RESEARCH ARTICLE

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

S. Santamarina[1,2] (iD), D. Montesinos[2,3] (iD), E. Alfaro-Saiz[1,4] (iD) & C. Acedo[1] (iD)

1 Research Team Taxonomy and Biodiversity Conservation TaCoBi, Department of Biodiversity and Environmental Management, University of León, León, Spain
2 Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Coimbra, Portugal
3 Australian Tropical Herbarium, James Cook University, Smithfield, Queensland, Australia
4 Herbarium LEB Jaime Andrés Rodríguez, CRAI Experimental, University of León, León, Spain

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 supressed 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;

Jarnevich & 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; Kawaletz 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 as *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. *Quercuslusitanica* 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 (Manofrígido, 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_ACJ).

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

$$RGR = \left(lnNL_{tf} - lnNL_{t0}\right)/t \qquad (1)$$

where NLt_0 is number of leaves per plant in week 12, NL_{tf} 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:

$$RII = (B_w - B_{0)}/(B_w + B_0) \qquad (2)$$

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 ± 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)	P	odds ratio (95% CI)	P
Q. lusitanica	∞ (3.163–∞)	**<0.001**	1.311 (0.308–5.861)	0.7554
P. lophantha	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.
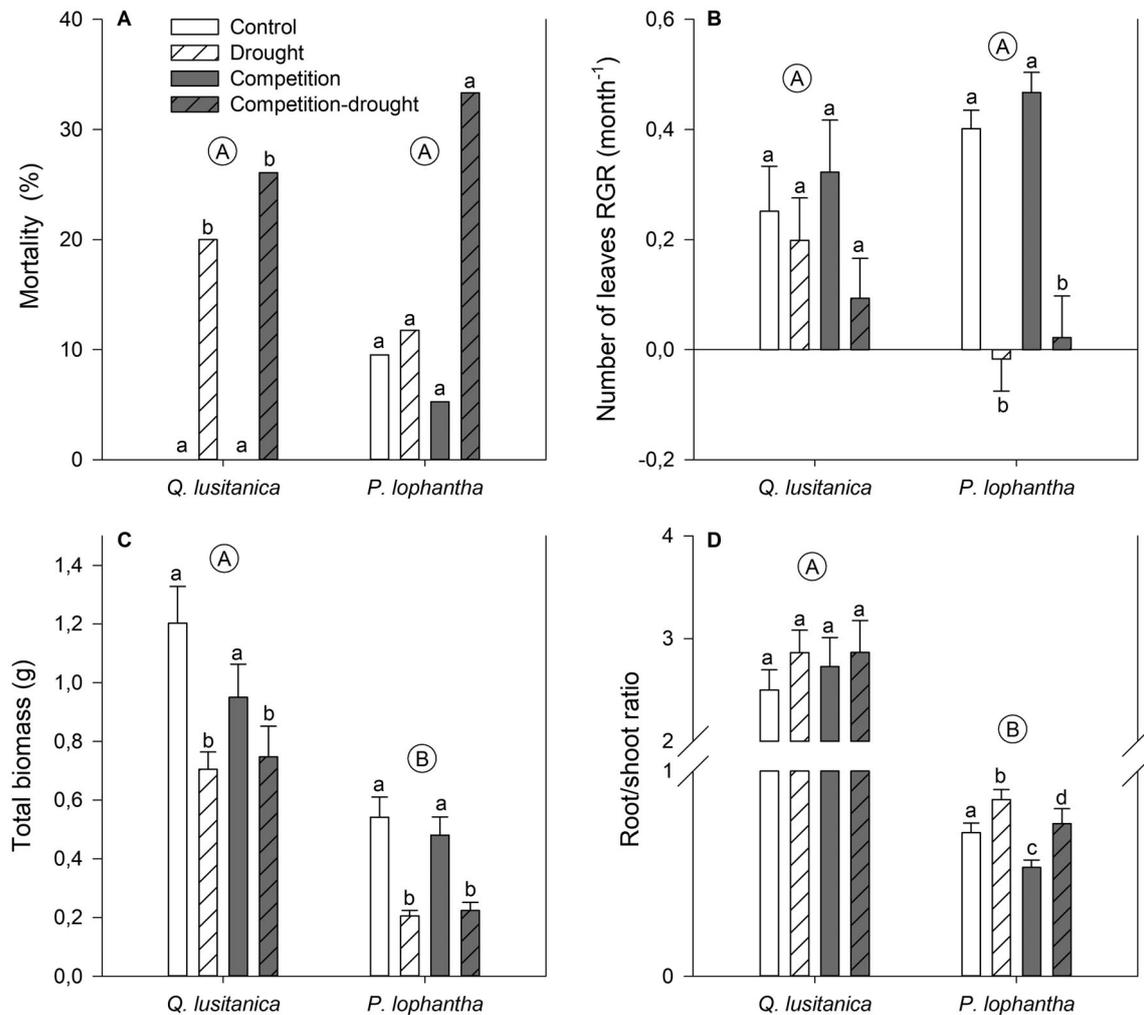
Fig. 1. Mortality (A); leaf RGR (B); total seedling biomass (C); and root/shoot ratio (D) for *Quercus lusitanica* and *Paraserianthes lophantha* in each treatment. Different uppercase or lowercase letters indicate statistically significant differences (*P* < 0.05) among species or between treatments, respectively. Bars represent mean ± 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)	*Q. lusitanica*	Drought + Competition	−1.493	0.141	−0.092	0.927	2.57	40.324
	P. lophantha	Drought + Competition	−8.654	**<0.001**	1.090	0.28	2.63	−19.579
Total biomass	*Q. lusitanica*	Drought + Competition	−3.263	**0.002**	−1.155	0.251	2.78	118.46
	P. lophantha	Drought + Competition	−5.653	**<0.001**	−0.479	0.633	2.61	−13.884
Root/shoot ratio	*Q. lusitanica*	Drought + Competition	1.011	0.315	0.520	0.604	2.78	254.74
	P. lophantha	Drought + Competition	3.696	**<0.001**	−2.896	**0.005**	2.61	−18.541
Relative Interaction Index	*Q. lusitanica*	Drought	2.265	**0.028**			47	0.573
	P. lophantha	Drought	0.995	0.325			43	20.775
Water potential	*Q. lusitanica*	Drought + Competition	2.538	**0.013**	−1.355	0.179	2.84	215.05
	P. lophantha	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*
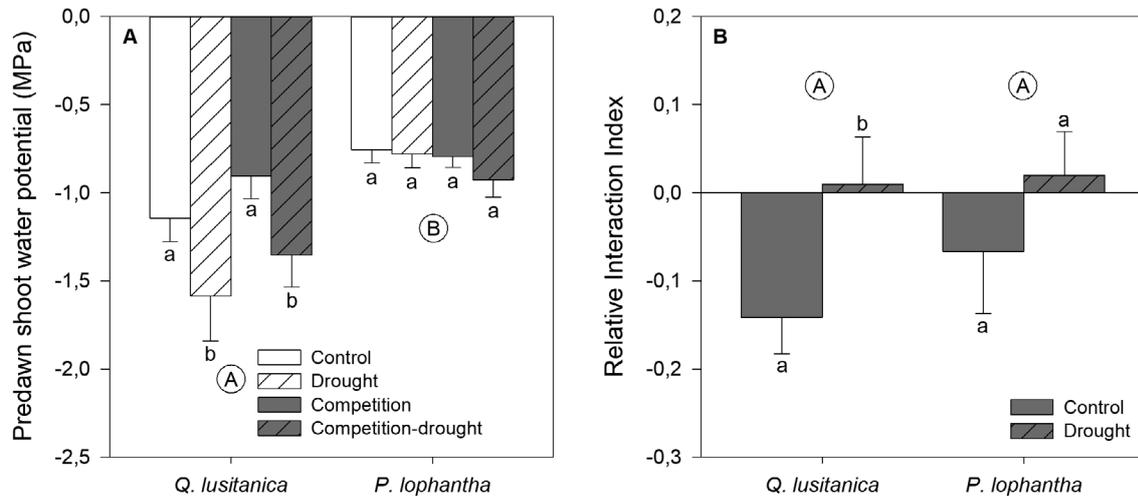
Fig. 2. Predawn shoot water potential (A) and Relative Interaction Index (B) for *Quercus lusitanica* and *Paraserianthes lophantha* in each treatment. Different uppercase or lowercase letters indicate statistically significant differences (P < 0.05) among species or between treatments, respectively. Bars represent mean ± 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.

ACKNOWLEDGEMENTS

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.

REFERENCES

Abbas A.M., Rubio-Casal A.E., De Cires A., Grewell B.J., Castillo J.M. (2019) Differential tolerance of native and invasive tree seedlings from arid African deserts to drought and shade. *South African Journal of Botany*, **123**, 228–240.

Abd El-Gawad A.M., Zotti M., Sarker T.C., Mazzoleni S., Bonanomi G. (2017) Does a plant detect its neighbor if it is kin or stranger? Evidence from a common garden experiment. *Community Ecology*, **18**, 305–310.

Akaike H. (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov B.N., Caski F. (Eds), *Proceedings of the Second International Symposium on Information Theory*. Akademiai Kiado, Budapest, Hungary, pp 267–281.

Amaral Franco J. (1990) Quercus L. In: Castroviejo S., Laínz M., López González G., Montserrat P., Muñoz Garmendia F., Piva J., Villar L. (Eds), *Flora Ibérica. Plantas vasculares de la Península Ibérica e Islas Baleares*. Real Jardín botánico. C.S.I.C, Madrid, Spain, pp 15–36.

Amigo J., Romero Buján M.I. (2018) La comunidad vegetal del carballo enano, Quercus lusitanica Lam. (Fagaceae, Magnoliopsida), en Monte Pindo (A Coruña, Noroeste ibérico) [The dwarf oak plant community, Quercus lusitanica Lam. Fagaceae, Magnoliopsida), in Monte Pindo (A Coruña, Northwest Iberian península)]. *Nova Acta Científica Compostelana (Bioloxía)*, **25**, 9–20.

Aref I.M.I. (1996) *Distribution and ecophysiology of Acacia species in south western zone of Saudi Arabia*. University of Edinburgh, UK.

Aref I.M., El-juhany L.I., Forssk A. (1995) Effects of drought stress on the growth of Acacia asak (Forssk.), A. tortilis (Forssk.) and A. gerrardii (Benth) ssp. negevensis (Zoh.). *Mansura University Journal of Agricultural Sciences*, **24**, 5627–5636.

Armas C., Ordiales R., Pugnaire F.I. (2004) Measuring plant interactions: a new comparative index. *Ecology*, **85**, 2682–2686.

Baider C., Florens F.B.V. (2011) Control of invasive alien weeds averts imminent plant extinction. *Biological Invasions*, **13**, 2641–2646.

Baldocchi D.D., Ma S., Rambal S., Misson L., Ourcival J.M., Limousin J.M., Pereira J., Papale D. (2010) On the differential advantages of evergreenness and deciduousness in mediterranean oak woodlands: a flux perspective. *Ecological Applications*, **20**, 1583–1597.

Barbeta A., Peñuelas J. (2016) Sequence of plant responses to droughts of different timescales: lessons from holm oak (Quercus ilex) forests. *Plant Ecology & Diversity*, **9**, 321–338.

Bell D.T., Rokich D.P., McChesney C.J., Plummer J.A. (1995) Effects of temperature, light and gibberellic acid on the germination of seeds of 43 species native to Western Australia. *Journal of Vegetation Science*, **6**, 797–806.

Bellard C., Jeschke J.M., Leroy B., Mace G.M. (2018) Insights from modeling studies on how climate change affects invasive alien species geography. *Ecology and Evolution*, **8**, 5688–5700.

Bertness M.D., Callaway R. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **5**, 191–193.

Bloom A.J., Chapin F.S., Mooney H.A. (1985) Resource limitation in plants: an economic analogy. *Annual Review of Ecology and Systematics*, **16**, 363–392.

Bonfil C. (1998) The effects of seed size, cotyledon reserves, and herbivory on seedling survival and growth in Quercus rugosa and Q. laurina (Fagaceae). *American Journal of Botany*, **85**, 79–87.

Bonito A., Varone L., Gratani L. (2011) Relationship between acorn size and seedling morphological and physiological traits of Quercus ilex L. from different climates. *Photosynthetica*, **49**, 75–86.

Bottollier-Curtet M., Planty-Tabacchi A.M., Tabacchi E. (2013) Competition between young exotic invasive and native dominant plant species: implications for invasions within riparian areas. *Journal of Vegetation Science*, **24**, 1033–1042.

Bueno A., Pritsch K., Simon J. (2019) Species-specific outcome in the competition for nitrogen between invasive and native tree seedlings. *Frontiers in Plant Science*, **10**, 337.

Bussotti F., Ferrini F., Pollastrini M., Fini A. (2014) The challenge of Mediterranean sclerophyllous vegetation under climate change: from acclimation to adaptation. *Environmental and Experimental Botany*, **103**, 80–98.

Castro M., Freire L., Prunell A. (1989) *Guía das árbores de Galicia: autóctonas e ornamentais*. Edicións Xerais de Galicia, D.L, Vigo, Spain, p 332.

Catford J.A., Bode M., Tilman D. (2018) Introduced species that overcome life history tradeoffs can cause native extinctions. *Nature Communications*, **9**, 2131.

Clemens J., Jones P.G., Gilbert N.H. (1977) Effect of seed treatments on germination in Acacia. *Australian Journal of Botany*, **25**, 269–276.

Correia M., Montesinos D., French K., Rodríguez-Echeverría S. (2016) Evidence for enemy release and increased seed production and size for two invasive Australian acacias. *Journal of Ecology*, **104**, 1391–1399.

Cowan R. (1988) Paraserianthes. In: McCarthy P. M. (Ed), *Flora of Australia Volume 12, Mimosaceae (excl. Acacia), Caesalpiniaceae*. ABRS/CSIRO Australia publishing, Melbourne, Australia, pp 33–36.

Czech B., Krausman P.R., Dobson A., Rodriguez J.P., Roberts W.M., Wilcove D.S. (1997) Distribution and causation of species endangerment in the United States. *Science*, **277**, 1116–1117.

Daehler C.C. (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 183–211.

David T.S., Henriques M.O., Kurz-Besson C., Nunes J., Valente F., Vaz M., Pereira J.S., Siegwolf R., Chaves M.M., Gazarini L.C., David J.S. (2007) Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought. *Tree Physiology*, **27**, 793–803.

Davidson A.M., Jennions M., Nicotra A.B. (2011) Do invasive species show higher phenotypic plasticity than native species and if so, is it adaptive? A meta-analysis. *Ecology Letters*, **14**, 419–431.

DOG. (2011) *DECRETO 167/2011, de 4 de agosto, por el que se modifica el Decreto 88/2007, de 19 de abril, por el que se regula el Catálogo gallego de especies amenazadas y se actualiza dicho catálogo.* Galicia Consellería de Medio Rural, pp. 23110–23113.

Domènech R., Vilà M. (2008) Response of the invader *Cortaderia selloana* and two coexisting natives to competition and water stress. *Biological Invasions*, **10**, 903–912.

Dukes J.S., Mooney H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology & Evolution*, **14**, 135–139.

European Union. (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities*, **206**, 7–50.

Fagúndez J. (2019) Plantas exóticas invasoras en Galicia. Doce años de avances en el conocimiento. In: Ramil-Rego P., Vales C. (Eds), *Especies Exóticas Invasoras: situación e propostas de mitigación, BADER: Mon.* Monografías do Ibader, Serie Biodiversidade, Lugo, pp 62–63.

Fernández-Martínez M., Belmonte J., Maria E.J. (2012) Masting in oaks: disentangling the effect of flowering phenology, airborne pollen load and drought. *Acta Oecologica*, **43**, 51–59.

Filazzola A., Liczner A.R., Westphal M., Lortie C.J. (2018) The effect of consumer pressure and abiotic stress on positive plant interactions are mediated by extreme climatic events. *New Phytologist*, **217**, 140–150.

Fisher R.A. (1956) *Statistical methods and scientific inference.* Hafner Publishing, New York, USA.

Forner A., Valladares R.F., Aranda I. (2018) Mediterranean trees coping with severe drought: avoidance might not be safe. *Environmental and Experimental Botany*, **155**, 529–540.

Forster M.A., Dalrymple R.L., Bonser S.P. (2016) A low watering treatment alters biomass allocation and growth rate but not heteroblastic development in an *Acacia* species. *Trees*, **30**, 2051–2059.

Fotelli M.N., Radoglou K.M., Constantinidou H. (2000) Water stress responses of seedlings of four Mediterranean oak species. *Tree Physiology*, **20**, 1065–1075.

Funk J.L. (2013) The physiology of invasive plants in low-resource environments. *Conservation Physiology*, **1**(1), cot026. https://doi.org/10.1093/conphys/cot026

Galiano L., Martínez-Vilalta J., Sabaté S., Lloret F. (2012) Determinants of drought effects on crown condition and their relationship with depletion of carbon reserves in a Mediterranean holm oak forest. *Tree Physiology*, **32**, 478–489.

Gallardo B., Aldridge D.C., González-Moreno P., Pergl J., Pizarro M., Pyšek P., Thuiller W., Yesson C., Vilà M. (2017) Protected areas offer refuge from invasive species spreading under climate change. *Global Change Biology*, **23**, 5331–5343.

GBIF.org. (2021) GBIF occurrence download. https://doi.org/10.15468/dl.d3f29w (accessed 26 November 2021).

Gentilesca T., Camarero J.J., Colangelo M., Nolè A., Ripullone F. (2017) Drought-induced oak decline in the western mediterranean region: an overview on current evidence, mechanisms and management options to improve forest resilience. iForest. *Biogeosciences and Forestry*, **10**, 796–806.

Goldberg D.E., Landa K. (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology*, **79**, 1013–1030.

Goldberg D.E., Rajaniemi T., Gurevitch J., Stewart-Oaten A. (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, **80**, 1118–1131.

González-Muñoz N., Castro-Díez P., Fierro-Brunnenmeister N. (2011) Establishment success of coexisting native and exotic trees under an experimental gradient of irradiance and soil moisture. *Environmental Management*, **48**, 764–773.

Grace J.B. (1995) On the measurement of plant competition intensity. *Ecology*, **76**, 305–308.

Grime P. (2012) *Plant strategies, vegetation processes, and ecosystem properties.* John Wiley & Sons, Chichester, UK.

Grotkopp E., Rejmánek M. (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *American Journal of Botany*, **94**, 526–532.

Harris C.J., Manea A., Moles A.T., Murray B.R., Leishman M.R. (2017) Differences in life-cycle stage components between native and introduced ranges of five woody Fabaceae species. *Austral Ecology*, **42**, 404–413.

Hellmann J.J., Byers J.E., Bierwagen B.G., Dukes J.S. (2008) Five potential consequences of climate change for invasive species. *Conservation Biology*, **22**, 534–543.

Herschel W. (1912) *Longevity of seeds. Bulletin of miscellaneous information*, Kew, **2**, p. 110.

Hughes L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution*, **15**, 56–61.

Hunt R. (1990) *Basic growth analysis. Plant growth analysis for beginners.* Unwin Hyman, London, UK.

Hyatt L.A. (2008) Does seedling ecology matter for biological invasions? In: Allessio Leck M., Thomas Parker V., Simpson R.L. (Eds), *Seedling ecology and evolution.* Cambridge University Press, Cambridge, UK, pp 295–306.

IPCC. (2014) *Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* IPCC, Geneva, Switzerland.

Jarnevich C.S., Stohlgren T.J. (2009) Near term climate projections for invasive species distributions. *Biological Invasions*, **11**, 1373–1379.

Jeschke J.M., Strayer D.L. (2008) Usefulness of bioclimatic models for studying climate change and invasive species. *Annals of the New York Academy of Sciences*, **1134**, 1–24.

Kawaletz H., Molder I., Zerbe S., Annighofer P., Terwei A., Ammer C. (2013) Exotic tree seedlings are much more competitive than natives but show underyielding when growing together. *Journal of Plant Ecology*, **6**, 305–315.

Kawaletz H., Mölder I., Annighöfer P., Terwei A., Zerbe S., Ammer C. (2014) Back to the roots: how do seedlings of native tree species react to the competition by exotic species? *Annals of Forest Science*, **71**, 337–347.

Kormanik P.P., Sung S.S., Kormanik T.L., Schlarbaum S.E., Zarnoch S.J. (1998) Effect of acorn size on development of northern red oak 1–0 seedlings. *Canadian Journal of Forest Research*, **28**, 1805–1813.

Kubiske M.E., Abrams M.D. (1992) Photosynthesis, water relations, and leaf morphology of xeric versus mesic *Quercus rubra* ecotypes in central Pennsylvania in relation to moisture stress. *Canadian Journal of Forest Research*, **22**, 1402–1407.

Kuebbing S.E., Nuñez M.A. (2016) Invasive non-native plants have a greater effect on neighbouring natives than other non-natives. *Nature Plants*, 16134.

Le Maitre D.C., Gaertner M., Marchante E., Ens E.J., Holmes P.M., Pauchard A., O'Farrell P.J., Rogers A.M., Blanchard R., Blignaut J., Richardson D.M. (2011) Impacts of invasive Australian acacias: implications for management and restoration. *Diversity and Distributions*, **17**, 1015–1029.

Leishman M.R., Wright I., Moles A., Westoby M. (2000) The evolutionary ecology of seed size. In: Fenner M. (Ed), *Seeds: the ecology of regeneration in plant communities*, 2nd edn. CABI Publishing, Wallingford, UK.

Leiva M.J., Fernández-Alés R. (1998) Variability in seedling water status during drought within a *Quercus ilex* subsp. *ballota* population, and its relation to seedling morphology. *Forest Ecology and Management*, **111**, 147–156.

Liu Y., Oduor A.M.O., Zhang Z., Manea A., Tooth I.M., Leishman M.R., Xu X., van Kleunen M. (2017) Do invasive alien plants benefit more from global environmental change than native plants? *Global Change Biology*, **23**, 3363–3370.

Llamas F., Lence C., Acedo C. (2003) Una nueva nothoespecie de *Quercus* L. (Fagaceae) en el NO de España. *Lagascalia*, **23**, 85–90.

Lloret F., Siscart D., Dalmases C. (2004) Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology*, **10**, 2092–2099.

Mainka S.A., Howard G.W. (2010) Climate change and invasive species: double jeopardy. *Integrative Zoology*, **5**, 102–111.

Martín Osório V., Wildpret de la Torre W., Jardim R., Silva L. (2008) *Paraserianthes lophantha* (Willd.) I.C. Nielsen. In: Silva L., Ojeda L., Elizabeth Rodríguez Luengo J. L. (Eds), *Flora e Fauna Terrestre Invasora na Macaronésia. TOP 100 nos Açores, Madeira e Canárias.* ARENA, Ponta Delgada, pp 285–287.

McDowell C.R., Moll E.J. (1981) Studies of seed germination and seedling competition in *Virgilia oroboides* (Berg.) Salter, *Albizia lophantha* (Willd.) Benth. and *Acacia longifolia* (Andr.) Willd. *Journal of South African Botany*, **47**, 653–685.

McKenzie B., Moll E.J., Campbell B.M. (1976) A suggested management plan for the indigenous vegetation of orange kloof, table mountain, based on a phytosociological survey. *South African Forestry Journal*, **99**, 1–6.

Mediavilla S., Escudero A. (2004) Stomatal responses to drought of mature trees and seedlings of two co-occurring Mediterranean oaks. *Forest Ecology and Management*, **187**, 281–294.

Milton S.J., Hall A.V. (1981) Reproductive biology of Australian acacias in the south-western cape province, South Africa. *Transactions of the Royal Society of South Africa*, **44**, 465–487.

Montesinos D. (2021) Fast invasives fastly become faster: invasive plants align largely with the fast side of the plant economics spectrum. *Journal of Ecology*, 1–5.

Morris T.L., Esler K.J., Barger N.N., Jacobs S.M., Cramer M.D. (2011) Ecophysiological traits associated with the competitive ability of invasive Australian acacias. *Diversity and Distributions*, **17**, 898–910.

Munné-Bosch S., Alegre L. (2004) Die and let live: Leaf senescence contributes to plant survival under drought stress. *Functional Plant Biology*, **31**, 203–216.

Navarro F.B., Jiménez M.N., Ripoll M.Á., Fernández-Ondoño E., Gallego E., De Simón E. (2006) Direct sowing of holm oak acorns: effects of acorn size and soil treatment. *Annals of Forest Science*, **63**, 961–967.

Osonubi O., Bakare O.N., Mulongoy K. (1992) Interactions between drought stress and vesicular-arbuscular mycorrhiza on the growth of *Faidherbia albida* (syn. *Acacia albida*) and *Acacia nilotica* in sterile and non-sterile soils. *Biology and Fertility of Soils*, **14**, 159–165.

Otieno D.O., Schmidt M.W.T., Adiku S., Tenhunen J. (2005) Physiological and morphological responses to water stress in two *Acacia* species from contrasting habitats. *Tree Physiology*, **25**, 361–371.

Peguero-Pina J.J., Vilagrosa A., Alonso-Forn D., Ferrio J.P., Sancho-Knapik D., Gil-Pelegrín E. (2020) Living in drylands: functional adaptations of trees and shrubs to cope with high temperatures and water scarcity. *Forests*, **11**, 1028.

Peperkorn R., Werner C., Beyschlag W. (2005) Phenotypic plasticity of an invasive acacia versus two native Mediterranean species. *Functional Plant Biology*, **32**, 933–944.

Pugnaire F.I., Morillo J.A., Peñuelas J., Reich P.B., Bardgett R.D., Gaxiola A., Wardle D.A., van der Putten W.H. (2019) Climate change effects on plant–soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. *Science Advances*, **5**(11).

Pyšek P., Richardson D.M. (2008) Traits associated with invasiveness in alien plants: where do we stand? (W. Nentwig, Ed.). *Biological Invasions Ecological Studies (Analysis and Synthesis)*, **193**, 97–125.

Qi Y., Wei W., Chen C., Chen L. (2019) Plant root–shoot biomass allocation over diverse biomes: a global synthesis. *Global Ecology and Conservation*, **18**, e00606.

R Core Team. (2019) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramírez-Valiente J.A., López R., Hipp A.L., Aranda I. (2020) Correlated evolution of morphology, gas exchange, growth rates and hydraulics as a response to precipitation and temperature regimes in oaks (*Quercus*). *New Phytologist*, **227**, 794–809.

Ramírez-Valiente J.A., Valladares F., Gil L., Aranda I. (2009) Population differences in juvenile survival under increasing drought are mediated by seed size in cork oak (*Quercus suber* L.). *Forest Ecology and Management*, **257**, 1676–1683.

Randall R.P. (Ed). (2017) *A global compendium of weeds*, 3rd edn. National Library of Australia, Perth, Australia.

Rico E. (2011) Primeros indicios de asilvestramiento de *Paraserianthes lophantha (*Willd.) I.C. Nielsen en Asturias. I. In: Fernández P.J., Vázquez V.M., Bueno Sánchez Á., Cires Rodríguez E., Nava Fernández H.S. (Eds), *Chorological, systematics and nomenclatural notes for the Vascular Plants Catalogue of the Principality of Asturias*. Bol. Cien. Nat. R.I.D.E.A, pp 75–76.

Rodríguez-Echeverría S., Afonso C., Correia M., Lorenzo P., Roiloa S.R. (2013) The effect of soil legacy on competition and invasion by *Acacia dealbata* Link. *Plant Ecology*, **214**, 1139–1146.

Rose S., Poorter L. (2000) The importance of seed mass for early regeneration in tropical forest: a review. In: ter Steege H. (Ed), *Long-term changes in tropical tree diversity: studies from the Guiana Shield, Africa, Borneo and Melanesia*. Wageningen, Tropenbos, pp 19–35.

Santamarina S., Alfaro-Saiz E., Llamas F., Acedo C. (2019) Different approaches to assess the local invasion risk on a threatened species: opportunities of using high-resolution species distribution models by selecting the optimal model complexity. *Global Ecology and Conservation*, **20**.

Sardans J., Peñuelas J. (2013) Plant–soil interactions in Mediterranean forest and shrublands: impacts of climatic change. *Plant and Soil*, **365**, 1–33.

Scheiner S., Gurevitch J. (Eds). (2001) *Design and analysis of ecological experiments*. Oxford University Press, Oxford, UK.

Seiwa K. (2000) Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints. *Oecologia*, **123**, 208–215.

Sork V.L. (1993) Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp.). *Vegetatio*, **107–108**, 133–147.

Ulrich E., Perkins L. (2014) *Bromus inermis* and *Elymus canadensis* but not *Poa pratensis* demonstrate strong competitive effects and all benefit from priority. *Plant Ecology*, **215**, 1269–1275.

Valladares F., Bastias C.C., Godoy O., Granda E., Escudero A. (2015) Species coexistence in a changing world. *Frontiers in Plant Science*, **6**, 866.

Valliere J.M., Escobedo E.B., Bucciarelli G.M., Sharifi M.R., Rundel P.W. (2019) Invasive annuals respond more negatively to drought than native species. *New Phytologist*, **223**, 1647–1656.

Verlinden M., van Kerkhove A., Nijs I. (2013) Effects of experimental climate warming and associated soil drought on the competition between three highly invasive West European alien plant species and native counterparts. *Plant Ecology*, **214**, 243–254.

Vilà M., Corbin J.D., Dukes J.S., Pino J., Smith S.D. (2007) Linking plant invasions to global environmental change. In: Canadell J.G., Pataki D.E., Pitelka L.F. (Eds), *Terrestrial ecosystems in a changing world. Global Changue—The IGBP series*. Springer, Berlin, Germany, pp 93–102.

Vilà M., Weiner J. (2004) Are invasive plant species better competitors than native plant species?—evidence from pair-wise experiments. *Oikos*, **105**, 229–238.

Violle C., Garnier E., Lecoeur J., Roumet C., Podeur C., Blanchard A., Navas M.L. (2009) Competition, traits and resource depletion in plant communities. *Oecologia*, **160**, 747–755.

Weigelt A., Jolliffe P. (2003) Indices of plant competition. *Journal of Ecology*, **91**, 707–720.

Werner C., Peperkorn R., Máguas C., Beyschlag W. (2008) Competitive balance between the alien invasive *Acacia longifolia* and native Mediterranean species. In: Tokarska-Guzik B., Brock J., Brundu G., Child L., Daehler C., Pyšek P. (Eds), *Plant invasions: human perception, ecological impacts and management*. Backhuys Publishers, Leiden, The Netherlands, pp 261–275.

Wickham H. (2011) The split-apply-combine strategy for data analysis. *Journal of Statistical Software*, **40**, 1–29.

Wickham H. (2016) *ggplot2: elegant graphics for data analysis*. Springer, New York, USA.

Wilcove D.S., Rothstein D., Dubow J., Phillips A., Losos E. (1998) Quantifying threats to imperilled species in the United States: assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease. *BioScience*, **48**, 607–615.

Witkowski E.T.F. (1991) Growth and competition between seedlings of *Protea repens* (L.) L. and the alien invasive, *Acacia saligna* (Labill.) Wendl. in relation to nutrient availability. *Functional Ecology*, **5**, 101.

Zavala M.A., Espelta J.M., Retana J. (2000) Constraints and trade-offs in Mediterranean plant communities: the case of holm oak–Aleppo pine forests. *Botanical Review*, **66**, 119–149.

Zolfaghari R., Fayyaz P., Nazari M., Valladares F. (2013) Interactive effects of seed size and drought stress on growth and allocation of *Quercus brantii* Lindl. seedlings from two provenances. *Turkish Journal of Agriculture and Forestry*, **37**, 361–368.