

RESEARCH ARTICLE

Drought affects the performance of native oak seedlings more strongly than competition with invasive crested wattle seedlings

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ABSTRACT

- Two of the most important processes threatening vulnerable plant species are competitive displacement by invasive alien species and water stress due to global warming. *Quercus lusitanica*, an oak shrub species with remarkable conservation interest, could be threatened by the expansion of the invasive alien tree *Paraserianthes lophantha*. However, it is unclear how competition would interact with predicted reductions in water availability due to global climate change. We set up a full factorial experiment to examine the direct interspecific competition between *P. lophantha* and *Q. lusitanica* seedlings under control and water-limited conditions.
- We measured seed biomass, germination, seedling emergence, leaf relative growth rate, biomass, root/shoot ratio, predawn shoot water potential and mortality to assess the individual and combined effects of water stress and interspecific competition on both species.
- Our results indicate that, at seedling stage, both species experience competitive effects and responses. However, water stress exhibited a stronger overall effect than competition. Although both species responded strongly to water stress, the invasive *P. lophantha* exhibited significantly less drought stress than the native *Q. lusitanica* based on predawn shoot water potential measurements.
- The findings of this study suggest that the competition with invasive *P. lophantha* in the short term must not be dismissed, but that the long-term conservation of the native shrub *Q. lusitanica* could be compromised by increased drought as a result of global change. Our work sheds light on the combined effects of biological invasions and climate change that can negatively affect vulnerable plant species.

INTRODUCTION

Competitive displacement by invasive alien species (IAS) is a major concern for the conservation of threatened native plants (Czech *et al.* 1997; Wilcove *et al.* 1998; Baider & Florens 2011; Catford *et al.* 2018). Changes in climatic patterns associated with global change could both accelerate the speed and increase the magnitude of displacement processes (Hughes 2000; Valladares *et al.* 2015; Liu *et al.* 2017; Catford *et al.* 2018). This is particularly important for slow-growing, vulnerable native species with contrasting resource use strategies to those of most invasive plants. Invasive plant species tend to have fast resource use strategies, often becoming even faster in their non-native ranges (Montesinos 2021).

Some recent meta-analyses reveal the role of competition in the interaction between native and invasive plants. These reported mounting evidence that invasive species are often better competitors than native species (Vilà & Weiner 2004;

Kuebbing & Nuñez 2016). Investigating competitive interactions during critical early plant life stages is worth attention to guide management strategies. Invasive seedlings are frequently easily competitively suppressed by native species (Hyatt 2008), and conservation efforts have focused on eradicating invasive mature trees. However, some invasive species can reduce native species recruitment at the seedling stage, *e.g.* by displacing native seedlings through germinating a large number of seedlings from persistent soil seed banks (Le Maitre *et al.* 2011). Furthermore, some invasive species show early competitive ability, which can be modified under disturbance events (Hyatt 2008; Bottollier-Curtet *et al.* 2013). The impact on the native seedlings is critical, since this can disrupt numerous cascading community and ecosystem dynamics (Grime 2012). If competitive dominance of invasive seedlings is confirmed, the need to focus management efforts on eradicating invasive seedlings will be reinforced.

There is increasing interest in predicting species responses to global change (Vilà *et al.* 2007; Jeschke & Strayer 2008;

Jarnevic & Stohlgren 2009; Gallardo *et al.* 2017; Bellard *et al.* 2018) and to compare the performance of native and non-native species under stress conditions, such as low water availability (Daehler 2003). Evidence suggests that, generally, precipitation will decrease in Southern Europe under changed climate conditions (IPCC 2014). Species native to Mediterranean areas, including some oaks (*Quercus* spp.), may be negatively affected by changed climate conditions if droughts become more frequent, longer and more extreme in these areas (Lloret *et al.* 2004; Galiano *et al.* 2012; Bussotti *et al.* 2014; Barbeta & Peñuelas 2016; Gentilesca *et al.* 2017). However, oaks have functional traits that confer some drought tolerance, such as hard and small leaves (Baldocchi *et al.* 2010; Peguero-Pina *et al.* 2020), higher allocation to deep belowground structures (Zavala *et al.* 2000; David *et al.* 2007; Sardans & Peñuelas 2013) and efficient hydraulic systems (Forner *et al.* 2018; Ramírez-Valiente *et al.* 2020).

An increase in water deficit could prove advantageous for co-occurring IAS. Invasive alien species from drier regions could be favoured if the new conditions become closer to their native range (Hellmann *et al.* 2008). Furthermore, an increase in water deficit could prove advantageous for IAS over native species because the former could have broader environmental tolerance (Dukes & Mooney 1999) and greater phenotypic plasticity (Davidson *et al.* 2011). However, a general relationship between climate change and the increased dominance of IAS over native species has yet to be established (Dukes & Mooney 1999). Recent evidence suggests that drought has larger detrimental effects on some IAS than on recipient native communities (Liu *et al.* 2017; Valliere *et al.* 2019). Species-specific research is still needed to confirm the accuracy of the predictions about which species may be favoured in each scenario (Verlinden *et al.* 2013).

Considering the effects of drought stress due to changing climate conditions, the competitive pressure of IAS and their interactions can play an important role when addressing native species conservation (Mainka & Howard 2010). Greenhouse experiments involving simple pairwise species mixtures in full factorial designs might be a suitable starting point to deal with such investigations (Scheiner & Gurevitch 2001). This type of experimental design allows us to study the response of functional traits that may be affected by the scarcity of water and by plant interactions. Parameters such as the root/shoot ratio (Leiva & Fernández-Alés 1998; Otieno *et al.* 2005; Kawalec *et al.* 2014; Abbas *et al.* 2019; Qi *et al.* 2019) or water potential (Fotelli *et al.* 2000; Violle *et al.* 2009) provide important information on plant responses to drought and/or competition stress. Besides, there are several competition intensity indices to quantify the magnitude of plant interactions (Grace 1995; Goldberg *et al.* 1999; Weigelt & Jolliffe 2003). The relative interaction index proposed by Armas *et al.* (2004) is a useful way to assess competitive interactions in a comparable manner. A number of studies have used this index to reveal the competitive outcomes between native and invasive species (Rodríguez-Echeverría *et al.* 2013; Ulrich & Perkins 2014; Abd El-Gawad *et al.* 2017) or under stress (Domènech & Vilà 2008; Filazzola *et al.* 2018).

In the Galician massif of Monte Pindo (NW Spain) the expansion of the Australian invasive species *Paraserianthes lophantha* (Willd.) I.C. Nielsen could threaten a small disjunct, isolated population of the native oak shrub *Quercus lusitanica* Lam. (Amigo & Romero Buján 2018; Santamarina *et al.* 2019),

although the potential mechanisms involved are unclear. The first record of *P. lophantha* in the locality is in 1989 (Castro *et al.* 1989). Since then, fires and human activity have played an important role in the expansion of this invasive species (García-Duro *et al.* 2019). Other non-native species, such *Eucalyptus globulus* Labill, *Acacia melanoxylon* R. Br or *Acacia dealbata* Link, are also present in the area (GBIF.org 2021). To date, there has been no detailed investigation, for this pair of species, of the competitive interaction between the native and the invasive species and increased drought caused by climate change. As a first approximation, we focused on the critical seedling stage. Specifically, we investigated if the competitive interaction of invasive *P. lophantha* seedlings and drought could synergistically risk preservation of the vulnerable native shrub species *Q. lusitanica*.

MATERIAL AND METHODS

Study species and sampling

Quercus lusitanica Lam. is a low-growing stoloniferous European oak with a shrubby habit, growing up to 1-m tall. It is native to several disjoint areas of the Iberian Peninsula and the north of Morocco (Amaral Franco 1990; Llamas *et al.* 2003). The species is considered vulnerable in the Spanish region of Galicia (Galician Decree 167/2011; DOG 2011) and occurs in the habitat 4030 'European dry heaths', in the list of Habitats of European Interest of the European Directive 92/43/EEC. *Paraserianthes lophantha* (Willd.) I.C. Nielsen is an evergreen spreading tree or shrub, with a height of up to 10 m, native to coastal and near-coastal areas in southwestern West Australia (Cowan 1988). The species has become invasive across numerous regions globally (Randall 2017).

Seeds from both species were obtained from the contact area of the two species in the Galician massif of Monte Pindo (NW Spain, 42.873372 N, -9.107041 W) in 2018. *Quercus lusitanica* acorns were collected in autumn (last week of October) from 26 different individuals; *P. lophantha* seeds were collected in late summer (August) from 26 different individuals. Although the timing of seed production is different for these two species, seedling emergence is observed during spring for both species (personal observation). Seeds were extracted from parent individuals at least 5 m apart, to avoid potential clone sampling. We deemed this sampling distance as adequate for *Q. lusitanica* in this specific location because the abrupt orography of the field site at Monte Pindo hinders the extensive growth of its short stolons.

Germination

To preserve seed viability, *Q. lusitanica* acorns, which are very sensitive to variations in humidity, were stored in porous paper bags at low temperature (0–5 °C) in open polyethylene bags for 1 week after collection, after which they were sown. Seeds of *P. lophantha* were dry-stored with silica gel in dark conditions in porous paper bags for 2 months. Although acorns are fruits, hereafter we refer to them as 'seeds' to facilitate comparisons with *P. lophantha* seeds.

Each seed used during the subsequent experiments was weighed to the nearest mg on an analytical balance (KERN, model ABS-N_ABJ-NM_ACS_ACJ, Kern & Sohn, Puchheim,

Germany). For *Q. lusitanica*, cupules were detached from acorns and discarded before weighing. To select viable seeds, acorns of *Q. lusitanica* were separated by flotation and soaked overnight (sunken acorns were discarded). To stimulate germination, acorns were scarified by cutting the pericarp near the end containing the embryo. They were subsequently buried in commercial potting soil at 4-cm depth and watered twice a week. Radicle emergence of acorns was examined twice a week to match germination times across species. The treatment to stimulate germination of *P. lophantha* seeds was conducted only when 50% of the acorns had germinated, on day 19 after burying the acorns. *P. lophantha* germination can be poor due to the hard seed coat that is resistant to water (Clemens *et al.* 1977), therefore seed dormancy was broken using thermal scarification by exposure to hot water (80 °C) for 10 min, followed by mechanical scarification by chipping the micropylar end of each seed with a scalpel. Scarified seeds were placed on damp cotton in Petri dishes at a constant temperature (28 °C) in complete darkness. Germinated seeds were removed when germination exceeded 50% and were transplanted into the experimental pots 24 h after scarification.

Competition and drought experiment

The interspecific competition and drought experiment was conducted in the greenhouses of the Botanical Garden of Coimbra (Portugal) over 22 weeks (from the last week of November 2018 to May 2019). The greenhouse air temperature was between 10 and 30 °C and natural light was provided through the covers of the greenhouse enclosure. Seeds were sown in 200 ml Ray Leach Cone-Trainers pots filled with an equal mixture of grit sand and commercial potting mix (1:1). Soil consisted of a mix of commercial peat moss and fine and coarse perlite.

Seeds of each of the two species were allocated to one of four experimental treatments (control, drought, competition, competition–drought). Each treatment combined one level of drought and one level of competition in a full factorial design. To reduce the influence of maternal and genetic effects, half sibling seeds from each mother tree were allocated to each treatment and thus seeds from any single parental individual were replicated only once within each treatment. The drought treatment consisted of a control group watered to saturation twice a week (control and competition treatments) and a drought group that was watered to saturation only once a week (drought and competition–drought). The greenhouse provided full shelter from any external precipitation. The reduction in water supply in the drought treatment simulates mild drought *versus* a non-water stress environment. Soil moisture content was controlled every 2 weeks with a hand-held conductimeter on a random subset of five pots in each treatment, showing a clear difference between pots in each group of more than three points (personal observation). The interspecific competition treatment consisted of a control group in which one seed of each species was grown in individual pots (control and drought treatments) and a competition group in which one seed of each species grew in competition with each other within the same pot (competition and drought–competition). Each experimental group was composed of 26 replicates (one per parental tree), giving 156 pots containing 208 individuals at the start of the experiment (104 of each species). Mortality reduced the

number to 99 and 78 *Q. lusitanica* and *P. lophantha* individuals, respectively, and only individuals surviving to the end of the experiment were included in the analysis.

We recorded seedling emergence (shoot apex visible above soil surface) once a month and plant leaf number in week 12 after the start of the experiment (seedlings ranging in age between 12 to 15 weeks) and in week 22 (22- to 25-week-old seedlings), immediately before harvesting. We harvested roots and shoots at predawn, for each individual plant, and used shoots to assess individual shoot water potential with a Scholander pressure chamber (Manofrigido, Amadora, Portugal). Shoot water potential is a sensitive indicator of plant water stress, in which the pressure needed to extract water from the plant indicates the plant water status; with higher pressures needed to extract water from stressed plants and lower pressures needed to extract water from well hydrated plants. After water potential measurements, we subsequently placed roots and shoots in paper bags, dried them at 70 °C for 48 h and weighed them to the nearest mg with an analytical balance (KERN, model ABS-N_ABJ-NM_ACS_ACS).

Relative growth rate (RGR) for number of leaves was calculated following Hunt (1990), based on the formula:

$$RGR = (\ln NL_{t_f} - \ln NL_{t_0})/t \quad (1)$$

where NL_{t_0} is number of leaves per plant in week 12, NL_{t_f} is final total number of leaves per plant in week 22 and t is number of months between the two measurements.

Plant biomass was used to determine root/shoot ratio (R/S), total biomass and relative interaction indices (RII hereafter; Armas *et al.* 2004). The RII formula was defined as:

$$RII = (B_w - B_0)/(B_w + B_0) \quad (2)$$

where B_w is total biomass of a seedling grown in competition with the other species in the same pot, and B_0 is biomass of control seedling grown alone in another pot. RII ranges between -1 and $+1$, where more negative values indicate stronger competition and positive values indicate facilitation.

Statistical analyses

All the statistical analyses were developed using packages *plyr* (Wickham 2011) and *stats* in R version 1.4 (R Core Team, 2019). Figures were generated with SigmaPlot (SigmaPlot version 12.5; Systat Software, San Jose, CA, USA, www.systatsoftware.com) and with R package *ggplot2* (Wickham 2016).

We used general linear models (GLMs) with *glm* procedure in package *stats* and a Gaussian link function to test for differences between the two species, and for effects of drought and competition (categorical explanatory variables) on *Q. lusitanica* and *P. lophantha* in terms of RGR, total biomass, R/S, RII and water potential as response variables. For each variable, we initially tested for differences between species using GLMs, and later developed GLMs for each species, with drought and competition as categorical explanatory variables, except for RII in which drought was the only explanatory variable. After running this analysis, we selected the models with the lowest Akaike information criterion (AIC) as those with the most explanatory power (Akaike 1973). Differences in mortality among

treatments for each species were detected using the Fisher exact test, which is often preferred when sample sizes are small (Fisher 1956). Linear regressions were used to assess the role of propagule weight in the final biomass allocation. The regressions were fitted separately for each treatment.

RESULTS

Seeds of *Q. lusitanica* were more than thirty times larger (3.609 ± 0.168 g; mean \pm SE) than those of *P. lophantha* (0.101 ± 0.002 g). Germination peaked after 4 weeks for the native *Q. lusitanica* (80% germination) and after only 5 days for the invasive *P. lophantha* (85%). Seed size correlated with final seedling biomass for the native, but *P. lophantha* final biomass was independent of initial seed size under all treatments (Figure S1). The invasive *P. lophantha* reached maximum seedling emergence after 1 month, whereas the native *Q. lusitanica* only reached maximum seedling emergence by month 5 (Figure S2).

Significant differences between the native and invasive species were found for several traits (Table S1). Mortality was similar for both species, but higher under drought conditions (drought and competition–drought) than for controls (control and competition) only for the native species. The invasive species only trended toward increased mortality when both competition and drought were combined (competition–drought), although it was not statistically significant (Table 1, Fig. 1A). Leaf relative growth rate (RGR) was similar for the two species overall, but *P. lophantha* leaf production was significantly reduced by drought (drought and competition–drought), which halved leaf production (Table 2, Fig. 1B).

Final seedling biomass of *Q. lusitanica* was significantly higher than that of *P. lophantha*, but the biomass of both species was significantly lower under drought treatments (drought and competition–drought; Table 2, Fig. 1C). Overall, root/shoot ratio (R/S) was significantly higher for *Q. lusitanica* than for *P. lophantha*, indicating larger proportional allocation of biomass to roots for the native species. There was no difference in R/S among *Q. lusitanica* experimental groups, but *P. lophantha* R/S significantly increased either in the presence of drought (drought and competition–drought) or in absence of competition with *Q. lusitanica* (control and drought; Table 2, Fig. 1D). Physiologically, *Q. lusitanica* individuals had more negative water potential than *P. lophantha*, indicating higher water stress for the native species (Fig. 2A). Water potential values for *Q. lusitanica* were significantly more negative under drought treatments (drought and competition–drought) than

controls, as expected. However, there were no significant differences among drought or competition treatments for *P. lophantha* individuals, indicating more resilient physiology of the invasive species (Table 2, Fig. 2A).

Relative Interaction Indices highlighted the important negative competitive interactions developing between the two species in the absence of drought (control), but the reductions in total biomass associated with drought overshadowed the competitive effects and responses for both species (drought). However, differences in the intensity of the competitive effects and responses between watering treatments were only significant for native *Q. lusitanica* but not for the invasive species (Table 2, Fig. 2B).

DISCUSSION

Seedlings of both the native *Q. lusitanica* and the invasive *P. lophantha* experienced competitive effects and responses, but neither species was clearly at a competitive disadvantage. Rather than competition, drought had an even greater impact on the two species. However, our results show a smaller decrease in water potential for *P. lophantha* than for *Q. lusitanica*, which suggests a more resilient response of the invasive seedlings than the native species under drier conditions.

Quercus lusitanica acorn weight was significantly correlated with subsequent seedling biomass, which may have initially given the native species a competitive advantage over *P. lophantha*. In contrast, the seed size of *P. lophantha* did not correlate with its seedling biomass, suggesting that this invasive species relies less on initial stored resources and more on current photoassimilates. High acorn mass can confer initial competitive advantage (Goldberg & Landa 1991; Seiwa 2000), which in turn have a positive effect in early development and successful establishment of this oak species (Bonfil 1998; Kormanik *et al.* 1998), even under drought stress (Ramírez-Valiente *et al.* 2009; Bonito *et al.* 2011; Zolfaghari *et al.* 2013). However, that competitive and ecological advantage may later diminish when competing with a fast growing species (Rose & Poorter 2000; Navarro *et al.* 2006).

Seedlings of the invasive *P. lophantha* allocated a significantly higher proportion of biomass to shoots than the native *Q. lusitanica*, and even more when growing in competition, or if water was not a limiting factor. *Q. lusitanica* had a larger root/shoot ratio than *P. lophantha*, thanks to its thickened taproot, a common trait in native Mediterranean resprouter species (Zavala *et al.* 2000). Under drought conditions, the invasive *P. lophantha* significantly reduced its leaf growth rate and increased allocation to roots. Reduced leaf production may be drought-induced stunting but also a consequence of leaf shedding, a trait frequently observed in invasive Australian wattles (Osonubi *et al.* 1992; Aref *et al.* 1995; Aref 1996; Forster *et al.* 2016), and which may play a major role in survival of drought-stressed plants (Munné-Bosch & Alegre 2004). Increased allocation to belowground growth than in non-stressed conspecifics has previously been reported in several other invasive species in low-resource environments (Funk 2013) and demonstrates positive associations with the ability of woody invasive plants to survive droughts (Grotkopp & Rejmánek 2007).

In our experiment, the invasive species was able to modulate early its biomass allocation to increment the acquisition of the

Table 1. Fisher's exact test for mortality of *Quercus lusitanica* and *Paraserianthes lophantha*.

variable	drought effect		competition effect	
	odds ratio (95% CI)	<i>P</i>	odds ratio (95% CI)	<i>P</i>
<i>Q. lusitanica</i>	∞ (3.163– ∞)	<0.001	1.311 (0.308–5.861)	0.7554
<i>P. lophantha</i>	3.764 (0.840–23.561)	0.063	2.105 (0.504–10.510)	0.349

Significant *P*-values (*P* < 0.05) are presented in bold.

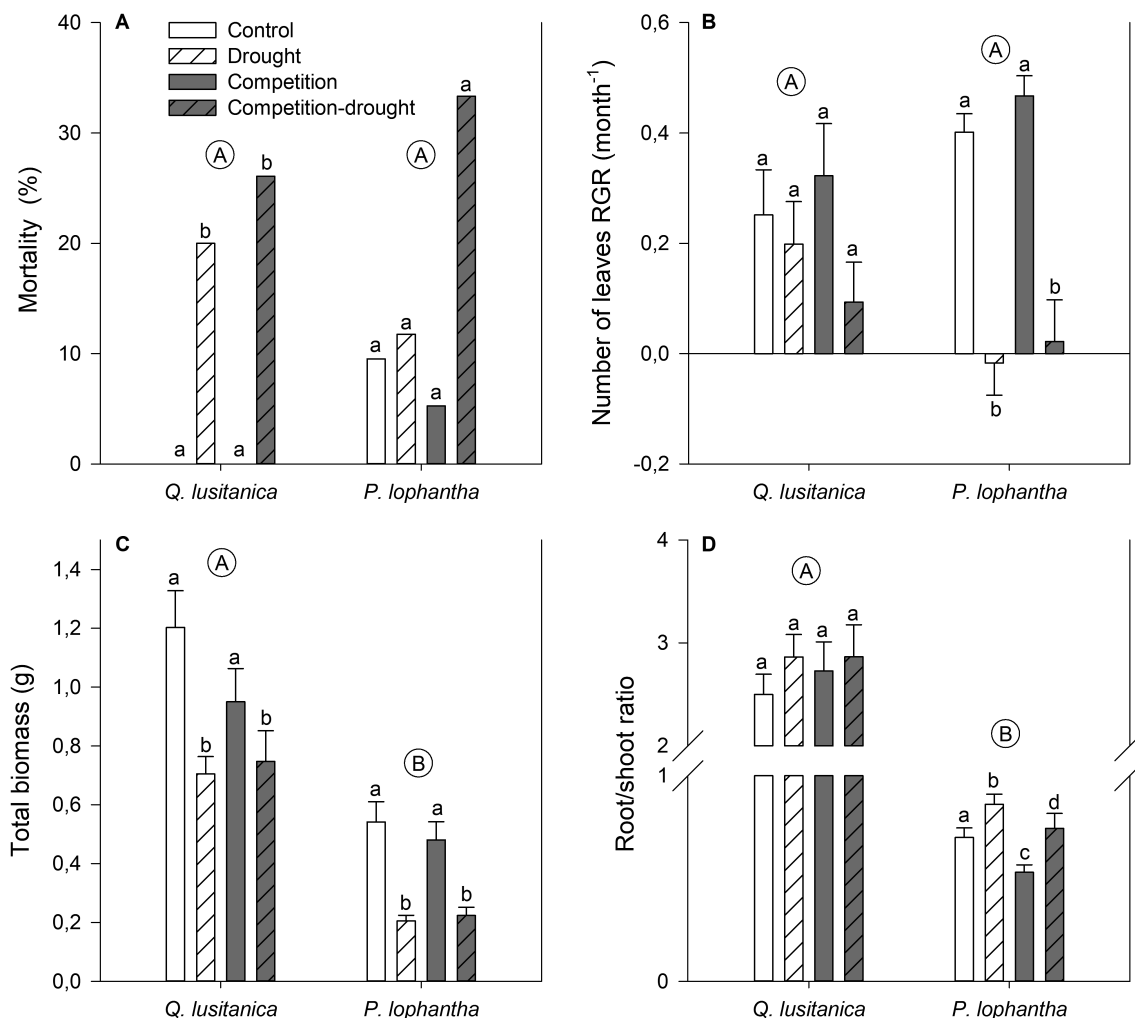


Fig. 1. Mortality (A); leaf RGR (B); total seedling biomass (C); and root/shoot ratio (D) for *Quercus lusitanica* and *Paraserianthes lophantha* in each treatment. Different uppercase or lowercase letters indicate statistically significant differences ($P < 0.05$) among species or between treatments, respectively. Bars represent mean \pm SE.

Table 2. Results for the best models selected by akaike information criterion (AIC) from all general linear models fitted on the effects of drought and competition on *Quercus lusitanica* and *Paraserianthes lophantha*.

variable	species	selected model	drought		competition		df	AIC
			t	P	t	P		
Leaf relative growth rate (RGR)	<i>Q. lusitanica</i>	Drought + Competition	-1.493	0.141	-0.092	0.927	2.57	40.324
	<i>P. lophantha</i>	Drought + Competition	-8.654	<0.001	1.090	0.28	2.63	-19.579
Total biomass	<i>Q. lusitanica</i>	Drought + Competition	-3.263	0.002	-1.155	0.251	2.78	118.46
	<i>P. lophantha</i>	Drought + Competition	-5.653	<0.001	-0.479	0.633	2.61	-13.884
Root/shoot ratio	<i>Q. lusitanica</i>	Drought + Competition	1.011	0.315	0.520	0.604	2.78	254.74
	<i>P. lophantha</i>	Drought + Competition	3.696	<0.001	-2.896	0.005	2.61	-18.541
Relative Interaction Index	<i>Q. lusitanica</i>	Drought	2.265	0.028			47	0.573
	<i>P. lophantha</i>	Drought	0.995	0.325			43	20.775
Water potential	<i>Q. lusitanica</i>	Drought + Competition	2.538	0.013	-1.355	0.179	2.84	215.05
	<i>P. lophantha</i>	Drought + Competition	0.982	0.330	1.114	0.269	2.63	38.53

Additive models are indicated by +. Significant P -values ($P < 0.05$) are shown in bold.

resources that most strongly limit its growth, such as light or water (Bloom *et al.* 1985). This is a response often related to competitive ability in other invasive Australian wattles (Morris

et al. 2011), which can be of overall importance for invasive success (Witkowski 1991; Grotkopp & Rejmánek 2007; Pyšek & Richardson 2008). In contrast, the native *Q. lusitanica*

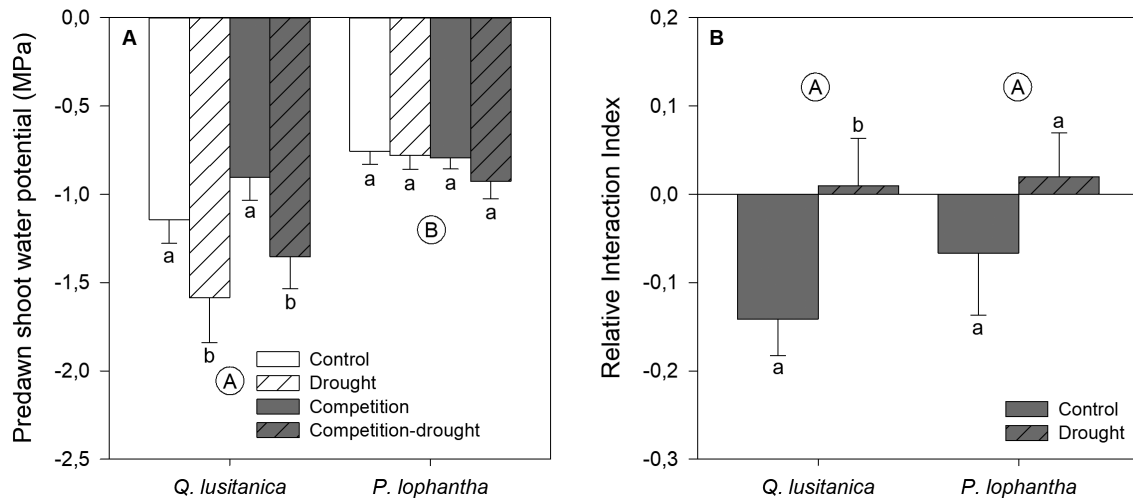


Fig. 2. Predawn shoot water potential (A) and Relative Interaction Index (B) for *Quercus lusitanica* and *Parasarianthes lophantha* in each treatment. Different uppercase or lowercase letters indicate statistically significant differences ($P < 0.05$) among species or between treatments, respectively. Bars represent mean \pm SE.

consistently allocated a higher proportion of biomass to roots than the invasive *P. lophantha*, but this proportional allocation did not respond to changes in water availability or competition for the native species. This is consistent with results from previous studies, in which oak species did not significantly change their proportional investment to root growth under water deprivation (Kubiske & Abrams 1992; Fotelli *et al.* 2000) or competitive environments (Bueno *et al.* 2019).

This one-to-one experiment did not determine a clear competitive winner. Our findings differ from those of other studies with similar leguminous invasive trees which frequently prove better competitors than native tree or shrub species (Witkowski 1991; Peperkorn *et al.* 2005; Morris *et al.* 2011; Kawaletz *et al.* 2013, 2014; Rodríguez-Echeverría *et al.* 2013). However, *P. lophantha* could exert competitive pressure on the native *Q. lusitanica* under field conditions more severe than observed in our study. *P. lophantha* reaches reproductive maturity after only 2 years, when it starts intense reproduction, producing seed every year (Martín Osório *et al.* 2008), whereas the native species is a masting oak that produces fewer propagules, and only in alternate years (Sork 1993; Fernández-Martínez *et al.* 2012). Therefore, *P. lophantha* creates large and persistent seed banks (Herschel 1912; McKenzie *et al.* 1976; McDowell & Moll 1981; Milton & Hall 1981; Bell *et al.* 1995; Rico 2011; Harris *et al.* 2017), a common trait among many closely related genera, such as *Acacia* (*e.g.* Correia *et al.* 2016). The production of abundant small seeds could boost its invasive colonization success (Leishman *et al.* 2000; Pyšek & Richardson 2008). Furthermore, as demonstrated in our experiment, the invasive seedlings emerged faster than the native seedlings, which would allow it to quickly occupy the space and out-compete the native species for light (González-Muñoz *et al.* 2011). This is supported by the fact that *P. lophantha* significantly allocated more biomass to shoots in the presence of competition with *Q. lusitanica*, which suggests that competition may be most significant for aboveground biomass. The leguminous invasive tree can then create a dense canopy that limits the amount of light available to native individuals, changes soil conditions through highly nutritious leaf litter and the association of bacteria with

the roots, so altering the invaded area (Morris *et al.* 2011; Fagúndez 2019; Pugnaire *et al.* 2019). Therefore, under natural conditions, the propagule pressure of *P. lophantha* is highly likely to tip towards the invasive.

Our study provides further support to the 'stress-gradient hypothesis' which states that under high physical stress, competition may be less important (Bertness & Callaway 1994). The stress-related reduction in competitive interactions between *Q. lusitanica* and *P. lophantha* could be explained by the fact that seedlings of both species were smaller than the controls, and water availability was a greater driver of performance of each species than competition *per se*. This highlights the overarching importance of water stress over competition. Furthermore, when experiencing water stress, the native *Q. lusitanica* was the only species to have a significantly lower water potential and higher mortality. These findings have important implications for laying the foundations on where conservation actions on populations of *Q. lusitanica* should be directed in the future. Competitive displacement by invasive *P. lophantha* will not be increased if overall precipitation decreases as is predicted by Global Circulation Models (IPCC 2014). In this sense, conservation actions in the future should be prioritized to counteract the potential risks associated with drier environmental conditions on native oaks.

Our greenhouse pot study focused on one life stage on the interaction between an invasive tree and a vulnerable native species. The establishment and seedling stages are critically important for population dynamics, but we cannot yet infer how this interaction will develop at later life stages (Werner *et al.* 2008; Kawaletz *et al.* 2014). Physiological variables can vary between seedlings and mature trees in some Mediterranean oak species (Mediavilla & Escudero 2004), and our study conditions could not be fully representative of those in nature. Our results, however, show previously unknown mechanisms occurring during the crucially important early establishment of these two species.

Competitive interactions between invasive *P. lophantha* and native *Q. lusitanica* seedlings must not be dismissed but

might be less critical than the effects of drought stress associated with global change. However, it might be necessary to act in the short term to protect the vulnerable, slow-growing native species *Q. lusitanica* against the invasive *P. lophantha* to ensure that the native species has the best possible conditions to face future climate scenarios. Our results provide useful data to make conservation decisions on sensitive native populations when they are in contact with invasive tree species under potential water stress due to global warming.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Linear regressions between seed weight (g) and seedling biomass (g) of *Quercus lusitanica* (left column) and *Paraserianthes lophantha* (right column). The regressions were fitted individually for each treatment.

Figure S2. Cumulative seedling shoot emergence for *Quercus lusitanica* and *Paraserianthes lophantha* expressed as a percentage of the maximum emergence observed at the end of the experiment.

Table S1. Statistical results of General Linear Models with mortality, leaf relative growth rate (RGR), total biomass, root-shoot ratio, Relative Interaction Index, and water potential as dependent variables, and species as categorical explanatory variable. Significant differences ($P < 0.05$) are presented in bold.

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