).

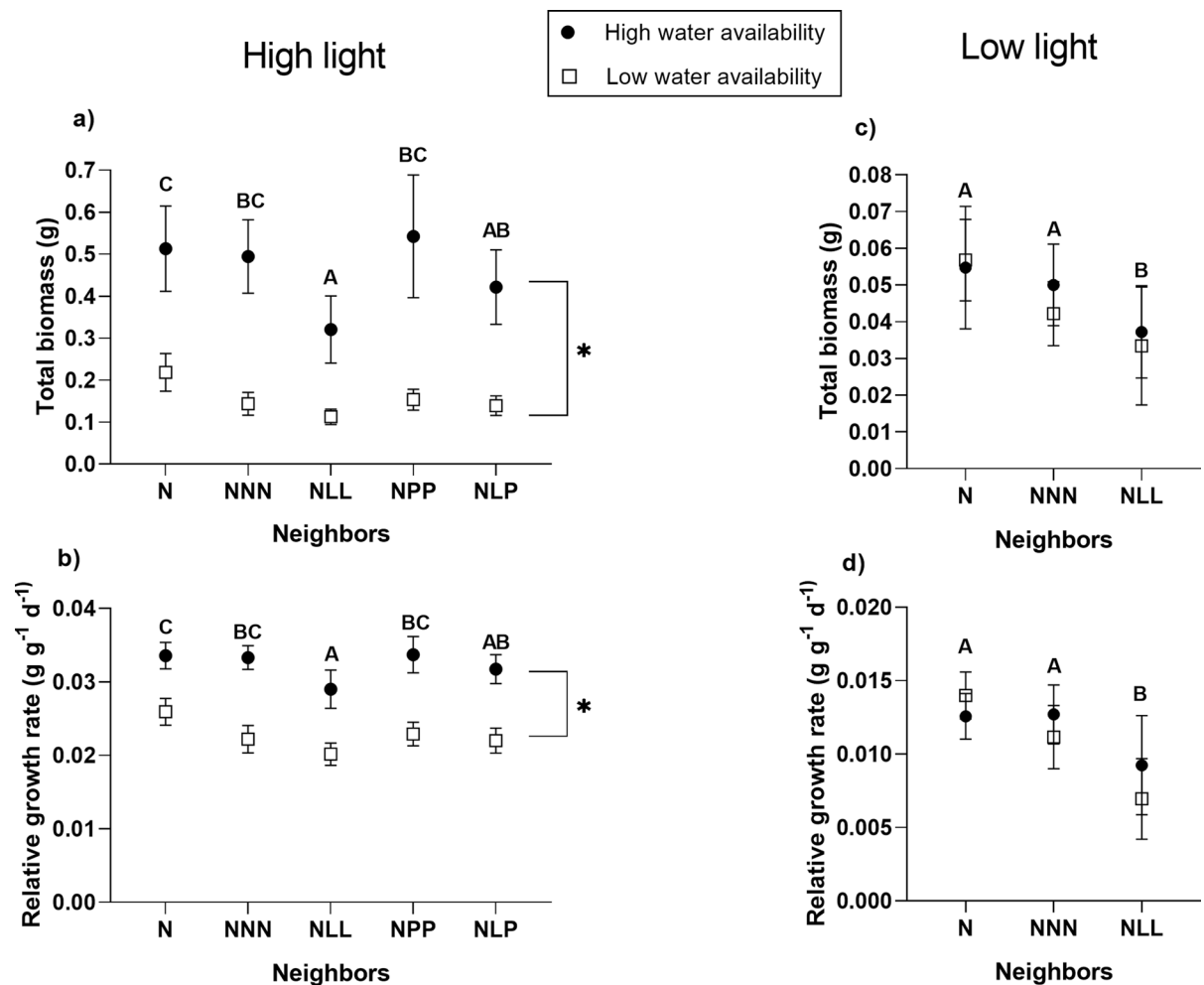


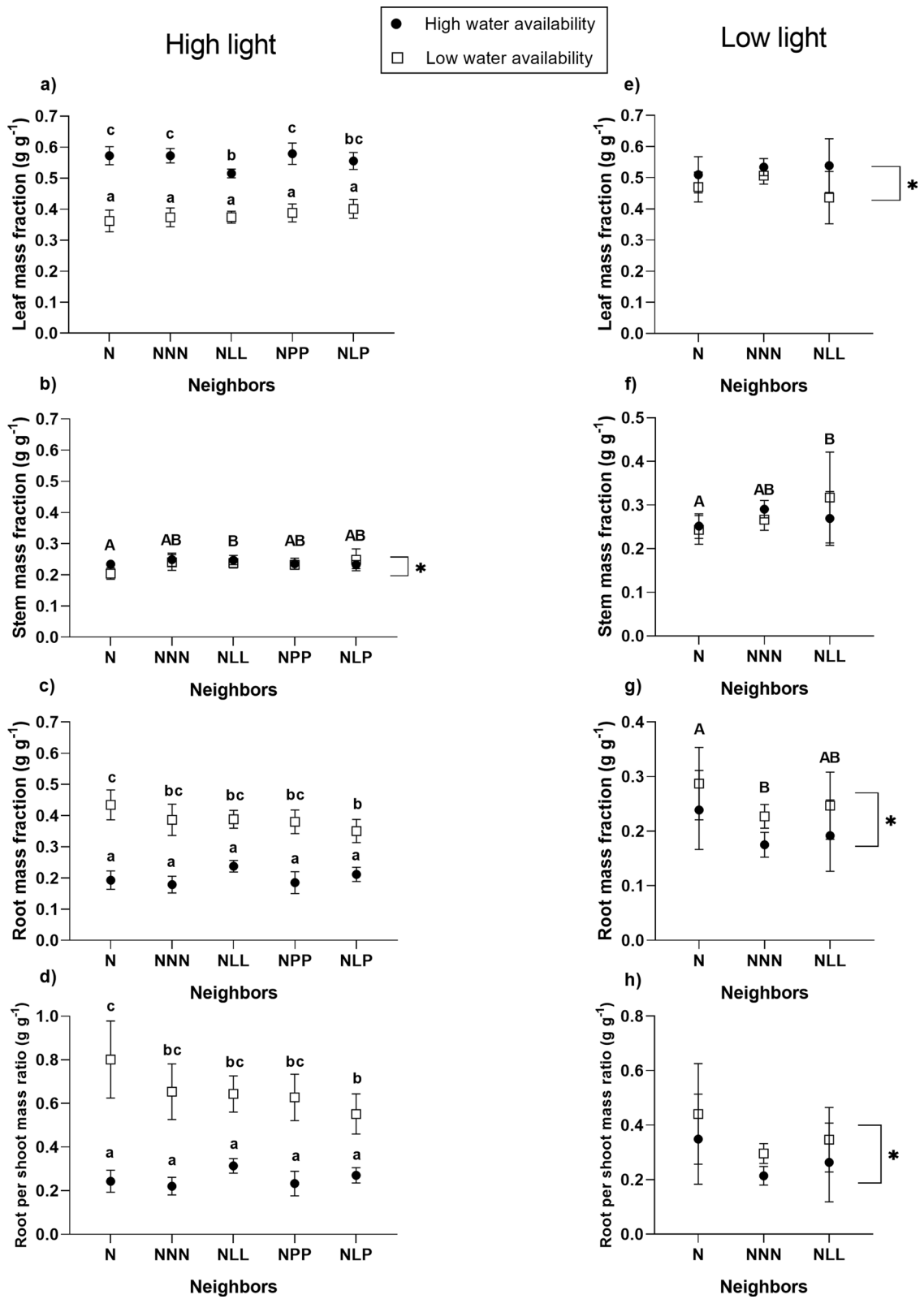
Fig. 1 Response of *L. molleoides* seedlings subjected to changes in water availability and neighbors (i.e., competition) under two different light conditions. **a** and **b** Total Biomass, **c** and **d** RGR (relative growth rate). Neighbor treatment: N=*L. molleoides* seedlings growing alone (control), NNN=intraspecific competition, NLL=interspecific competition of *L. molleoides* with *L. lucidum*, NPP=interspecific competition of *L.*

molleoides with *P. angustifolia*, NPL=interspecific competition with both nonnatives, *L. molleoides* with *L. lucidum* and *P. angustifolia*. The graphs show the average value and confidence intervals at 95%. Capital letters indicate significant differences among neighbors; * in the brackets indicates differences between water availability levels ($p < 0.05$)

Discussion

It is widely known that competition is one of the main mechanisms determining the composition of communities and the development of plant invasions (Davis et al. 2000; Shea and Chesson 2002; Fargione et al. 2003; Brooker 2006; Kuebbing and Nuñez 2016). However, the number of nonnative invasive species interacting with natives and the role that resource availability can play in competition outcome were rarely considered in previous works (but see Ferenc

et al. 2021). In our study, the native species exhibited changes in performance in response to the identity of the interacting species and the level of resource availability. In particular, we found that interspecific competition from the nonnative invasive species *L. lucidum* had a higher negative effect on the performance of the native species than intraspecific competition. In general, we did not observe a joint effect of both nonnative invasives on the native species. However, root biomass allocation did exhibit a joint effect of both non-native invasive species under low water



◀**Fig. 2** Biomass allocation of *L. molleoides* seedlings subjected to changes in water availability and neighbors (i.e., competition) under two different light conditions. **a** and **b** LMF (leaf mass fraction), **c** and **d** SMF (shoot mass fraction), **e** and **f** RMF (root mass fraction), **g** and **h** RM/SM (root/shoot mass ratio). Neighbor treatment: N=*L. molleoides* seedlings growing alone (control), NNN=intraspecific competition, NLL=interspecific competition of *L. molleoides* with *L. lucidum*, NPP=interspecific competition of *L. molleoides* with *P. angustifolia*, and NPL=interspecific competition with both nonnatives, *L. molleoides* with *L. lucidum* and *P. angustifolia*. The graphs show the average value and confidence intervals at 95%. Lower case letters are used for differences among the interaction levels of water availability and neighbors; capital letters indicate significant differences among neighbors and * in the brackets indicates differences between water availability levels ($p < 0.05$)

availability. This effect is remarkable, since roots play a key role in seedling competition in water scarcity situations (Zou et al. 2009; Bueno et al. 2021). Finally, the reduced performance of the native species when growing with *L. lucidum* was observed under a variety of resource conditions; however, there was a trend toward stronger negative effects under high resource availability.

Intraspecific versus interspecific competition with each nonnative invasive species separately under different resource conditions

As reported in other studies involving nonnative invasive species, our results showed that interspecific competition from *L. lucidum* was higher than intraspecific competition (Vilà and Weiner 2004; Skálová et al. 2013; Gioria and Osborne 2014; Kuebbing and Nuñez 2016; Guido et al. 2019). This higher competition by *L. lucidum* could be the result of the higher, more efficient or different resource acquisition generally described for nonnative invasive species than for natives (Gurvich et al. 2005; van Kleunen et al. 2010; Godoy et al. 2011). In particular, under both light conditions, our results showed that interspecific competition by the nonnative invasive species *L. lucidum* decreased the native species performance in most of the analyzed variables. In fact, total biomass, height and basal stem diameter, which are closely related to species competitive capacity and seedling survival (Lasky et al. 2015; Ferenc and Sheppard 2020; Ferenc et al. 2021), were significantly reduced in native seedlings growing in competition with the nonnative invasive *L. lucidum*. Additionally, even

though the interspecific competition was observed in both resource levels, there was a trend toward a stronger negative effect on the native species performance under high resource availability (e.g., Fig. 1). This resource trend was previously highlighted in other works that analyzed competition (Grime 1977; Davis et al. 2000; Mangla et al. 2011; Rozendaal et al. 2020). The interspecific competition exerted by *P. angustifolia*, the other nonnative invasive species was in general non-significant. In fact, this species showed high mortality under the low light condition; this result was also recently observed in another experimental study of seedlings under contrasting light and water conditions, which included this species (Simian 2021). All in all, our data suggest that the outcome of competition between native and nonnative invasive species depends on the identity of the interacting species. Indeed, previous studies attempting to obtain generalizations in the field of biological invasions observed that the identity of the nonnative species can determine changes in the response variables (Bottollier-Curtet et al. 2013; Čuda et al. 2015; Tabassum and Leishman 2016; Bueno et al. 2021).

The different competition outcomes obtained by the two nonnative invasive species could be related to their position within the resource use and acquisition spectrum (Díaz et al. 2004; Reich 2014). That is, even though both tree species could be included within a “conservative syndrome”, the position of *L. lucidum* within that spectrum is closer to that of species with an “acquisitive syndrome” (Tecco et al. 2013), which might explain the stronger competitive ability of this nonnative invasive species. In fact, this species has a remarkably high growth rate (Fernandez et al. 2020). It is also important to highlight that under field conditions, propagule pressure might play a key role in seedling establishment (Simberloff 2009). Since both species are among the most frequent and abundant nonnative invasive species in the area, their high propagule pressure (Ferrerías et al. 2008; Vergara-Tabares et al. 2018a) could modify competitive interactions (Sheppard and Burns 2014; Pik et al. 2020).

We did not observe a significant effect of intraspecific competition on the performance of the native *L. molleoides* seedlings. Undoubtedly, intraspecific competition might change with seedling density (Sheppard and Burns 2014) and ontogenetic stage (Gibson et al. 1999; Mangla et al. 2011), which deserves further studies. Finally,

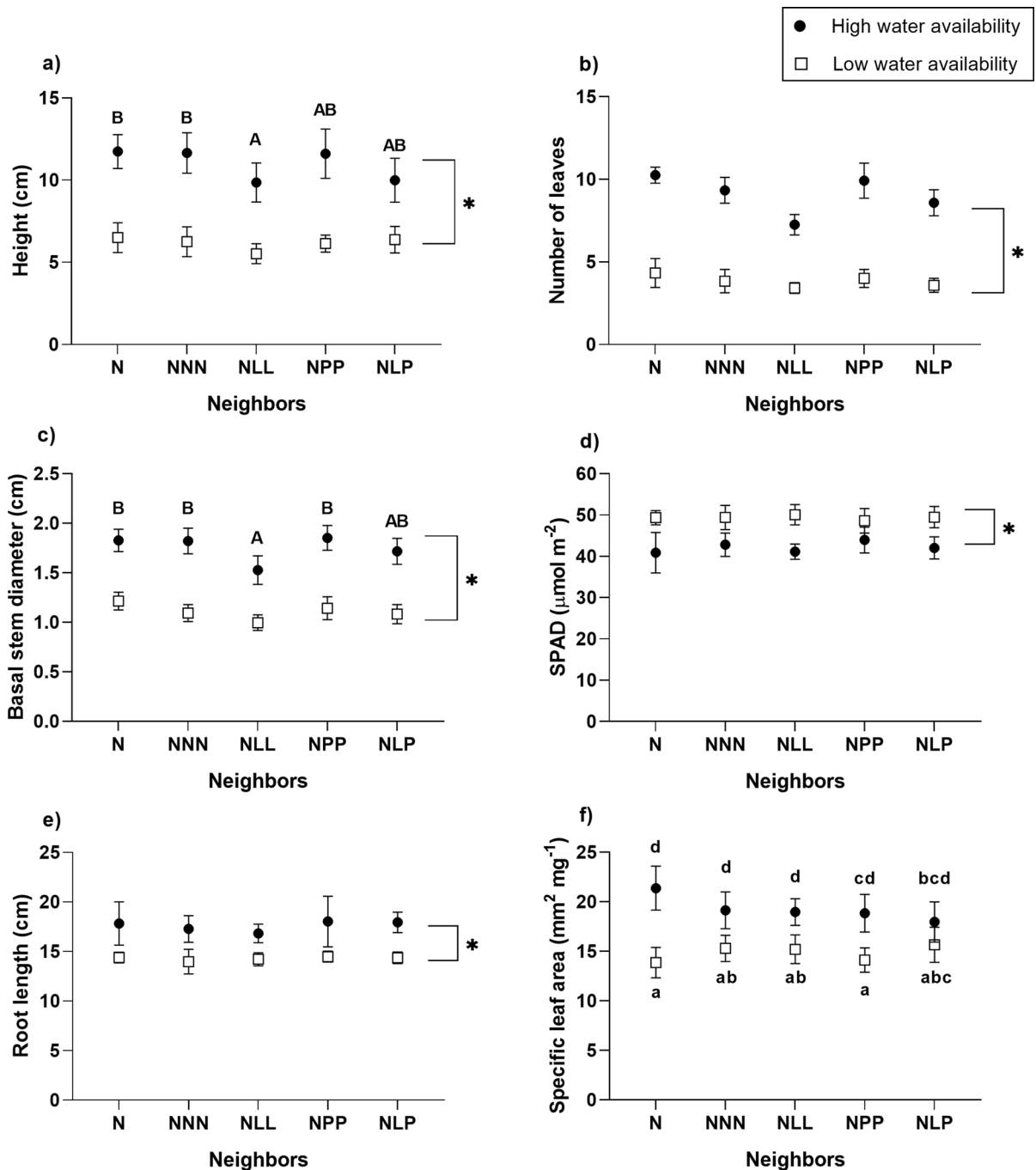
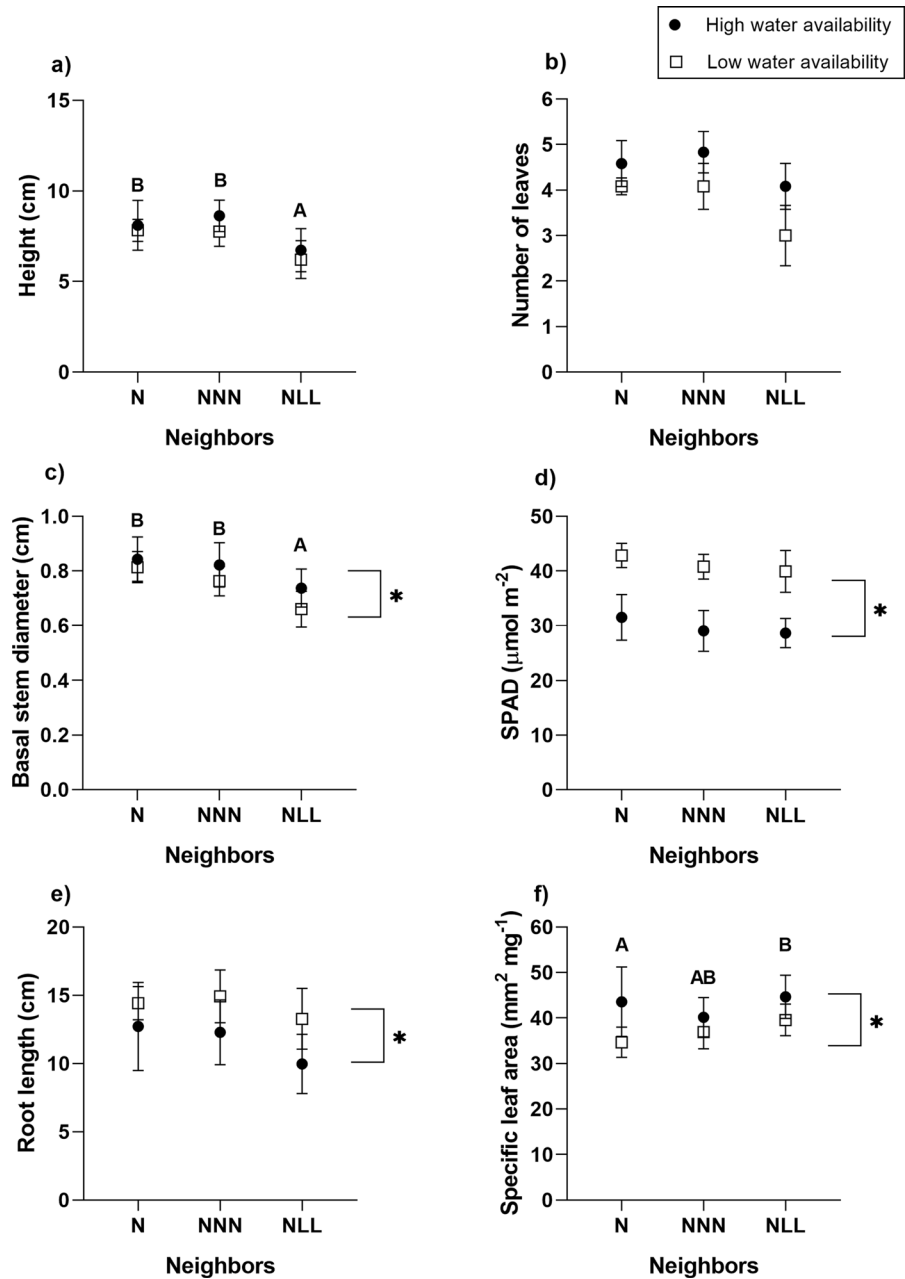


Fig. 3 Performance indicators and functional traits of *L. molleoides* seedlings subjected to changes in water availability and neighbors (i.e., competition) under high light condition. **a** and **g** height, **b** and **h** number of leaves, **c** and **i** basal stem diameter, **d** and **j** SPAD, **e** and **k** root length, **f** and **l** specific leaf area. Neighbor treatment: N=*L. molleoides* seedlings growing alone (control), NNN=intraspecific competition, NLL=interspecific competition of *L. molleoides* with *L. lucidum*, NPP=interspecific competition of *L. molleoides* with

P. angustifolia, NPL=interspecific competition with both nonnatives, *L. molleoides* with *L. lucidum* and *P. angustifolia*. The graphs show the average value and confidence intervals at 95%. Lower case letters are used for differences among levels for the interactions between water availability and neighbors; capital letters indicate significant differences among neighbors and * in the brackets indicates differences between water availability levels ($p < 0.05$)

Fig. 4 Performance indicators and functional traits of *L. molleoides* seedling subjected to changes in water availability and neighbors (i.e., competition) under low light condition. **a** and **g** height, **b** and **h** number of leaves, **c** and **i** basal stem diameter, **d** and **j** SPAD, **e** and **k** root length, **f** and **l** specific leaf area. Neighbor treatment: N = *L. molleoides* seedlings growing alone (control), NNN = intraspecific competition, NLL = interspecific competition of *L. molleoides* with *L. lucidum*, NPP = interspecific competition of *L. molleoides* with *P. angustifolia*, NPL = interspecific competition with both nonnatives, *L. molleoides* with *L. lucidum* and *P. angustifolia*. The graphs show the average value and confidence intervals at 95%. Lower case letters are used for differences among levels for the interaction between water availability and neighbors; capital letters indicate significant differences among neighbors and * in the brackets indicates differences between water availability ($p < 0.05$)



although performance was modified by competition and resource conditions, the native species showed a high survival in all the treatments evaluated. This result agrees with previous studies in the area, in which *L. molleoides* showed a high survival under low light availability conditions, such as seedlings that grew under a native species (Torres and Renison 2015) or in nonnative forests (Ferrerias et al.

2019). Our results also agree with previous studies on trees under competition in South American and African forests, in which the authors also observed that competition affects performance but not survival (Rozendaal et al. 2020). However, as those authors claim, the performance effect could indirectly affect mortality in other stages of plant development.

Competition exerted by two nonnative species under different resource conditions

In general, both nonnative invasive species together did not produce a stronger negative effect on the native species under the high light condition. However, the greatest reduction of *L. molleoides* root biomass was recorded under low water condition when it grew with both nonnative invasive species. Under low water conditions, a higher amount of biomass invested in roots is related to higher chances of facing the scarcity of this resource (Zou et al. 2009; Wang and Taub 2010; Bueno et al. 2021). This higher negative effect on the native species could be due to the different growth forms of both nonnative invasive species, i.e. *L. lucidum* is a tree, while *P. angustifolia* is a shrub. These growth forms were associated with a different root architecture, with the root system being more superficial in shrubs and deeper in trees (Becker and Castillo 1990). Thus, at the seedling stage, the combination of both root systems in a low water environment might deplete most of the available water in the entire soil column, constraining the native species root development. This depletion could have severe consequences, particularly in semiarid systems as the one where these species coexist. A previous study analyzing the effect of two nonnative invasive species on a native -but not including changes in resource availability-, noted that the performance of the native species changed with species identity (i.e., when growing with two nonnative invasive species, some native species showed a significant decrease in their performance, whereas others showed a slight decrease, no effect or even a facilitating effect on native performance; Ferenc et al. 2021). In this sense, our study also warns that the differences might appear in a singular trait and under a particular resource condition. All in all, there is a need to increase the works about competition with more than one nonnative invasive species to elucidate general patterns regarding multi-species interactions.

Under the low light condition, the effect of both nonnative invasive species was not analyzed due to the high mortality of *P. angustifolia*. Thus, it is clear that the combination of both nonnative invasive species might not be a threat under this condition.

Resource availability versus competition

In general, the low light environment caused a greater reduction in the performance variables of the native species than the different levels of water availability or competition. Even though the effect of light conditions was not compared statistically, the reduction of seedling biomass under the low light condition was highly remarkable (Fig. 1a, c; when the native grew in the low light environment, total biomass decreased seven times with respect to the high light environment). By contrast, a previous work in herbs found that competition caused a greater reduction in plant performance than resource availability (Čuda et al. 2015). However, that work involved a lower reduction in water availability (21.2% in the low water availability treatment) and less severe water reduction between water treatments. Moreover, the different growth forms involved in that work and ours might have different responses to those factors (Tabassum and Leishman 2016). In addition, our results agree with previous studies that found a more marked reduction in seedling performance under reduced light conditions than under reduced water conditions (Zou et al. 2009). Despite the strong effect of light availability, our study showed that under all the resource conditions, competition, particularly interspecific, could affect native seedling development. In this sense, our study agrees with results reported by Skálová et al. (2013), who observed a competition effect of nonnatives on natives in different resource levels. However, in our work the effect of competition seems to be greater with higher resource availability, as previously suggested by other authors (Grime 1977; Rozendaal et al. 2020). All in all, even though the results from greenhouses cannot be extrapolated to field conditions (Franzese et al. 2022), depending on where it grows, *L. molleoides* seedling establishment might be threatened by competition by nonnative invasive species or light scarcity. That is, the area where these species coexist has a heterogeneous vegetation cover (Giorgis et al. 2017; Zeballos et al. 2014), generating distinct light environments. Thus, in conserved native woodlands or in highly invaded areas, where light is generally scarce (Ferrerias et al. 2019), the low availability of this resource could be the main threat to native species recruitment, whereas in open areas, the main threat might be competition by *L. lucidum*. In addition, the effect of water availability on seedling

development might vary throughout the year. That is, during the early growing season, when water availability can exhibit large fluctuations (with periods when temperatures largely exceed precipitations, i.e. dry periods), water scarcity could have a strong negative influence on seedling development; in turn, by the end of the growing season, when water availability is generally high, competition, particularly in open areas, might have a strong negative influence on the performance of native seedlings.

Conclusions and future perspective

The seedling stage usually exhibits high mortality (Fenner and Thompson 2005). Moreover, it is deeply influenced by intra- and interspecific competition (Leck et al. 2008; Mangla et al. 2011). Our work addressed competition of woody native and nonnative invasive seedlings including two little explored factors: the effect of two nonnative invasive species on a native and the potential different outcome of contrasting resource levels. First, we found that the effect of nonnative invasive species is species-specific (Ferenc et al. 2021). Second, we found a joint effect of both nonnative invasive species on one of our response variables under a particular resource condition. Thus, our results highlight the advantages of considering multiple response variables and resource conditions in seedlings, and opens new questions about sampling protocols. Third, our study suggests that, in general, competition would be stronger with higher resource availability. Finally, we found a high survival of *L. molleoides*, independently of the treatment applied; however, considering that this native is a dominant species, a greater negative effect of these factors on other native species could be expected. Most of the studies focusing on competition effects generally take into account total biomass and survival (Molina-Montenegro et al. 2012; Skálová et al. 2013; Müller et al. 2016; El-Barougy et al. 2020; Ferenc et al. 2021). Even though these factors could be considered the most important variables, we think that including several traits will help to make clearer predictions about the consequences of invasions across different environmental conditions. In addition, the inclusion of several variables would help to make generalizations of the effect of multiple nonnative invasive species on native species (Ferenc et al. 2021).

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Declarations

Conflict of interest The authors have not disclosed any competing interests.

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