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Interacting water, nutrients, and shrub age control steppe grass-on-shrub competition: Implications for restoration

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Abstract

Understanding the factors that control grass–shrub interactions and coexistence is critical to the design of dryland management and restoration strategies. Using *Stipa tenacissima* tussocks as adult neighbor and *Olea europaea* var. *sylvestris* as target woody species, we performed a 5-year-long, large-scale manipulative experiment to investigate the independent and combined effects of water and nutrient availability, and the modulating effects of *O. europaea* ontogeny on the net outcome of grass–shrub interaction. At two contrasting dryland sites, we conducted experimental plantings of *Olea* seedlings on two microsites: contiguous to a *Stipa* tussock (*Stipa* microsite) and on the inter-tussock bare-soil areas (Open microsite), and manipulated resource availability by combining nutrient and water addition. The experiment followed a full factorial design, with all treatment combinations applied at each site. We monitored survival, height, and stem basal diameter of *Olea* individuals over a study period of 5 years. All across the wide range of conditions considered, negative effects of *Stipa* on *Olea* largely prevailed during the first 2 years after the plantation. We found that competition was stronger in the drier steppe, where extra inputs of water favored neutral interactions. Conversely, nutrient addition increased competition strength, particularly when combined with water inputs, pointing to the contrasting role of different resources and the importance of interactions between them in the control of plant–plant interaction outcome. The competition effects of *Stipa* faded with time and gradually shifted to neutral interaction as *Olea* individuals aged. Our results are particularly relevant to guide restoration efforts in formerly wooded xeric grasslands and rangelands.

KEYWORDS
drylands, grass–shrub competition, *Olea europaea* var. *sylvestris*, plant–plant interactions, *Stipa tenacissima*

INTRODUCTION

Plant–plant interactions are determinants of the spatial structure, diversity, and dynamics of plant communities (Bazzaz, 1990; Cavieres & Badano, 2009; Goldberg & Barton, 1992; Stoll & Bergius, 2005; Tilman, 1982), and hence a critical factor to be considered in managing natural ecosystems, rangelands, and farmlands (Brooker et al., 2008; Gómez-Aparicio et al., 2004; Pyke & Archer, 1991; Sweeney et al., 2002). Understanding the factors and species attributes that modulate plant interactions is valuable in predicting the consequences of environmental changes in plant communities and designing the most appropriate conservation, adaptation, and restoration measures (Tylianakis et al., 2008). In the particular case of drylands, the understanding of grass–shrub interactions and coexistence is critical to the design of land management and restoration strategies (Cipriotti et al., 2014).

The coexistence of woody plants and grasses that characterizes many drylands worldwide is thought to depend on disturbances, water availability, and nutrient availability (Sankaran et al., 2004), with all these factors having the potential to control the outcome of grass–shrub interactions (Scholes & Archer, 1997; Soliveres et al., 2011; Verwijmeren et al., 2014). Depending on the degree of rooting depth overlap, dryland shrubs and grasses may compete more or less intensely for belowground resources (Cipriotti et al., 2014; Knoop & Walker, 1985; Ward et al., 2013), but this competition may be offset by a variety of facilitative effects, such as microhabitat amelioration or protection from herbivory, resulting in a net positive interaction outcome (Holzaptel & Mahall, 1999; Maestre et al., 2003). Supporting the stress-gradient hypothesis (Bertness & Callaway, 1994), many studies found that positive interactions increased in frequency or strength with increasing stress (He et al., 2013), yet facilitation could collapse or fade in extreme environmental conditions (de Bello et al., 2011; Michalet et al., 2014; Verwijmeren et al., 2019). However, when the stress gradient is driven by a resource, there is empirical support for both increasing and decreasing net facilitation between shrubs and grasses with increasing environmental stress (Holzaptel et al., 2006; Maestre et al., 2003; Zhang, Zhao, et al., 2018). Most previous studies that analyzed resource-availability effects on the sign and strength of grass–shrub and shrub–grass interactions in drylands were based on natural gradients (e.g., aridity and fertility gradients), along which many other factors (also physical stress) may vary and exhibit confounding or interacting effects. Furthermore, a lumped or additive effect of the availability of various types of resources, such as water and nutrients, is often implicit in the resource gradient considered (e.g., Armas et al., 2011; Moustakas et al., 2013). It can be expected, however, that the differential use of different

essential resources by neighbor plants influences the outcome of their interaction (Tilman, 1982). Surprisingly, the experimental assessment of both the independent and joint effects of the availability of several essential soil resources on grass–shrub interactions, and on plant interactions in general, is scarce, yet findings so far suggest that the response of the plant interactions may not be consistent for the various resources considered (e.g., le Bagousse-Pinguet et al., 2013; Wilberts et al., 2014; Zhang, Lü, et al., 2018), even for different sources of nitrogen (Trinder et al., 2012).

In combination with abiotic factors, plant interactions can also be modulated by a variety of biotic attributes such as the functional group, competitive ability, phylogenetic distance, and niche difference of the interacting species (Graff & Aguiar, 2017; Maestre et al., 2005; Mayfield & Levine, 2010; Morcillo et al., 2019), which may in turn contribute to a relevant role of species identity (Weigelt et al., 2002). Furthermore, the relative importance of the mechanisms involved in herbaceous–woody plant interactions often changes as plants age, resulting in ontogeny-mediated shifts in the outcome of the interactions, which in turn may vary in response to variations in abiotic conditions (le Roux et al., 2013; Soliveres et al., 2010). Overall, a growing body of literature points to the interplay between multiple factors regulating grass–shrub coexistence and interactions, yet there are still very few insights about the relative role and combined effects of the factors involved (Cipriotti et al., 2014; le Roux et al., 2013; Soliveres et al., 2015; Zhang, Lü, et al., 2018). The understanding of such interplay remains very limited, hampering our ability to predict the response of herbaceous–woody assemblages to changing climatic and disturbance regimes, and incorporate this knowledge into land management and restoration actions. Moreover, while a great deal of research has focused on the effects of woody plants on the subcanopy herbaceous vegetation (Belsky et al., 1989; Dohn et al., 2013; Holzaptel et al., 2006), very few studies have investigated the impacts of grasses on woody plants (Maestre et al., 2001, 2003; Sala et al., 1989).

In this paper, we investigated the interplay between water and nutrient availability and plant ontogeny in shaping the outcome of grass–shrub interaction in drylands. We focused our study on alpha-grass steppes, which are widely distributed in the western Mediterranean basin. Alpha-grass (*Stipa tenacissima* L.) is a perennial tussock grass that naturally co-occurs with shrubs and small trees. However, the removal of woody plants to favor the expansion of alpha-grass for fiber cropping, combined with grazing and repeated burning (le Houérou, 2001), resulted in vast areas of low-diversity, degraded steppe communities. Maestre et al. (2001) demonstrated for the first time the potential of using facilitation by grasses (*Stipa* tussocks) to re-establish shrubs on semiarid degraded steppes, and several further

studies supported the facilitating role of *S. tenacissima* in the establishment of woody species (e.g., García-Fayos & Gasque, 2002; Navarro et al., 2008). However, *S. tenacissima* can also be a strong competitor of neighbor plants (Maestre et al., 2003; Soliveres et al., 2011), and when facilitation prevails, it is mostly due to the positive effect of shade (Maestre et al., 2003). Alpha-grass steppes offer a well-studied model system with a critical mass of knowledge on plant–plant interactions to move forward and further investigate interactions between controlling factors.

Using *S. tenacissima* L. as adult neighbor and *Olea europaea* var. *sylvestris* (Mill.) Brot. as target species, we performed a 5-year-long, large-scale manipulative experiment to investigate (1) the independent and combined effects of water and nutrient availability on the net outcome of the interaction between *S. tenacissima* tussocks and *O. europaea* saplings, and (2) the modulating effects of *O. europaea* ontogeny on such interaction. Also, by reviewing previous works that considered *S. tenacissima* as neighbor plant, we comparatively evaluated the role played by the target interacting species in the outcome of the interaction with *S. tenacissima*.

METHODS

Study area

We conducted the experiment at two sites in southeastern Spain: Crevillent (38°14′37″ N, 0°52′16″ W, 160° aspect, 12° slope, 460 m above sea level) and Petrer (38°28′2″ N, 0°40′42″ W, 190° aspect, 15° slope, 495 m above sea level), 30 km apart from each other. Climate is Mediterranean semiarid, characterized by high intra- and interannual variability in precipitation and an intense summer drought. Mean annual precipitation (long term, 1999–2020, records at the nearest weather stations) is slightly lower in Crevillent (274 mm, 38°15′20″ N, 0°50′7″ W) than in Petrer (289 mm, 38°26′16″ N, 0°38′25″ W), yet on-site records showed that total rainfall over the study period (2009–2014) was much lower in Crevillent than in Petrer (1005 vs. 1868 mm, respectively), with both sites experiencing a severe drought during 2014. In both sites, soils are sandy loam-textured, developed over marl, and limestone colluvium. Organic matter, total nitrogen, and available phosphorous in the 0- to 10-cm mineral soil are lower in Crevillent (1.67% ± 0.49% OM, 0.13% ± 0.02% total N, and 4.6 ± 1.2 ppm P; mean ± SE) than in Petrer (4.36% ± 0.48% OM, 0.22% ± 0.03% total N, 13.6 ± 1.2 ppm P). Vegetation is dominated by *S. tenacissima* (synonym: *Macrochloa tenacissima* [Loefl. ex L.] Kunth), with other perennial grasses, such as *Brachypodium retusum* (Pers.) Beauv.,

and small shrubs and chamaephytes such as *Globularia alypum* L., *Thymus vulgaris* L., and several species of the genus *Helianthemum*, as accompanying species at both sites. Vegetation is distributed in patches, mainly *Stipa* tussocks, in a matrix of bare ground, with slightly higher and denser patches in Crevillent (51% patch cover, 122 cm average tussock width) than in Petrer (40% patch cover, 105 cm average tussock width). The target woody species, *O. europaea* var. *sylvestris*, is an emblematic Mediterranean broad-leaved sclerophyll tree, which can be found on many varied geopedological substrates and in a wide range of environments from arid maquis to subtropical fog forests, yet the species exhibits its full potential in the most xeric areas of the biogeographic region (Gianguzzi & Bazan, 2019). This species contributes to the woody component of healthy steppes together with other tall shrubs and trees such as *Pistacia lentiscus* L., *Quercus coccifera* L., *Rhamnus lycioides* L., and *Pinus halepensis* Mill., and a variety of shrubs and subshrubs.

Experimental design and measurements

To evaluate the interaction between *S. tenacissima* (adult neighbor, hereafter *Stipa*) and *O. europaea* var. *sylvestris* (target species, hereafter *Olea*), we conducted experimental plantings of *Olea* seedlings on two microsites: *Stipa*, located upslope and contiguous to a *Stipa* tussock, and Open, located in the intertussock bare-soil areas. We manipulated resource availability by combining two treatments: nutrient (N) and water (W) addition, resulting in four resource combinations: control (N^-W^-); nutrient addition (N^+W^-); water addition (N^-W^+); and nutrient and water addition (N^+W^+). The experiment followed a full factorial design, with all treatment combinations applied at each site.

The *Olea* seedlings used in the plantation were grown for 9 months in a nearby forestry nursery (Viver Lopez, S. L, Alicante, Spain). On average, at the planting time, height and basal stem diameter of *Olea* seedlings were 44.5 ± 2.0 cm and 6.0 ± 0.2 mm, respectively. Before planting, we selected 200 *Stipa* and 200 Open planting points per site. For the *Stipa* sampling points, we systematically selected isolated individual *Stipa* tussocks of medium size (ranging between 50 and 120 cm in canopy diameter) available in a relatively homogeneous steppe area from each site. For the Open planting points, we selected the central point of intertussock bare-soil areas. Each *Stipa* microsite was located at a maximum distance of 15 cm from the upslope side of an individual *Stipa* tussock, while each Open microsite was located at a minimum distance of 60 cm from the nearest *Stipa* tussock. The root mass of *S. tenacissima* tussocks is known to be about one order of magnitude lower in bare-soil areas

between the tussocks than in the soil at the edge of the tussocks (Armas & Pugnaire, 2011), supporting the use of Open and *Stipa* microsites to test the competition effect of *Stipa* tussocks on the species of interest. We then randomly distributed 50 planting points for each combination of resource treatments, microsite and site. Planting holes ($40 \times 40 \times 40$ cm^3 in size) were prepared using a Retro Kaiser (S1 4×4 Cross), with a resulting density of 500 holes per hectare. The nutrient-addition treatment was implemented few days before planting by adding 0.6 kg (fresh weight) of biosolid (composted sludge) to the soil in the planting hole, which increased 0.84% in organic matter, 0.03% in total nitrogen, and 31.8 ppm in available phosphorus at Crevillent site, and 0.88% in organic matter, 0.01% in total nitrogen, and 15.4 ppm in available phosphorus at the Petrer site. Compared with the natural nutrient availability at the experimental sites, the biosolids fertilization treatment particularly increased available phosphorus, which tends to be the most limiting nutrient in semiarid calcareous soils (Sardans et al., 2004). The water-addition treatment was implemented by eight pulses of deep irrigation (1.5 L each time), applied to the planting points in critical periods, such as before and after the summer, during the first 3 years after the plantation (four applications in 2009, two in 2010, and two in 2011). Before planting, we installed one PVC tube per planting hole for those points selected to receive water inputs (N^-W^+ and N^+W^+ treatments). The tubes were installed connecting the bottom of the planting hole (40 cm depth) and the surface, allowing irrigation directly on the seedling root area by pouring water through the surface opening. We planted the seedlings in late winter (March 2009) and monitored the experiments for 5 years.

Few days after planting, we installed vertical moisture probes at 0- to 25-cm soil depth, in 9 randomly selected planting holes per treatment and microsite. We monitored soil moisture at 8- to 10-week intervals between April 2009 and March 2011 using time-domain reflectometry (TDR; Topp & Davis, 1985) with the Campbell TDR100 (Campbell Scientific, Edmonton, AB, Canada) equipment. We assessed the performance dynamics of *Olea* individuals by monitoring survival, plant height, and stem basal diameter (SBD) on all the individuals planted over a study period of 5 years. Height and SBD relative growth rates for the seedling establishment (first 2 years), post-establishment (last 3 years), and whole (5 years) growth periods were calculated as: (Ln X_{final} − Ln $X_{initial}$)/($t_{final} − t_{initial}$), where X_{final} and $X_{initial}$ are the respective height and SBD final and initial values, and t is time (years). We estimated the intensity of the interaction of *Olea* with *Stipa* for different *Olea* age values using the relative interaction index (RII; Armas et al., 2004) on survival and SBD relative growth rate. Since *Olea* individuals growing on

Open and *Stipa* microsites were not paired, we estimated RII from the average values of SBD relative growth rate and from the overall survival percentage of *Olea* seedlings per resource-addition treatment. Thus, for each level of the resource-addition treatment and ages of interest, RII on each performance variable was calculated as: RII = ($X_{Stipa} − X_{Open}$)/($X_{Stipa} + X_{Open}$), where X_{Open} and X_{Stipa} represent the overall performance of *Olea* individuals on Open microsites and *Stipa* microsites, respectively. Negative values for RII indicate the prevalence of competition, and positive values, the prevalence of facilitation; values close to zero indicate a neutral outcome.

Data analyses

Treatment effects were analyzed using the generalized linear model (binomial family) on *Olea* survival data and linear model (ANOVA) on *Olea* growth data and average soil moisture data, considering three fixed factors: microsite (M), nutrient addition (N), and water addition (W), in a full factorial design. These analyses were performed using R (R Core Team, 2017). Data on soil moisture dynamics were analyzed using a repeated-measures ANOVA, with M as a between-subjects factor and time as a within-subject factor, performed with SPSS v.17.0 statistical software package (SPSS, Chicago, IL). Homogeneity of variances was tested using Levene's test, and data of heteroskedastic variables were transformed by logarithm. All the analyses were performed separately for each experimental site.

RESULTS

Soil moisture

Soil moisture at the drier site, Crevillent, was higher for the Open than for the *Stipa* microsite, while between-microsite differences in soil moisture in the wetter site, Petrer, were not significant (Appendix S1: Figure S1 and Table S1). Neither nutrient (N) nor water (W) addition showed any significant effect on soil moisture average for any of the two experimental sites, yet there were significant interactions between microsite (M) and W, and between M, W, and N in Petrer, and a trend toward lower soil moisture for N^+W^+ compared with N^-W^+ in Crevillent (Appendix S1: Figure S2 and Table S2).

Plant survival

Five years after seedling plantation, survival of *Olea* individuals was much lower in Crevillent (ranging from 18%

to 65%) than in Petrer (ranging from 71% to 96%). Survival decreased during the first 9 months after the plantation and then remained almost constant for more than 3 years, decreasing again during the last year of the study period under the influence of an extreme and long drought. At both sites, *Olea* survival was higher for the Open microsite, yet differences between microsites were much higher in Crevillent. Water addition increased *Olea* survival in Crevillent, and marginally at the Petrer site, while nutrient addition did not show any significant effect on survival (Figure 1; Table 1). The RII for *Olea* survival indicated a net competition effect of *Stipa* on *Olea*, particularly in Crevillent, that was more intense for treatment combinations including nutrient addition (N$^+$). The treatments with the highest competition effect were N$^+$W$^+$ in Crevillent and N$^+$W$^-$ in Petrer.

Plant growth

Five years after planting, SBD of *Olea* individuals growing on the Open microsite ranged from 7.9 ± 0.3 mm for N$^-$W$^-$ in Crevillent to 18.0 ± 0.7 mm for N$^+$W$^+$ in Petrer. This performance gradient in response to site conditions and resource-input treatments was less clear for plant height, which ranged from 23.4 ± 2.3 mm for N$^-$W$^+$ in Crevillent to 56.0 ± 3.4 cm for N$^+$W$^-$ in Petrer (Appendix S2: Figures S1 and S2). Overall, both SBD and height relative growth of *Olea* individuals were lower in Crevillent than in Petrer (Figures 2 and 3), with height growth for the whole study period being null or negative in Crevillent. Height and SBD growth were significantly lower for the *Stipa* microsite than for the Open microsite, but this effect vanished after the first 2 years after
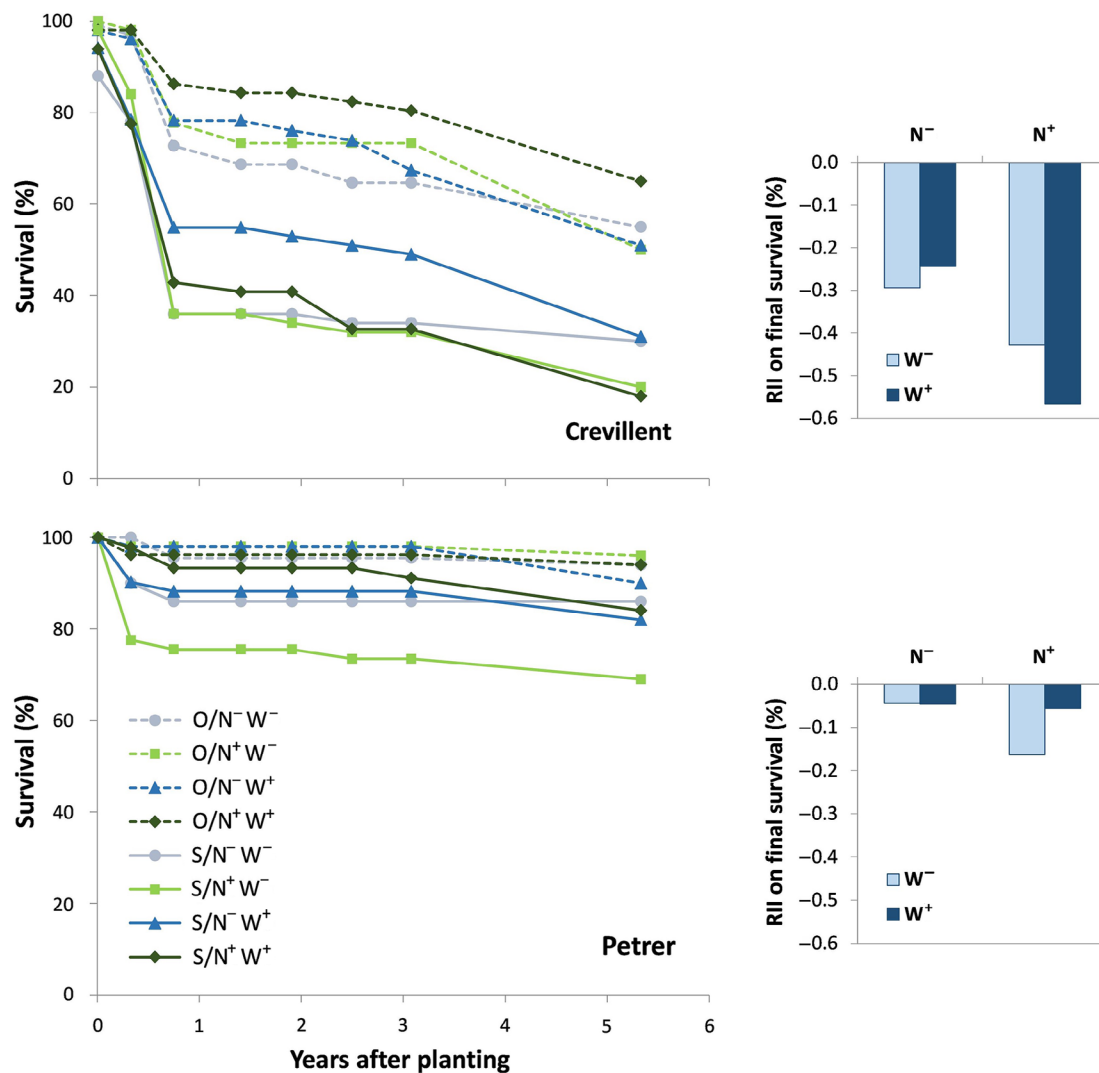

FIGURE 1 Left panels: Survival (%) dynamics of *Olea europaea* individuals for the various combinations of water and nutrient addition on *Stipa* (S; solid lines) and Open (O; dashed lines) microsites for the first 5 years after the experimental plantations at Crevillent and Petrer sites. N$^+$/N$^-$ represents nutrient addition/no addition; W$^+$/W$^-$ represents water addition/no addition. Right panels: Net effect (relative interaction index [RII]) of the interaction with *Stipa* tussocks for *O. europaea* survival 5 years after the plantation.

TABLE 1 Summary statistics of the generalized linear model, expressed as χ^2 with p values in parentheses, for *Olea europaea* survival data 5 years after plantation at Crevillent and Petrer sites.

Factors	Crevillent	Petrer site
M	**53.94 (<0.001)**	**29.1 (<0.001)**
N	0.01 (0.983)	0.17 (0.684)
W	**5.36 (0.021)**	***3.33 (0.068)***
M × N	2.07 (0.151)	0.15 (0.702)
M × W	0.01 (0.970)	0.48 (0.488)
N × W	0.05 (0.832)	0.72 (0.398)
M × N × W	0.64 (0.424)	2.35 (0.126)

Note: Values in boldface indicate significant treatment effects ($p \leq 0.05$), and boldface italics indicate marginally significant effects ($p \leq 0.07$).
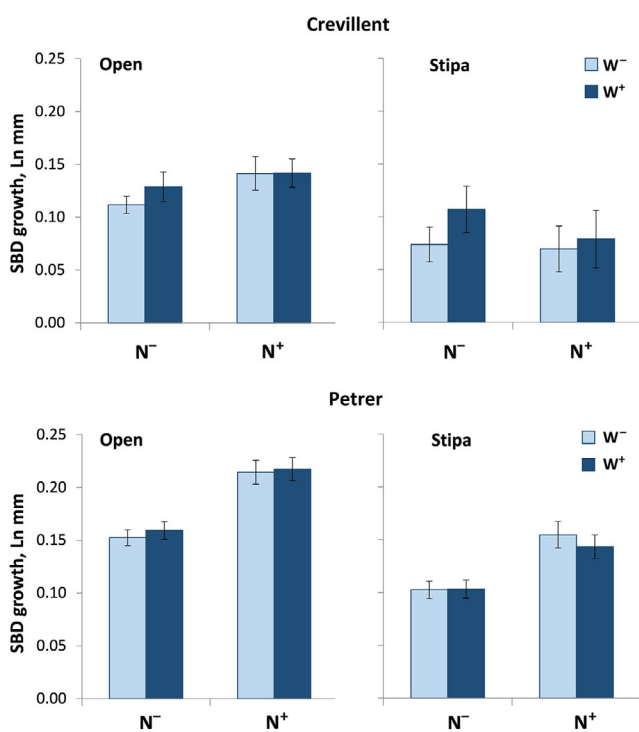Abbreviations: M, microsite; N, nutrient input; W, water input.

FIGURE 2 Relative growth rate in stem basal diameter (SBD) (Ln, in millimeters) of *Olea europaea* individuals growing on Open (left) and *Stipa* (right) microsites at Crevillent and Petrer sites for the 5-year study period as a function of the various combinations of water and nutrient addition. N^+/N^- represents nutrient addition/ no addition; W^+/W^- represents water addition/no addition. Bars are mean values ±1 SE.
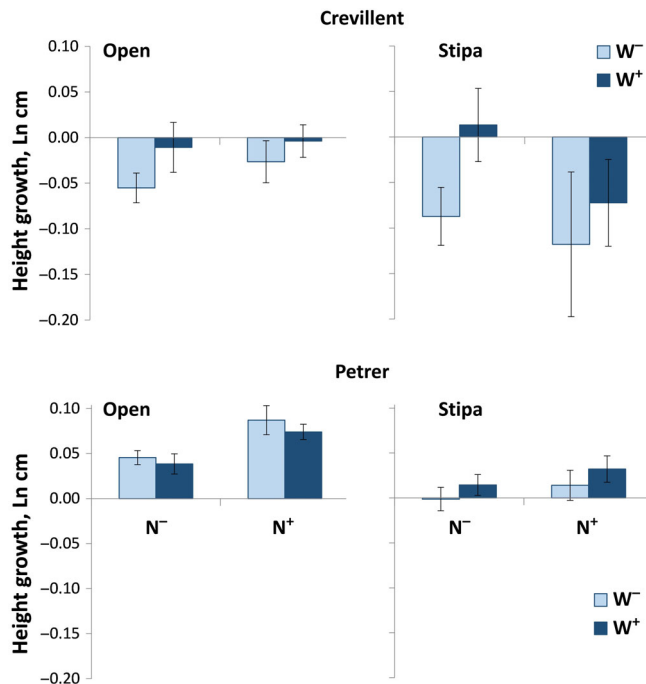

FIGURE 3 Relative growth rate in height (Ln, in centimeters) of *Olea europaea* individuals growing on Open (left) and *Stipa* (right) microsites at Crevillent and Petrer sites for the 5-year study period as a function of the various combinations of water and nutrient addition. N^+/N^- represents nutrient addition/no addition; W^+/W^- represents water addition/no addition. Bars are mean values ±1 SE.

planting (Table 2). Nutrient addition (N^+) significantly increased height and SBD growth rate in Petrer, but not in Crevillent. In both sites, there were significant or marginally significant M × N interaction effects, reflecting the stronger positive effect of N^+ for the Open microsite. Water addition slightly increased *Olea* height growth in Crevillent, and marginally increased SBD in Petrer. A marginally significant interaction M × N × W for height growth in Crevillent (Table 2) reflected the negative effect of water addition when combined with nutrient addition on height growth of *Olea* individuals growing on the *Stipa* microsite (Figure 2).

For the whole study period, the RII values for SBD relative growth were negative (Figure 4), particularly in Crevillent. These values, however, rapidly increased during the first 2 years after the plantation and then stabilized around slightly negative, near-zero values. In Crevillent, the treatments with the lowest (most negative) and highest RII values were N^+W^+ and N^-W^+, respectively. In Petrer, RII dynamics hardly varied among treatments.

DISCUSSION

Five-year monitoring of a large-scale field manipulative experiment on grass–shrub interactions in two alphagrass steppes showed that the net effect of neighbor tussocks of *S. tenacissima* on *O. europaea* saplings varied

T A B L E 2 Summary statistics of the linear model (ANOVA table; expressed as *F* with *p* values in parentheses) with microsite (M), nutrients (N), and water (W) as fixed factors for *Olea europaea* growth data (height and stem basal diameter [SBD]) for the whole study period (5 years), the seedling establishment period (first 2 years), and the post-establishment period (last 3 years) at Crevillent and Petrer sites.

	Crevillent site			Petrer site		
Factors	Whole period (0–5 years)	Establishment (0–2 years)	Post-establishment (2–5 years)	Whole period (0–5 years)	Establishment (0–2 years)	Post-establishment (2–5 years)
Height growth						
M	**3.3 (0.073)**	**6.9 (0.009)**	0.0 (0.993)	**29.1 (<0.001)**	**48.3 (<0.001)**	*2.9 (0.088)*
N	0.7 (0.388)	0.5 (0.472)	0.5 (0.465)	**7.4 (0.007)**	0.5 (0.466)	**6.3 (0.013)**
W	**5.2 (0.023)**	0.3 (0.571)	1.9 (0.170)	0.0 (0.940)	0.0 (0.918)	0.6 (0.424)
M × N	2.7 (0.105)	0.0 (0.890)	**4.6 (0.033)**	2.3 (0.131)	1.0 (0.328)	*3.4 (0.065)*
M × W	0.7 (0.398)	0.3 (0.582)	2.8 (0.094)	1.4 (0.238)	0.6 (0.432)	0.0 (0.946)
N × W	0.7 (0.411)	0.4 (0.545)	0.0 (0.866)	0.2 (0.692)	0.5 (0.489)	0.6 (0.427)
M × N × W	0.1 (0.723)	*2.7 (0.100)*	0.6 (0.449)	0.0 (0.937)	0.8 (0.363)	0.4 (0.531)
SBD growth						
M	**14.4 (<0.001)**	**22.7 (<0.001)**	*2.8 (0.098)*	**76.7 (<0.001)**	**13.9 (<0.001)**	1.2 (0.266)
N	0.3 (0.869)	0.2 (0.660)	0.1 (0.722)	**56.7 (<0.001)**	**8.0 (0.005)**	**5.0 (<0.001)**
W	1.5 (0.226)	0.1 (0.726)	0.5 (0.492)	0.0 (0.983)	0.7 (0.409)	*3.7 (0.055)*
M × N	2.2 (0.142)	*2.8 (0.095)*	1.3 (0.265)	0.7 (0.393)	**4.1 (0.044)**	0.0 (0.889)
M × W	0.2 (0.657)	0.0 (0.827)	2.2 (0.141)	0.5 (0.483)	1.6 (0.213)	0.3 (0.604)
N × W	0.7 (0.419)	1.1 (0.294)	1.1 (0.285)	0.3 (0.576)	0.6 (0.456)	0.5 (0.493)
M × N × W	0.0 (0.950)	0.0 (0.829)	0.0 (0.919)	0.1 (0.772)	0.0 (0.964)	0.4 (0.503)

Note: Values in boldface indicate significant treatment effects ($p \leq 0.05$), and boldface italics indicate marginally significant effects ($p \leq 0.1$).
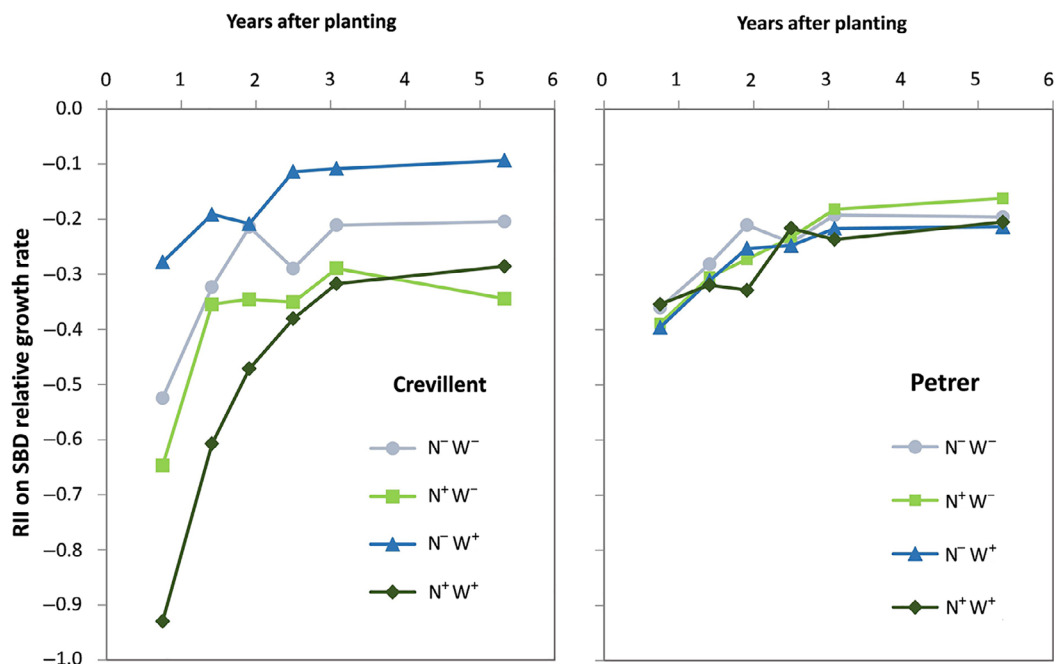

F I G U R E 4 Net effect (relative interaction index [RII]) of the interaction with *Stipa* tussocks for *Olea europaea* stem basal diameter (SBD) relative growth rates for the various combinations of resource addition and increasing age of *Olea* plants over the 5-year period after the plantation. N^+/N^- represents nutrient addition/no addition; W^+/W^- represents water addition/no addition. Symbols and error lines represent mean values ± 1 SE.

between competition and neutral outcomes depending on the interplay between *Olea* sapling age and water and nutrient availability. In general, the competition effects of *Stipa* on *Olea* dominated the first 2 years after planting, fading with time and gradually shifting to neutral interaction as *Olea* individuals aged. Competition was stronger in the drier steppe, where soil moisture was lower in the *Stipa* microsite than in the Open microsite. The extra addition of water favored neutral interactions. Conversely, nutrient addition increased competition strength, even more so when combined with water addition.

Contrasting effects of water and nutrient availability on the outcome of grass–shrub interaction

For the *Olea* saplings growing in the Open microsite, the nutrient-addition treatment increased plant growth in Petrer but not in Crevillent, while water addition resulted in the opposite pattern, which points to nutrient availability as the most limiting factor in the less dry site and to water availability in the drier site. Regardless the nature of the most limiting factor, all across the wide range of conditions considered (which resulted from baseline differences between sites combined with the resource-addition treatments), negative effects of *Stipa* on *Olea* largely prevailed during the first years after the plantation. However, while water addition reduced the competition effects of *Stipa*, nutrient addition enhanced these negative effects. Moreover, in the drier site, the positive effect of water addition shifted to negative when combined with nutrient addition. Our results demonstrate interaction effects between the various resources that modulate the competition strength, questioning the assumption of additive effects for the combined influence of several resources, as well as the use of overall resource availability as a single control factor in plant–plant interactions. The contrasting microsite effect of nutrient addition on *Olea* individuals could be partly explained by the baseline difference in nutrient availability between the two microsites, as soils underneath and near *Stipa* tussocks typically exhibit higher organic carbon and nutrient content than intertussock bare soils (Bochet et al., 1999; Maestre et al., 2001), and therefore, extra nutrient addition would be less relevant for *Olea* plants growing on the *Stipa* microsite. However, the fact that the combined addition of water and nutrient at the Crevillent site resulted in the strongest competition effect suggests that, provided that enough nutrient supply is available, *Stipa* is more efficient than *Olea* in making the most of intermittent pulses of water in a dry environmental context. le Bagousse-Pinguet et al. (2013) found that

fertilization benefited neighbor adult shrubs and not the small individuals of the target species transplanted underneath the shrub, which was attributed to differences in size and associated capacity for nutrient uptake. Our results also point to *Stipa* plasticity in resource acquisition (Pugnaire & Haase, 1996) as a major contributor to the competitive ability of this species. Since many semiarid grass species quickly respond to resource-enrichment pulses (Reyes & Aguiar, 2019), increasing heterogeneity in resource supply could increase negative neighbor effects of grasses (Novoplansky & Goldberg, 2001). According to our results, the debate on the effect of gradients of resource-driven stress on the strength of plant–plant interactions cannot be reduced to the alternatives of monotonic versus unimodal variation with increasing stress (Maestre, Bowker, et al., 2009), as interactions between different resources and the spatial and temporal variation in resource supply seem to be relevant sources of variation for the outcome of plant–plant interactions.

Water addition clearly improved *Olea* survival in both sites, which highlights that even when plant growth does not appear to be water-limited, pulses of water in critical periods can be essential for the survival of seedlings and young individuals (Valdecantos et al., 2014). Although water addition barely modified the interaction effect of *Stipa* on *Olea* survival, the direction and sign of the mild effect on survival were consistent with the effects on plant growth.

Ontogeny as modulating factor of grass–shrub interaction

Eventually, ontogeny overrode other factors in driving the outcome of the interaction between *Olea* and *Stipa*. The aging of *Olea* plants resulted in a gradual decrease in competition intensity, with the net outcome of the interaction with *Stipa* becoming neutral or marginally negative around 2 years after the plantation. Seedlings and saplings of trees and shrubs are often outcompeted by established perennial grasses, but the outcome of this interaction may wane or even reverse at later life stages of the woody species (Grime, 2001). Niche differentiation between species, such as contrasting rooting depths, has been suggested as a plausible explanation for the lack of competition between neighboring plants (Armas & Pugnaire, 2005; Briones et al., 1998; Mayfield & Levine, 2010). Although young *Olea* saplings, less than 2–3 years old, concentrate most active roots at the 0- to 20-cm soil layer, this distribution changes with sapling age, increasing root density below 20 cm of soil depth (Masmoudi-Charfi, 2013). The root system of *Stipa* is more superficial, with most roots of adult plants located at the 10- to 20-cm

soil layer (Puigdefábregas et al., 1999). This age-driven increasing contrast in root distribution between *Olea* and *Stipa* could explain the waning of their competitive interaction. However, given the high colonization capacity of *Stipa* roots, derived from the extensive branching of its rhizomes (Alados et al., 2006), and the opportunistic growth of this species (Pugnaire & Haase, 1996), *Stipa* roots could easily exploit the rooting area of the interacting young *Olea* individuals in response to sudden increases in resource concentration under *Olea* (e.g., from stemflow; or concentrated irrigation as in this study). There is clear evidence that the mechanisms involved in plant–plant interactions may change as plants age, resulting in ontogeny-mediated shifts in the outcome of the interactions (le Roux et al., 2013; Quero et al., 2008; Schiffers & Tielbörger, 2006). Our results provide another example of decreasing competition with the aging of the target plant, which might further change toward the suppression of *Stipa* by adult *Olea* individuals due to shading (Gasque & García-Fayos, 2004).

The role of the target shrub species

As in our work, some studies performed in similar alpha-grass steppes observed a net competition effect of *Stipa* on seedlings and juveniles of shrub species, such as *Lepidium subulatum* (Soliveres et al., 2010), *Retama sphaerocarpa* (Soliveres et al., 2011), and *Pistacia lentiscus* (Maestre & Cortina, 2004), yet the interaction effect on *P. lentiscus* shifted from competition to facilitation for intermediate values of environmental stress. Conversely, several other studies found that *Stipa* tussocks have a positive effect on the establishment of woody species, such as *Medicago arborea*, *Quercus coccifera*, *P. lentiscus* (Maestre et al., 2001), and *Pinus halepensis* (Gasque & García-Fayos, 2004), perennial herbs such as *Haplophyllum bastetanum* (Navarro et al., 2008), and annual plants (Pescador et al., 2018).

The canopy architecture of *S. tenacissima*, with its dense, steep foliage, provides moderate self-shading and protection to smaller neighboring plants against excessive radiation (Valladares & Pugnaire, 1999), which combined with increased fertility underneath and in the vicinity of the *Stipa* tussocks explains the facilitation potential of *Stipa* (Maestre et al., 2003). As compared to common coexisting grass species, *S. tenacissima* is a weak competitor at the seedling and juvenile stages (Morcillo et al., 2019). However, adult tussocks exert a strong competition effect on neighboring juveniles of woody species (Maestre et al., 2003), probably associated with the strong plasticity of *Stipa*, which opportunistically maximizes resource acquisition and growth whenever there are resource pulses (Pugnaire & Haase, 1996; Ramírez et al., 2007). A net competition effect of *Stipa* tussocks on

neighbor shrub saplings can be expected when the microsite amelioration promoted by *Stipa* is not that critical to the target species or does not counteract the impact of the resource-acquisition pulses of *Stipa*.

Our results show that *Olea* can perform well over a wide range of conditions. Also, seedling and sapling survival rates are commonly higher for *Olea* than for similar woody species that coexist with *Olea* in semiarid lands, such as *P. halepensis, P. lentiscus*, *Q. coccifera*, and *Rhamnus lycioides* (Chirino et al., 2009), which reflects the well-acknowledged plasticity and tolerance to stress of this species (de Casas et al., 2011). These features can explain why young *Olea* individuals may not benefit enough from the shade and improved soil conditions provided by *Stipa* tussocks to outweigh competition for resources. As in the case of the *Stipa*–*Olea* interaction, a net effect of competition between *Stipa* and juvenile individuals of shrub species such as *L. subulatum* and *R. sphaerocarpa* can be explained in part by the lack of a positive effect of the shade provided by *Stipa* tussocks. Thus, *L. subulatum* avoids water stress by dropping the leaves during summer and other extended drought periods (Palacio et al., 2007), making photoprotection by *Stipa* dispensable, and *R. sphaerocarpa*, a leafless leguminous shrub, concentrates the photosynthetic area on its cladodes and exhibits high light requirements (Valladares et al., 2003).

APPLICATIONS TO RESTORATION

Increasing the abundance of native woody plants in grass-dominated ecosystem (often referred to as shrub encroachment) has been identified as an indicator of ecological degradation in drylands (Millennium Ecosystem Assessment, 2005). However, the overall ecological effects of such encroachment depend on a variety of factors, including previous and current land use, climate, soil and topographic properties, and woody species traits (Eldridge et al., 2011; Maestre et al., 2016; Nunes et al., 2019). Alpha-grass steppes are one of the most representative ecosystems of semiarid areas of the Mediterranean basin. For more than 4000 years, these steppes have been used by humans for livestock grazing and for the collection of the alpha-grass fiber, which often involved intentional removal of woody vegetation to reduce competition with grasses, causing a significant loss of biodiversity, as well as soil degradation and erosion (le Houérou, 2001). Reintroducing highly functional woody species that were locally lost from degraded alpha-grass steppes is considered critical to the reversal of their degradation (Cortina et al., 2009). Regardless of the overall impact of increased shrub density, understanding the factors that control shrub establishment in

grass-dominated drylands is essential for designing appropriate management and restoration measures for these ecosystems.

This work demonstrated contrasting and interacting effects of nutrient and water availability on grass–shrub interaction. Water inputs, even if small and sporadic, reduce the effect of competition with *Stipa*, which offers the opportunity of benefiting from its potential positive effects exerted through shading and improved soil condition. However, nutrient addition increases the competition effect of the grass, counteracting the potential benefits from extra water inputs. Therefore, when using facilitation by *Stipa* to promote the establishment of late-successional, slow-growing woody species in degraded steppes (Maestre et al., 2001), it would be advisable to rely on the naturally enhanced fertility of the soil underneath and in the vicinity of *Stipa* tussocks and avoid any fertilization input. Conversely, seedlings planted in intertussock bare-soil areas will largely benefit from fertilization.

The competition effect of *Stipa* tussocks on juvenile *Olea* shrubs vanishes with shrub age, probably due to an increasing difference in rooting depth. Various eco-technological treatments could help to dampen or reduce competition with *Stipa* and tilt the net balance of the grass–shrub interaction toward a neutral or positive interaction. For example, techniques that promote niche differentiation between shrubs and grasses, such as the use of long containers for seedling production to promote deeper rooting (de la Fuente et al., 2017), combined with deep planting (Oliet et al., 2012) and/or deep preparation of the soil for planting (Chirino et al., 2009), can help to overcome the initial overlap of rooting depths earlier, accelerating one of the effects of the natural ontogeny process on slow-growing tall shrubs.

A review of the works that assessed the interaction effects of *S. tenacissima* on juvenile individuals of woody species provides evidence of the important role played by the target species in shaping the net outcome of the grass–shrub interaction. Even for species that can be considered as morphologically and functionally similar (e.g., Mediterranean, late-successional, and tall evergreen shrubs), slight variations in their functional traits can lead to contrasting results, ranging from competition to facilitation. A positive net interaction outcome is more likely when the water and radiation stress tolerance of the target woody species is not particularly strong and/or when the shrub is capable of rapidly rooting deeper than the grass. In contrast, woody species that are highly stress-tolerant and shade-intolerant, or have relatively shallow roots are good candidates for avoiding the *Stipa* neighborhood as planting microsites.

Our results are of particular importance to guide restoration efforts in alpha-grass steppes and other formerly wooded xeric grasslands and rangelands for which the loss of woody plants has commonly resulted in decreased functioning.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Morcillo & Bautista, 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.16569162.v1.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.