Promoting oak (*Quercus pubescens* Willd.) seedling development: finding the balance between canopy opening and grass competition under water stress

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Abstract

To adapt Mediterranean forests to increasingly harsh climatic conditions by promoting genetic diversity, thinning is often considered an effective strategy to enhance sexual regeneration. However, determining an optimal thinning level that both increases light availability and maintains favorable microclimatic conditions for germination, without excessively promoting herbaceous competition, remains challenging. To better understand how abiotic and biotic factors influence oak seedling development and to help identify a balanced thinning level under climate change, we conducted a semi-controlled experiment testing the combined effects of competition with a grass species (Poaceae), two canopy opening levels, and water stress. Our results highlight the crucial role of competition with Poaceae species - in our case *Festuca ovina* - in oak regeneration. Their presence not only intensifies competition for essential resources, but also modifies soil properties and alters belowground interactions, overall creating conditions less favorable for oak seedling establishment. In addition, our results highlight the significant impact of key abiotic factors that are canopy opening (which influences light availability) and hydric conditions, as well as their interactions with the effects of competition. We observed a consistent need for adequate light to ensure optimal seedling performance, suggesting that successful regeneration depends on balancing sufficient canopy opening to improve light availability with maintaining sufficient cover to mitigate water stress and limit grass competition. Overall, our study contributes to the broader debate on sustainable forest management strategies under changing climatic conditions.

Keywords:

Quercus pubescens; Semi-controlled experiment; Grass competition, *Festuca ovina*, Water stress, Canopy opening, Mediterranean forest

1. Introduction

In Europe, forests cover 227 million hectares (from Portugal to Russia and Turkey), representing 35% of total land area (Forest Europe, 2020). With natural forests currently representing less than 1% of European forests, almost all Europe's native forests have been altered by more or less intensive management practices (Paillet et al., 2010; Vanbergen et al., 2005). Forests provide multiple ecological, economic and social services (Aggestam et al., 2020), with timber production through forestry being a key factor influencing management decisions (Bottalico et al., 2014; Nocentini et al., 2022; Palahi et al., 2008). As an example, about 75% of forest area in Europe is available for timber supply (FORST EUROPE, 2020). Human activities have profoundly altered the forest species distribution, as well as the structure and composition of forest communities (Blondel, 2006; Quézel & Barbero, 1990).

The genus *Quercus* has often been favored in Europe by foresters to the detriment of other species due to the economic value of its species (Marchi et al., 2016; Timbal & Aussenac, 1996). A large part of the oak forests has been traditionally managed as coppices, supplying timber for firewood and charcoal production for centuries (Marchi et al., 2016; Nocentini & Coll, 2013; Picchio et al., 2011). This ancient and simple management method relies on vegetative regeneration with harvest rotations generally ranging from 15 to 35 years depending on the tree species, growth conditions and desired products (Bottalico et al., 2014; Chirici et al., 2020; Spinelli et al., 2016). Stump sprouting and rapid growth after felling (mainly clearcutting) allows shorter harvest intervals than in high forests that are regenerated by seeds (Ducrey & Turrel, 1992; Giovannini et al., 1992).

Oak coppices are widespread worldwide and especially common in Mediterranean countries such as France, Italy or Spain (Fabbio, 2016; Marchi et al., 2016). However, after the Second World War, coppicing was largely abandoned in favor of other energy sources (Prévosto et al., 2013; Salomón et al., 2017; Vadell et al., 2022), which implies a significant reduction of the vegetative regeneration due to reduced sprouting efficiency in abandoned and ageing coppices (Ladier et al., 2014; Prévosto et al., 2013). This limitation on regeneration poses a major challenge to forest management, at a time when

biomass has returned to the forefront as a potential energy source thanks to its renewable nature (Santi et al., 2024).

Furthermore, Mediterranean forests will face increasing water deficit combined to rising temperatures due to ongoing climate change (IPCC 2023; Lionello et al. 2014; Lionello et al. 2008). These unfavorable abiotic conditions for tree growth are often combined with an increase in insect outbreaks or fungal attacks, affecting forest health and potentially leading to dieback, defoliation and even mortality (Allen et al., 2015; Lemaire et al., 2022). In this context, adaptive solutions that effectively strengthen the long-term resilience of forests, and in particular their capacity to regenerate from seeds (sexual regeneration), are needed (Vilà-Cabrera et al., 2018). Sexual regeneration involves genetic mixing and environmental selection of seedlings, ensuring better adaptation to the environment (Bussotti et al., 2015; Vilà-Cabrera et al., 2018). However, particularly since the beginning of the 21st century, this regeneration pathway has faced significant challenges (Plieninger et al., 2010; and Tyler et al., 2006 for Californian oaks): insufficient recruitment, slow-growing seedlings and low survival rates (Gauquelin et al., 2016; Prévosto, 2020).

To adapt forest systems to these new and harsher climatic conditions, thinning is often considered an effective method to enhance tree growth, improve their health status and favor seed regeneration by reducing competition for resources between remaining trees (Kerr & Haufe, 2011) and limiting the impact of drought on growth (Cabon et al., 2018; Sohn et al., 2016). Thinning is also an adaptive solution that can contribute to carbon sequestration (Mäkipää et al., 2023; Zhang et al., 2018), biodiversity provisioning (Li et al., 2020) and fire risk reduction (Taylor et al., 2021). Furthermore, compared to coppicing, this management method is considered an adaptive solution for promoting sexual regeneration by enhancing seed production (Otto et al., 2012) and favoring long-term establishment of seedlings by promoting their survival and growth (Bran et al., 1990; Espelta et al., 1995; Retana et al., 1999).

Seedling development stages are influenced by numerous ecological filters, such as soil properties and microclimatic conditions (*e.g.*, soil moisture, light availability or temperature fluctuations)

(Mendoza et al., 2009). Both abiotic and biotic factors influence seedling establishment and growth, making it difficult to strike a balanced thinning level (Mölder et al., 2019). Light and water availability for instance, play a key role but are influenced by the intensity of thinning (Prévosto et al., 2011; Retana et al., 1999). First, seedling growth benefits from increased light level due to opening of the canopy (Lusk et al., 2008; Niinemets, 2006; Quero et al., 2007). However, the canopy is known to create favorable microclimatic conditions for seed germination (Mölder et al., 2019; Retana et al., 1999), with the forest cover acting as a buffer against climatic conditions, for instance by reducing extreme temperatures and the vapor pressure deficit (Prévosto, 2020; Valladares et al., 2016). Moreover, the positive effect of opening on seedling growth could offset by reduced water availability and competition for soil nutrients with the herbaceous stratum that is promoted by forest opening (Gaudio et al., 2011; Wagner et al., 2010). In particular, grass species of the Poaceae family are known to produce a dense root system with a high physiological ability to uptake water and nutrients (Gibson & Newman, 2001; Yamada, 2011), and are recognized as strong competitors to tree seedlings (Balandier et al., 2006; Schaller et al., 2003; Vernay et al., 2018). For example, Collet et al. (1996) observed that young *Quercus petraea* seedlings competing with *Avenella flexuosa* (formerly *Deschampsia flexuosa*) were shorter in height, had fewer branches and a smaller root system. Similarly, Fernandez et al. (2023) observed that *Molinia caerulea* restricted both *Q. petraea* roots and ectomycorrhization rate.

To better understand how abiotic and biotic factors influence the development of oak seedlings and help identify a balanced thinning level in a climate change context, we conducted an experiment under semi-controlled conditions to test the effects of competition with a Poaceae species, combined with two levels of simulated canopy opening and water deficit. We analyzed the effects of these factors on the different biomass allocation to the different plant compartments, as well as on some key morphological and physiological variables in young *Quercus pubescens* seedlings, a deciduous oak native to the Mediterranean basin. As competition with grass species can influence the nutritional status and water supply of oak seedlings, we also examined the seedling root mycorrhization and soil physico-chemical characteristics. We studied the interactions between these three factors (*i.e.*, canopy

opening, hydric conditions and competition) and made the following hypotheses: 1) seedling development and mycorrhization are limited when forest canopy opening is low and water deficit is high; 2) competition with a grass species has a negative effect on seedling morphological and physiological traits and on mycorrhization; 3) the negative effect of competition is limited by low canopy opening level and unfavorable hydric conditions.

2. Materials & Methods

2.1. Plant materials

Target species: *Quercus pubescens* Willd.

Quercus pubescens Willd. (Fagaceae), commonly called downy oak, is characteristic of the supramediterranean bioclimate (Quezel, 1979) and is found from southern Europe to southwestern Asia (Ganatsas & Tsakaldimi, 2013), on hillsides generally between 200 and 800 m a.s.l. (Pasta et al., 2016) and up to 1400 m a.s.l. in France (Rameau et al., 2008). This species exhibits good tolerance to moderate summer drought and low winter temperatures, but is vulnerable to extreme climatic events, including recurrent frost and intense droughts, which are characteristic of continental climates (Pasta et al., 2016). It grows on both acidic and calcareous soils, though it shows a marked preference for the latter, and is characterized by a heliophilous and thermophilous ecological strategy (Contran et al., 2013; Pasta et al., 2016). In France, *Q. pubescens* is the dominant species on approximately 1.41 million hectares, of which 841,000 hectares are forests where it comprises more than 75% of the canopy cover (IGN, 2024). In southeastern France, these forests are mainly managed as coppices. However, the cutting frequency has decreased over the past few decades, and many *Q. pubescens* stands are now left without management and ageing (Ladier et al., 2014).

For our experiment, we used *Q. pubescens* acorns collected at an experimental site in Saint-Christol d'Albion, SE France, 44°02'58.0''N 5°32'35.8''E, 875 m a.s.l., which was established as part of the H2020 HoliSoils project (https://holisoils.eu). This stand is a *Q. pubescens* mature coppice with the last cut occurring 70 to 80 years ago (see Brasseur et al. (2025) and Ménival et al. (2025) for further study site description). Saint-Christol-d'Albion is characterized by a supramediterranean bioclimate with an average annual precipitation of 980 ± 47 mm and an annual mean temperature of 10.1 ± 1.1 °C (mean ± standard error calculated for the 1995-2024 period with the Saint-Christol-d'Albion climatological station data, Météo-France (2024))

In October 2022, over 100 acorns were collected (after visual inspection and controlled with the floating method) and stored at 4°C in humid sand until germination. In January 2023, they were planted in individual 1L pots filled with a substrate composed of 50% universal peat-free potting substrate (coconut fiber, vegetable compost and bark compost mix) and 50% soil collected from the naturalized green spaces of Saint Jérôme campus of Aix Marseille University (AMU). The pots were placed for a year in the greenhouse of the IMBE experimental garden (AMU Saint Jérôme Campus, Marseille, France) (Figure 1).

Competing species: *Festuca ovina* L.

The genus *Festuca* L. (Poaceae) is commonly found in the meadows and steppes of North America and Eurasia (Daniel, 2001). It is a perennial plant growing in dense clumps and occasionally spreads through short rhizomes (Yamada, 2011). This genus is particularly known for its drought tolerance thanks to a fibrous and extensive root system (Gibson & Newman, 2001; Yamada, 2011).

Festuca rubra L. and *Festuca glauca* L. are both present at the Saint-Christol experimental site, particularly in the most open plots. Due to the plant material accessibility, we are using *Festuca ovina* L. as study species. *Festuca ovina* seeds were supplied by Les Semences du Puy SARL (origin Denmark, harvest in 2019) and are sown in March 2023 in 10 cm deep trays filled with 2/3 universal potting substrate and 1/3 perlites and the plants were grown in the greenhouse (Figure 1).

2.2. Experimental design

The experimentation was set up at the IMBE experimental garden (Aix Marseille University, Saint-Jérôme Campus, Marseille, France). The climate is typically Mediterranean with a mean annual temperature of 17.1 ± 2.7 °C and mean annual precipitations of 443.7 ± 63.9 mm mainly distributed from September to January and from April to May (mean ± standard error calculated for the 2019-2024 period with the Marseille Observatory climatological station data, Météo-France (2024)).

160 The experimental design was set up three interacting factors: 2 competition levels (with/without)
161 x 2 canopy opening levels (high/low) x 2 hydric condition levels (water deficit/favorable hydric
162 condition), with 12 replicates per combination for a total of 96 pots.

163 In October 2023, *Q. pubescens* seedlings were transplanted in 6L pots (19 × 19 cm and 21 cm
164 deep): 48 seedlings transplanted alone in the pots (*i.e.*, without competition treatment) and 48
165 seedlings transplanted next to a 10 × 10 cm^2 *F. ovina* clumps (*i.e.*, with competition treatment) (Figure
166 1). The substrate used was composed of 1/3 soil collected on the Saint-Christol-d'Albion study site and
167 2/3 universal potting soil (physico-chemical analysis of the substrates at the beginning of the
168 experiment is presented in Table 1). The use of natural soil guarantees the presence in the pots of
169 microorganisms naturally present in the *Q. pubescens* forest of Saint-Christol-d'Albion, while the use
170 of "universal soil" ensures good drainage due to relatively high clay content of the forest soil. The
171 plants were kept under a plastic tunnel in the same watering (70-100% field capacity) and canopy
172 opening conditions for 6 months. Watering conditions were controlled by monitoring pot weights
173 every 2-3 days.

174 In April 2024, pots with and without competition are divided into high and low canopy opening
175 levels (Figure 1). One tunnel was set up in an open area of the experimental garden (high canopy
176 opening), and another under the tree canopy (low canopy opening). Three Photosynthetically Active
177 Radiation (PAR) detectors (tube of 30 cm length, ©SOLEMS DPAR/LEC1C#) were placed in each tunnel
178 to assess light transmission. Three additional detectors were placed in open conditions, outside the
179 experimental garden (*i.e.*, under full light conditions). Measurements were recorded every minute for
180 24 h, in April 2024 on a clear-sky day. Light transmittance was computed as the ratio of light availability
181 in each opening condition to light availability under full light conditions. Light transmittance was
182 uniform under each tunnel, 37% under the high opening treatment, compared to only 10% under the
183 low opening treatment. A similar percentage difference is observed at the Saint-Christol-d'Albion study
184 site between unthinned control plots and plots thinned at 75% of the initial basal area (Brasseur et al.,
185 2025). Temperature and relative humidity were recorded throughout the experiment every 5 min

using a HOBO data logger (Onset Computer Corporation, Bourne, MA, USA) in both tunnels (Table 2). Vapor pressure deficit (VPD) was calculated according to the function: $VPD = e_s - e_a$ with e_s as the saturation vapor pressure with:

$$e_s = 0.6108 \times \exp\left(\frac{17.27 \times T}{T + 237.3}\right)$$ with T the temperature in °C.

and e_a as the actual vapor pressure with:

$$e_a = e_s \times \left(1 - \frac{RH}{100}\right)$$ with RH the relative humidity in %.

For three months, from July 2024 to September 2024, half of the pots in each canopy opening treatment were subjected to reduced water supply to maintain them at 30–40% of their field capacity, corresponding to a water stress treatment, while the other half were maintained at 70–80% of their field capacity (favorable hydric conditions) (Figure 1). Soil moisture was maintained using an automatic, controlled drip irrigation system and monitored by weighing the pots every 2 to 3 days.

2.3. *Festuca ovina* measurements

In September 2024, *F. ovina* clumps were harvested, and the above- and belowground parts were separated. Roots were carefully washed over a sieve to remove soil particles without loss. The above- and belowground parts were then frozen, freeze-dried and weighed.

2.4. *Quercus pubescens* growth measurements

Quercus pubescens seedlings size (principal stem height - from the root collar to the apical bud - in cm and diameter at the root collar in mm) was measured at the beginning of the experiment (October 2023), during the growing season before water stress was introduced (July 2024), and at the end of the experiment (September 2024). We calculated the Relative Growth Rate (RGR) for height and diameter as:

$$RGR = \frac{X_{final} - X_{initial}}{X_{initial}} \times 100$$ with $X_{initial}$ and X_{final} the height or diameter at the beginning and at the end of the experiment, respectively.

209 The height/diameter ratio was calculated and the number of leaves was also recorded for each
210 seedling.

211 In September 2024, *Q. pubescens* seedlings were harvested, and their root systems were carefully
212 separated from *F. ovina* clumps. The root systems were then washed over a sieve to remove soil
213 particles without losing any roots. Seedlings were separated into leaves, stems, primary roots
214 (diameter > 2 mm) and fine roots (diameter < 2 mm) then frozen, freeze-dried and weighed.

215 ## 2.5. *Quercus pubescens* physiological response and mycorrhization

216 In September 2024, we measured the chlorophyll index on 3 leaves per seedling, expressing the
217 relative chlorophyll content per unit leaf area, using a SPAD-502 Plus Chl (Konica Minolta Optics,
218 Japan). We also measured the area of each leaf of each seedling to estimate the SLA (mm^2/mg).

219 To quantitatively assess mycorrhizal colonization of *Q. pubescens* fine roots, we used Phospholipid
220 fatty acid (PLFA) analysis following the method described in Biryol et al. (2024). We measured
221 mycorrhizal biomass in µg per gram of dry fine root previously grounded with a ball mill (Retch)
222 (collection and freeze-drying process described above). PLFA 18:2ω6,9 was used as a marker molecule
223 for fungal biomass (Bååth & Anderson, 2003; Frostegård & Bååth, 1996; Klamer & Bååth, 2004;
224 Wallander et al., 2013). This fungal biomarker is commonly used in soil microbial community studies
225 but has also been found in plant tissues (Laczko et al., 2004; Olsson, 1999; Zelles, 1997). However, as
226 described by Kaiser et al. (2010), most of the PLFAs measured in roots originate from ectomycorrhizal
227 fungi growing inside the roots.

228 ## 2.6. Soil physico-chemical analyses

229 Initial substrate samples were collected at the biggening of the experiment and soil samples were
230 collected and at the end of the experiment in September 2024 during seedling harvesting, then dried
231 (60°C for 48h in a drying oven) and sieved using a 2 mm sieve. The soil physico-chemical analyses were
232 then carried out by Teyssier laboratory (Bordeaux, France, www.laboratoire-teyssier.com). Soil pH
233 (measured in water and KCl), total organic matter and organic carbon (C, determination after dry

combustion), total nitrogen (N, Kjeldahl method), phosphorous (P as P_2O_5, Olsen method), potassium (K as K_2O), magnesium (Mg as MgO), calcium (Ca as CaO), sodium (Na as Na_2O) and cation exchange capacity (CEC) were analyzed for each soil samples (methods are specified in Supplementary material Table S1).

2.7. Statistical analyses

All statistical analyses were performed using the R software 2024.12.1 +563 (R version 4.3.1, Foundation for Statistical Computing, Vienna, Austria). The normality of residuals was assessed through histogram inspection, Shapiro-Wilk test, and Q-Q plot visualization. Transformed data were used when needed to ensure residuals normality for linear models. Quasipoisson family models were used in case of overdispersion of Poisson family models. All models, data transformation performed and *p*-value of Shapiro-Wilk tests and R^2 associated are summarized in Supplementary materials (Supplementary Tables S2, S3, S4, S5. B and S7). If model diagnostics indicated the presence of one influential observation (studentized residual > 3 and high Cook's distance), the data point was considered an outlier and was excluded from the analysis to meet model assumptions of normality and homoscedasticity (also indicated in Supplementary Tables S3). Model predictions were plotted according to the different modalities with the 95% confidence intervals calculated as: $\hat{y} \pm t_{(1-\propto/2,df)} \times SE(\hat{y})$ where $\hat{y}$ is the predicted value, $t_{(1-\propto/2,df)}$ is the critical value of Student's t distribution according to the degree of freedom and $SE(\hat{y})$ is the standard error of the predicted value.

The effects of canopy opening and hydric condition, as well as their two-ways interaction on *F. ovina* belowground and aboveground biomass were tested using linear models and type III analysis of variance.

The effects of competition, canopy opening, humidity, their two-way interactions and the three-way interactions on *Q. pubescens* morphological and physiological traits (height and diameter at the end of the experiment, height/diameter ratio, aboveground biomass, belowground biomass, aboveground/belowground biomass ratio, number of leaves, SLA, mycorrhization) and on each soil

259 physico-chemical parameter were tested using linear or generalized linear models and type III ANOVA
260 depending on the evaluated trait.

261 The effects of time, competition, canopy opening, hydric condition and their two-way interactions
262 on *Q. pubescens* growth parameters (height, diameter and height/diameter ratio) were tested using
263 linear models (with log(x) transformation) and type III analysis of variance (ANOVA).

264 Residual's normality was not verified for chlorophyll index data. We therefore used non-
265 parametric tests. We performed a Kruskal-Wallis test with post hoc Dunn test (with false discovery rate
266 correction) to determine which modalities differ significantly from the others.

267 To assess the effect of competition, canopy opening and hydric condition on soil physico-chemical
268 profiles, we used a Principal Component Analysis (PCA) on standardized data. We performed a
269 permutational multivariate analysis of variance (PERMANOVA) on the PCA individual coordinates using
270 the adonis function of the Vegan package.

3. Results

Festuca ovina biomass

The aboveground and belowground biomass of *F. ovina* were respectively 1.6-fold and 2.7-fold higher under high compared to low canopy opening. (Table 3, Figure 2. A). The aboveground biomass was negatively affected by the water deficit only at high canopy opening level (-28.6%), while the belowground biomass was not influenced by the hydric conditions (Table 3, Figure 2. A).

Quercus pubescens growth

First, a significant positive correlation was observed between time and *Q. pubescens* seedling growth (Table S5 and Figure S1 in Supplementary material) with an average height relative growth rate (RGR) of 124.8% and an average diameter RGR of 64.6% across all treatments between the beginning and the end of the experiment. Although growth over time was influenced by the biotic and abiotic factors tested (Table S5. A in Supplementary material), the difference in height and diameter growth between the beginning and the end of the experiment was always significant (Figure S1. A, B in Supplementary material).

In absence of competition, *Q. pubescens* seedling height and diameter at the end of the experiment were 108.2% and 21.1% higher at a high canopy opening level than at a low level (Table 4 and Figure 3). At a high canopy opening level, a negative effect of water deficit was observed only on height (-46.6%) (Table 4 and Figure 3). At a low canopy opening level, hydric conditions did not influence height or diameter.

At a high canopy opening level and under favorable hydric conditions, the presence of *F. ovina* significantly reduced *Q. pubescens* growth in height (-63.3%) and diameter (-24.4%) at the end of the experiment (Table 4 and Figure 3). We observed a height RGR between the beginning and the end of the experiment of 395.6% for *Q. pubescens* alone, while height RGR reached only 93.8% in presence of *F. ovina* (Table S5 and Figure S1. A in Supplementary material). A similar trend was noted for the

295 diameter but with less intense effect of the grass species: a 112.1% RGR without competition
296 compared to a 71.3% RGR in presence of *F. ovina* (Table S5 and Figure S1. B in Supplementary material).

297 At a low canopy opening level, the negative effect of competition on height growth was not
298 significant. However, a lower canopy opening level attenuated the effect of competition on diameter
299 growth (-21.0% *versus* -24.4% (Table 4 and Figure 3)).

300 Hydric conditions modulated the effect of competition on *Q. pubescens* growth (significant
301 interaction between Competition × Hydric condition for height growth, Table 4). Under water deficit,
302 the negative effect of competition on growth was strongly attenuated for height (-32.2% *versus* -
303 63.3%) and alleviated for diameter (not significant) (Figure 3).

304 Low canopy opening and water stress alleviated the effect of competition on both height and
305 diameter growth (Figure 3).

306 ## *Quercus pubescens* biomass

307 In absence of competition, the *Q. pubescens* seedling of both aboveground and belowground
308 biomass increased with a high canopy opening level (Table 5 and Figure 4. A). Under favorable hydric
309 conditions, the aboveground and belowground biomasses were 424.6% and 167.5% higher under high
310 compared to low canopy opening, respectively.

311 A negative effect of water deficit on the aboveground biomass was observed, but only at a
312 high canopy opening level (-67.0%) (significant interaction between canopy opening × hydric condition,
313 Table 5). Belowground biomass was not influenced by hydric conditions (Figure 4. A).

314 The same response pattern was observed for most seedling biomass compartments (leaves,
315 stems and fine roots biomass) as well as for the number of leaves and the ratio between aboveground
316 and belowground biomass (Table 5, Figure 4. B, D, E and Figure S2 in Supplementary material), in
317 response to canopy opening and water stress, while primary roots biomass followed a similar trend to
318 that of total belowground biomass (Table 5, Figure 4. F).

At a high canopy opening level and under favorable hydric conditions, the presence of *F. ovina* significantly reduced *Q. pubescens* aboveground (-84.2%) and belowground (-54.0%) biomasses (Table 5 and Figure 4. A). A same response pattern to competition was observed for all seedling biomass compartments (leaves, stems, fine roots biomass), for the number of leaves and for the aboveground/belowground ratio (Table 5, Figure 4. B, D, E and Figure S2. A, C in Supplementary material).

The negative effect of competition on aboveground and belowground biomass disappeared when canopy opening level decreased (significant interaction between competition × canopy opening, Table 5, Figure 4. A). Water deficit attenuated the negative effect of competition on aboveground biomass (-69.5% *versus* -84.2%) and alleviated the effect of competition on belowground biomass (significant interaction between competition × hydric condition, Table 5, Figure 4. A).

Low canopy opening and water stress alleviated the effect of competition on both aboveground and belowground biomasses (Figure 4. A).

A similar response pattern to that described for aboveground biomass was observed for abiotic control of competition impact on *Q. pubescens* leaf, stem and primary roots biomasses, as well as on the ratio between aboveground and belowground biomass. Fine roots biomass and leaf number followed the same response pattern of belowground biomass (Table 5, Figure 4. B, D, E, F and Figure S2 in Supplementary material).

Quercus pubescens leaf traits

Quercus pubescens leaf area was not affected by canopy opening, hydric condition or competition (Table 5, and Figure S2 in Supplementary material). However, the SLA of seedlings grown in a high canopy opening level, without *F. ovina* and under favorable hydric conditions was significantly smaller than that of seedlings grown with *F. ovina* under at least one stressful abiotic condition (low light, water deficit, or both) (Table 5 and Figure 4. C).

Quercus pubescens chlorophyll index

In absence of competition, *Q. pubescens* chlorophyll index was 6.6% lower at low than at a high canopy opening level. We observed a positive effect of water deficit on the chlorophyll index (+5.3%) but only at a high canopy opening level (Figure 5). At a low canopy opening level, hydric conditions did not influence the chlorophyll index.

At a high canopy opening level and under favorable hydric conditions, the presence of *F. ovina* reduced the *Q. pubescens* chlorophyll index (-33.4%), but this negative effect of competition was attenuated at a low canopy opening level (-12.3%) (Figure 5). Hydric conditions did not influence the effect of competition on chlorophyll index.

Mycorrhization

In absence of competition, fungal abundance associated with *Q. pubescens* roots was not affected by canopy opening levels or hydric conditions (Figure 6).

At a high canopy opening level, and under favorable hydric conditions, the presence of *F.* ovina induced a marked decrease in fungal abundance associated to *Q. pubescens* roots (-44.6%) (Figure 6). Under water stress, this negative effect of competition on fugal abundance was slightly attenuated but still significant (-42.7%). At a low light canopy opening level, the presence of *F. ovina* did not influence the fugal abundance (Figure 6).

Soil physico-chemical parameters

Principal component analysis (PCA) of soil physico-chemical parameters showed that the first PCA axis explaining 44.5% variation was determined by high scores of CEC, pH (water and KCl) and Ca, Mg and Na cations concentrations) (Figure 7. A), and differenced soil profiles according to the presence or absence of *F. ovina* ($P_{permanova} < 0.001$, Figure 7. B). The presence of *F. ovina* positively influenced the cation-exchange capacity (CEC), regardless of abiotic conditions (Table S6 and Figure S3 in Supplementary material). Under favorable hydric conditions, the presence of *F. ovina* positively

367 influenced the pH, and the concentration in MgO, CaO and Na_2O (Table S6 and Figure S3 in

368 Supplementary material).

4. Discussion

Effects of abiotic factors on *Q. pubescens* seedlings

Our experiment allows us to highlight the positive effect of canopy opening on *Quercus pubescens* growth. Canopy opening leads to an increase in both temperature and light availability (Mölder et al., 2019), the latter being the primary driver of growth stimulation (Espelta et al., 1995). *Quercus pubescens* is considered to have a heliophilic ecological strategy (Contran et al., 2013; Pasta et al., 2016), and light availability is known to be particularly important for oak regeneration (Mölder et al., 2019). Consistent with other studies on deciduous oak species (Sevillano et al., 2016; Wang & Bauerle, 2006; Welander & Ottosson, 1998), our results demonstrate an increase in both aboveground and belowground seedling biomass with increasing light availability (Sevillano et al., 2016; Wang & Bauerle, 2006; Welander & Ottosson, 1998). We observed that *Q. pubescens* seedlings tend to allocate more biomass to their aboveground than their belowground parts under high light availability, indicating a preferential investment in photosynthetic organs under optimal conditions (Kozlowski & Pallardy, 2002). The concomitant increase in leaf number and total leaf plant area observed corroborates this pattern of resource allocation. Enhanced photosynthetic activity under high light availability increases carbon assimilation, which in turn supports greater height and diameter growth (Lambers et al., 2008), as demonstrated in the present study. Limited light availability in the understory of mature forests is widely recognized as a major constraint on the survival and growth of oak seedlings (Dey et al., 2012), a pattern that our results also confirm by highlighting limited growth under low light conditions. This limitation explains the traditional reliance on clear-cutting to stimulate regeneration, though this primarily favors vegetatively reproduction (*i.e.*, for oaks, sprouts over seedlings from acorns) (Brasseur et al., 2025) and competition by the ground vegetation (see discussion below). On the other hand, consistent with the findings of Kwak et al. (2011) on *Q. suber*, we observed that chlorophyll content was higher under low compared to high light conditions. This suggests that *Q. pubescens* is able to maintain and preserve its photosynthetic apparatus under limited light conditions,

as also demonstrated under drought stress (Gallé et al., 2007; Laoué, Gea-Izquierdo, et al., 2024; Laoué, Havaux, et al., 2024). We also observed no significant difference in the abundance of root-associated fungi between high and low light conditions. This contrasts with studies on other species such as that of Shi et al. (2014) or Shukla et al. (2009) who reported a positive effect of light on root mycorrhizal colonization, suggesting a species-specific or context-dependent response.

Our study demonstrates that water stress negatively affects *Q. pubescens* growth, particularly in aboveground parts, leading to decreases in height, leaf number and leaf and stem biomass. Despite the slowdown in growth, *Q. pubescens* – a species known for its drought tolerance (Gallé et al., 2007; Haldimann et al., 2008; Saunier et al., 2022) - exhibited several strategies to cope with water stress. First, seedlings showed a shift in biomass allocation toward belowground parts, with an investment concentrated in primary roots, which did not appear to be affected by water stress. This pattern suggests an adaptative strategy aimed at increasing the volume of soil exploited for water supply, as already observed by Di Iorio et al. (2011). We further observed a reduction in fine roots biomass that could imply an increased vulnerability of fine roots to desiccation but also indicate a shedding strategy (Di Iorio et al., 2011): *Q. pubescens* seedlings reduce maintenance costs under water stress and enhance the role of thicker roots as temporary water storage organs (Eissenstat & Yanai, 1997). Conversely, water stress caused an increase in leaf chlorophyll content, indicating that *Q. pubescens* can stimulate its photosynthetic apparatus under limiting conditions, a response that we also observed when *Q. pubescens* is under low light availability. Finally, drought did not affect the abundance of root-associated fungi. While water stress can variably influence mycorrhizal colonization (positively or negatively), maintaining an effective mycorrhizal symbiosis is essential for plant drought tolerance as it helps increase water uptake by the plant.

Fi Finally, drought did not affect fungal abundance when expressed per unit of root mass. This result should be interpreted in light of the observed decrease in fine root biomass. Although fungal abundance at the root level was not influenced by water stress, the overall reduction in fine root biomass was not counterbalanced by an increase in mycorrhizal colonization. However, effective

mycorrhizal symbiosis is essential for plant drought tolerance, as it can improve water and nutrient uptake and mitigate stress (Augé, 2001; Domínguez Núñez et al., 2009; Mohan et al., 2014). Augé (2001) reported that drought can have contrasting effects on root colonization but that it more frequently leads to increased colonization, particularly under field conditions. Since the present study was conducted as a pot experiment, future field-based research will be vital to clarify whether these patterns hold true in more complex ecosystems.

For most of the morphological traits measured, we observed a strong interaction in their response to canopy opening (*i.e.*, light availability) and water stress. According to the facilitation hypothesis, under drought conditions, the negative effects of light limitation may be outweighed by its benefits for plant water status (Callaway, 1995; Sack, 2004; Valladares et al., 2016). Our study appears to confirm this hypothesis, as we observed a limited effect of water stress on most *Q. pubescens* seedlings traits under low light conditions. As discussed by Maestre et al. (2003), Quero et al. (2006) or Sánchez-Gómez et al. (2006), the facilitating role of shade during periods of drought could be involved in the regeneration process in Mediterranean environments. This has direct implications for forest management practices that modulate forest canopy cover, such as thinning. However, it should be noted that, under combined shade and drought conditions, we observed that *Q. pubescens* seedlings failed to enhance photosynthesis, in contrast to single stress conditions. Similar findings for *Q. suber* suggest that shade can impair the development of key drought-tolerance mechanisms, including osmotic adjustment and water loss regulation (Aranda et al., 2005). Our results also indicate that only the combined effect of shade and water stress significantly limits root colonization by mycorrhizae. Further analyses could provide a better understanding of the observed effects, such as strict distinctions between mycorrhizal groups (ecto-mycorrhizal and arbuscular mycorrhizal fungi), which may have different responses to abiotic factors (Mohan et al., 2014).

Effects of competition on *Q. pubescens* seedlings

First, our results highlight the effect of competition with a Poaceae species on *Q. pubescens* seedling growth, confirming the importance of considering the herbaceous stratum in the regeneration

process (Thrippleton et al., 2016). Indeed, in the presence of *Festuca ovina*, we observed reduced growth (height, diameter, above- and belowground biomass) as well as a lower above-/belowground biomass ratio compared to *Q. pubescens* seedlings developed without *F. ovina.* This latter observation indicates a higher investment in root biomass in order to resist competition for water and nutrient resources, which is in line with the findings of Kunstler et al. (2006). Our results are also consistent with those of Tonioli et al. (2001), who demonstrated in a field experiment that the surrounding vegetation, even though it plays a facilitating role during emergence, competes with young *Q. pubescens* seedlings for their growth. Another pot experiments, described by Coll et al. (2004), on *Fagus sylvatica* demonstrated the strong competitiveness of Poaceae species, particularly for water resources, thanks to their extensive root systems. Here, we also observed that the presence of *F. ovina* exerts a negative impact on the belowground biomass of *Q. pubescens*, affecting both fine and primary roots, but also inducing a reduction in chlorophyll index. In absence of *F. ovina*, oak seedlings displayed adaptative strategies to cope with water stress, such as an increase in chlorophyll index (see discussion above). In contrast, no such compensatory responses were detected under competition in favorable hydric conditions, suggesting the stronger constraining effect of competition. Similarly, we observed a significant reduction in the abundance of root-associated fungi in the presence of *F. ovina*, an effect that was not found under water stress or low light availability. Fernandez et al. (2023) studied the ectomycorrhization of *Q. petraea* seedlings growing with another Poaceae species, *Molinia caerulea,* and observed a reduced mycorrhizal association rate with oak roots. These inhibition patterns could be explained by allelopathic interactions, as discussed by Fernandez et al. (2023). Indeed, *F. ovina,* and more generally *Festuca* species, are known for their allelopathic potentialities (Bertin et al., 2007; de Bertoldi et al., 2012; Lipińska et al., 2013). Further experiments analyzing root exudates would provide valuable insights into the effects of *F. ovina* on *Q. pubescens* and its mycorrhization, by allowing us to distinguish between competitive effects and chemical interactions.

Furthermore, we observed that the presence of *F. ovina* also affects soil physicochemical characteristics. Our results highlight an increase in soil pH, cation exchange capacity (CEC), and the

concentration of certain exchangeable cations (MgO, CaO, Na_2O) in the presence of *F. ovina*. These results are consistent with previous studies indicating that grasses can alter soil chemistry (Koukoura et al., 2003; Wyszkowska et al., 2022), thereby influencing the growth of woody plants. Indeed, a change in soil chemistry can affect soil structure and the availability of nutrients for the plants. Our results suggest that the presence of *F. ovina* is associated with improved soil fertility (particularly due to higher CEC and pH). However, this benefit does not appear sufficient to offset the negative effects of the presence of *F. ovina* on *Q. pubescens* growth. Further research would be needed to clarify the underlying mechanisms of competition.

Finally, our results confirm, as discussed for example by Kohler et al. (2020), that large canopy openings can constrain the regeneration of target species by increasing light availability and promoting the development of herbaceous species (Floret et al., 1992; Palviainen et al., 2005; Kohler et al., 2020).

Our results also emphasize the interactions between biotic and abiotic factors, as we observed that the effects of competition depend on both canopy opening level and soil hydric conditions. Firstly, canopy opening, and therefore light availability, influences the competition between *F. ovina* and *Q. pubescens*. As expected for a Poaceae species (Xu et al., 2025), *F. ovina* above- and belowground biomass declined under low canopy opening, reflecting its sensitivity to light limitation. Furthermore, under low light conditions, the presence of *F. ovina* only marginally affected *Q. pubescens* seedling growth. In other words, as observed by Vernay et al. (2019) in the case of competition between *Q. petraea* and *Molinia caerulea*, competition interactions are amplified by light availability. Secondly, water stress also influences the competition between *F. ovina* and *Q. pubescens*. At high canopy opening level, we observed a negative effect of water stress on *F. ovina* aboveground biomass but not on its belowground biomass. This result corroborates previous observations indicating that the *Festuca* genus exhibits high drought tolerance, attributed to its fibrous rhizomes and extensive root system (Gibson & Newman, 2001; Yamada, 2011). Since water stress has a weaker impact on the growth of *F. ovina* than light limitation, competition between *F. ovina* and *Q. pubescens* is also less constrained by water stress than by low light availability. Indeed, under water stress, the presence of *F. ovina* still

498 negatively influenced *Q. pubescens* growth (*e.g.*, height, aboveground biomass or primary roots
499 biomass). These results further highlight that intensive canopy opening can hinder regeneration. By
500 increasing light availability, these openings intensify competitive interactions and exacerbate water
501 stress, which disadvantage oak seedlings compared to *F. ovina*. However, it should be noted that low
502 light availability imposes an equally strong limitation on oak seedling growth than water stress
503 combined with competition under high light availability, showing that both intensive and insufficient
504 canopy opening levels exert significant constraints.

505 Finally, our study contributes to the broader discussion on forest management
506 recommendations aiming at enhancing regeneration in a climate change context. First, we highlight
507 the role of competition with Poaceae species, in our case with a *Festuca* species, in oak regeneration.
508 The presence of Poaceae species not only increases competitive pressure for resources, but also
509 modifies soil properties and belowground interactions. Furthermore, our results emphasize the key
510 roles of light availability and hydric conditions on seedling development, whose levels are largely
511 dependent on silvicultural operations (Mölder et al., 2019). We revealed a persistent light requirement
512 for optimal seedling performance, indicating that regeneration success depends on achieving a balance
513 between sufficient canopy opening to provide light and enough cover to mitigate drought stress and
514 minimize grass competition. It would be interesting to continue our research with field studies to avoid
515 the biases introduced by pot experiments, but also over a longer period of time, during which
516 individuals experience several dry seasons.

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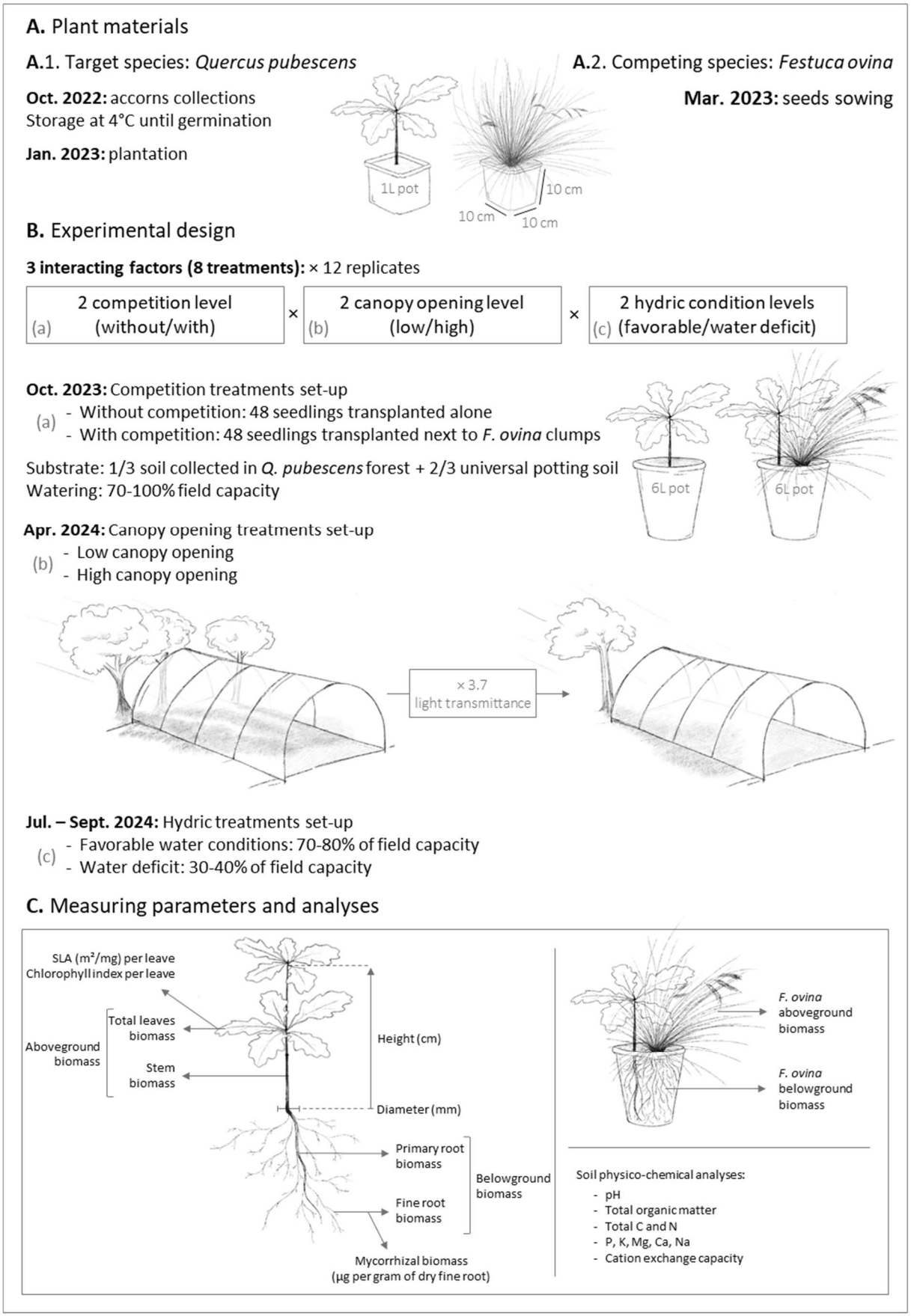
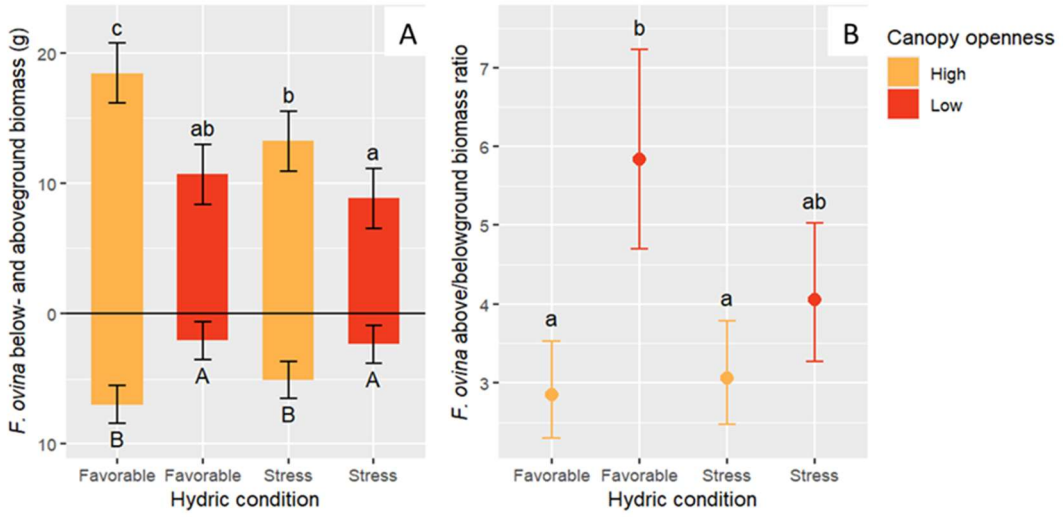
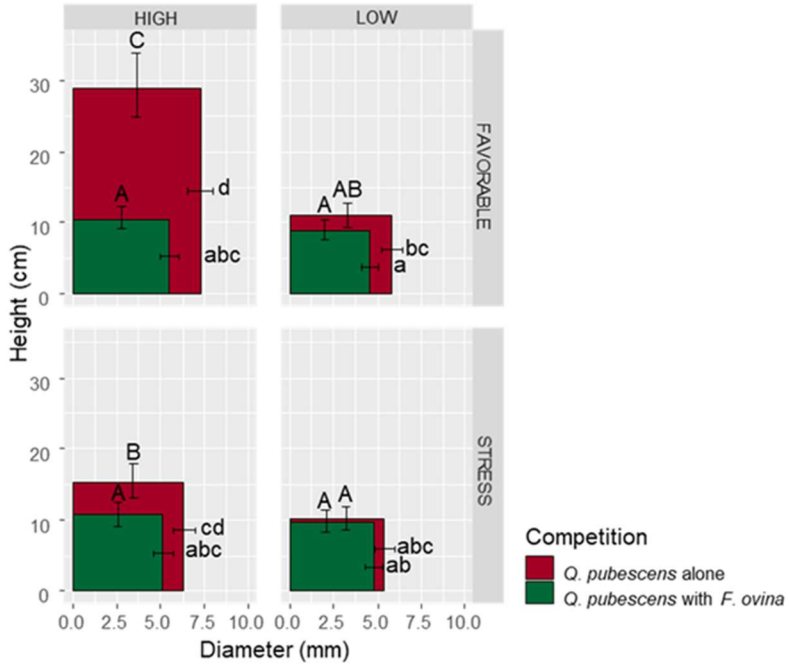


Figure 1. Experimental design testing 2 competition levels, 2 canopy opening level and 2 hydric conditions on Q. pubescens seedling growth.



912

913 Figure 2. Festuca ovina above- and belowground biomass in g (A) and above/belowground ratio (B). Bars represent means ±
914 standard error, n=12. Letters indicate significant differences between treatments based on post hoc Tukey tests (p-value <
915 0.05). (A) Uppercase letters below the bars indicate significant differences in belowground biomass; lowercase letters above
916 the bars refer to aboveground biomass.



917

918 Figure 3. Effects of competition, canopy opening, hydric conditions and their interactions on Q. pubescens growth in height
919 and diameter. Predicted values are obtained from linear and generalized linear models with Anova (type III). The letters
920 indicate significant differences (uppercase for height and lowercase for diameter) based on Tukey's post hoc comparisons (p-
921 value < 0.05) within each combination.

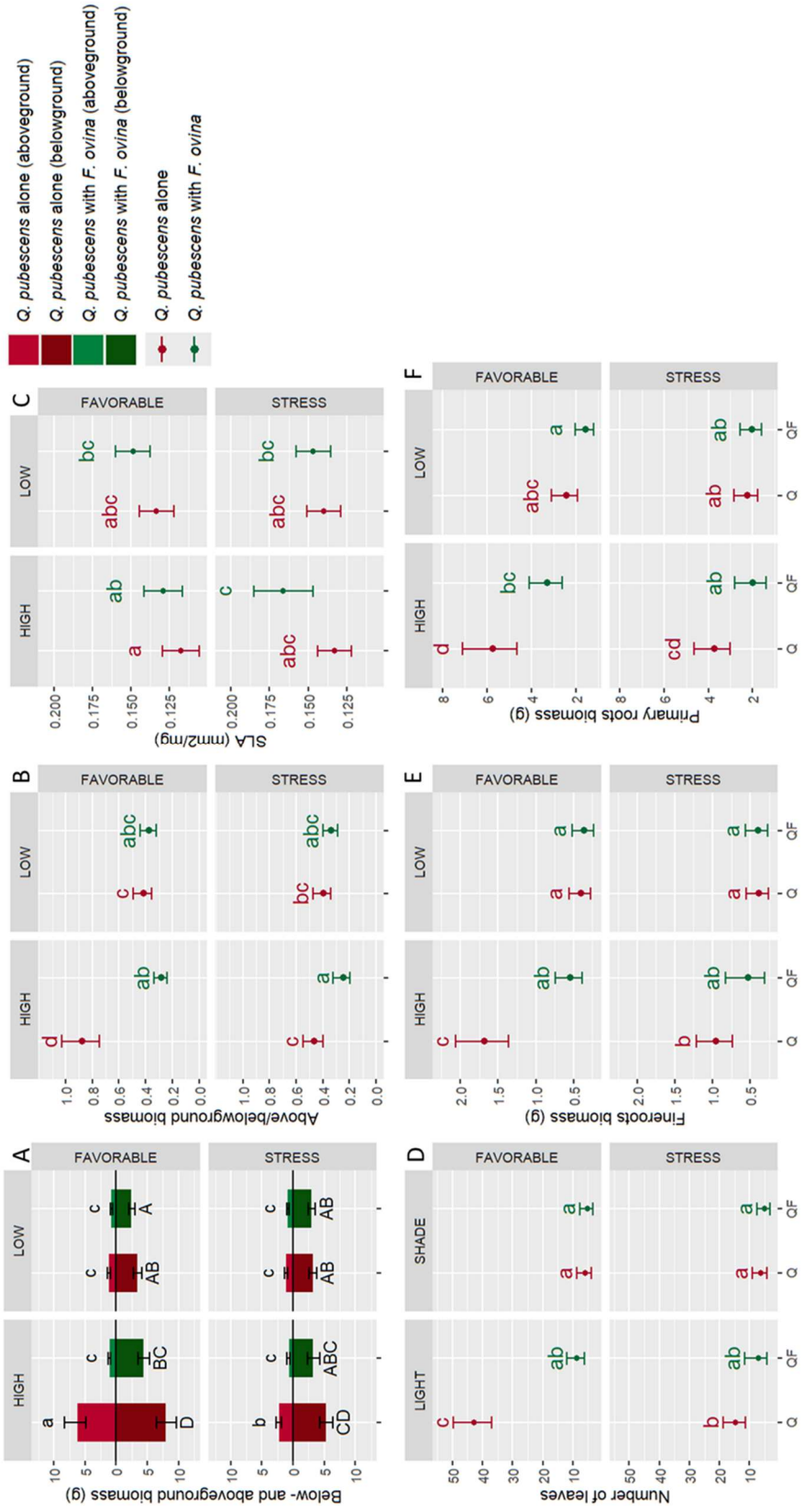
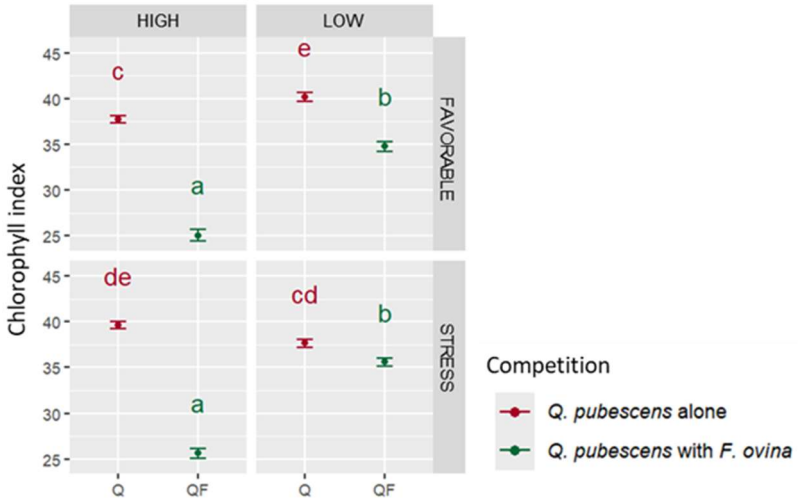
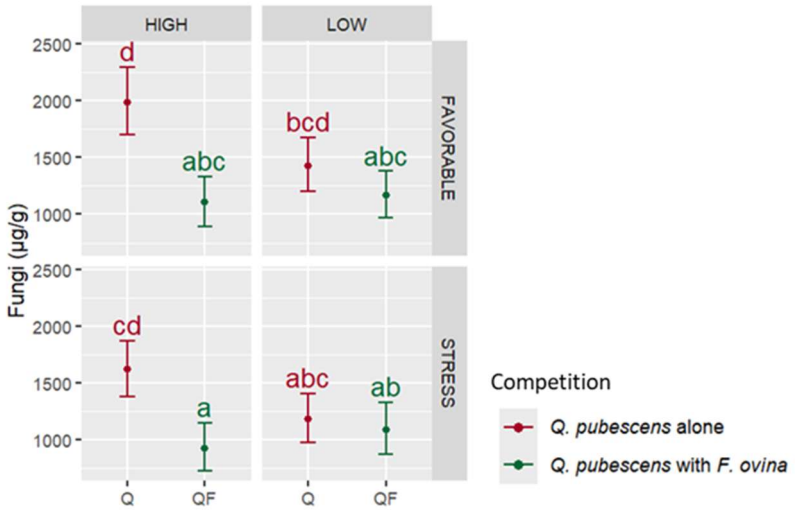


Figure 4. Effects of competition, canopy opening, hydric conditions and their interactions on Q. pubescens aboveground and underground biomass per individual (A), aboveground/underground biomass ratio (B), SLA (C), Number of leaves per individual (D), Fine roots biomass per individual (E) and Primary roots biomass per individual (F). Predicted values are obtained from linear and generalized linear models (Table 5) with Anova (type III).



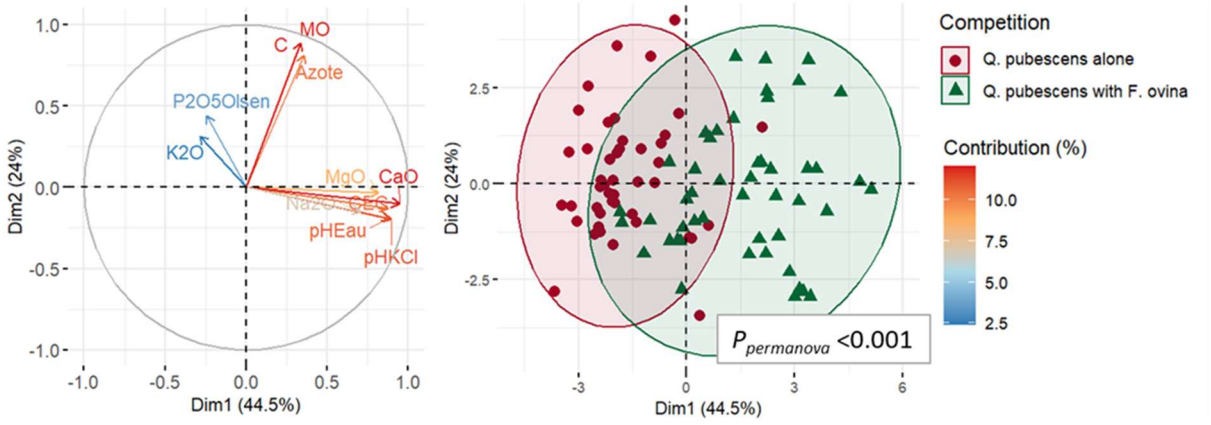
927

928 Figure 5. Effects of competition, canopy opening, hydric conditions and their interactions on Q. pubescens chlorophyll index
929 (mean ± se). Kruskal-Wallis p-value < $2.2e^{-16}$ and Dunn test results are shown with letters.



930

931 Figure 6. Effects of competition, canopy opening, hydric conditions and their interactions on the fungal abundance associated
932 to Q. pubescens roots (µg/g of dry fine roots). Predicted values are obtained from a linear model (Table 5) with Anova (type
933 III).



934

935 Figure 7. Principal component analysis (PCA) from the soil physico-chemical parameters according to competition levels and
936 main explanatory variables of PC1 and PC2.

Table 1. Means ± standard errors of substrate physico-chemical parameters at the beginning of the experiment (n=6).

CEC (meq/100 g)	20.6 ± 0.7
pH (Water)	5.4 ± 0
pH (KCl)	4.8 ± 0
Organic matter (%)	25.8 ± 1.2
P2O5 Olsen (%)	319.2 ± 8.7
K2O (mg/kg)	1011.2 ± 19.7
MgO (mg/kg)	501.7 ± 8.4
CaO (mg/kg)	3940 ± 99.6
Na2O (mg/kg)	103 ± 2.2
N (mg/kg)	3674.2 ± 180.6
C (g/kg)	149.9 ± 7.1
C/N ratio	40.8 ± 0.9

Table 2. Means ± standard errors of daily mean, maximum, and minimum temperature (in °C), daily mean relative humidity values (in %) and daily VPD (Vapor Pressure Deficit in kPa) over the experimental period. Different letters indicate significant differences between canopy opening levels (Kruskal Wallis tests with *p*-value threshold = 0.05).

Canopy opening level	**Daily mean temperature (°C)**	**Daily max temperature (°C)**	**Daily min temperature (°C)**	**Daily mean relative humidity (%)**	**VPD (kPa)**
High	24.4 ± 0.4 (a)	41.5 ± 0.6 (a)	16.1 ± 0.3 (a)	59.8 ± 0.7 (a)	1.8 ± 0.7 (a)
Low	21.9 ± 0.3 (b)	29.4 ± 0.4 (b)	17.0 ± 0.3 (b)	60.8 ± 0.8 (a)	1.2 ± 0.4 (b)

Table 3. Results of type III ANOVA and associated P values testing for the effects of canopy opening (O), hydric conditions (H) and their interaction on *F. ovina* traits. (Notes: * for P < 0.5, ** for P < 0.01 and *** for P < 0.005)

	Canopy Opening (O)	Hydric conditions (H)	O × H
*F. ovina a*boveground biomass (g)	**28.11*** **	**9.49** **	2.18^{ns}
*F. ovina below*ground biomass (g)	**135.96*** **	**28.97*** **	1.29^{ns}
Aboveground/belowground ratio	**624.96*** **	**22.01*** **	1.88^{ns}

950 Table 4. Results of type III ANOVA and associated P values testing for the effects of competition (C),
951 canopy opening (O), hydric conditions (H) and their interaction on *Q. pubescens* growth parameters
952 at the end of the experiment (height, diameter and height/diameter ratio). (Notes: * for P < 0.5, **
953 for P < 0.01 and *** for P < 0.005).

	Competition (C)	Canopy Opening (O)	Hydric conditions (H)	C × O	C × H	O × H	C × O × H
Height (cm)	**52.8*** **	**56.1*** **	**7.7** **	**25.1*** **	**13.4*** **	**8.5** **	**4.6***
Diameter (mm)	**36.5*** **	**20.2*** **	2.7^{ns}	0.8^{ns}	2.0^{ns}	2.0^{ns}	0.2^{ns}
Height/diameter	**12.0*** **	**20.8*** **	2.8^{ns}	**19.3*** **	**7.4** **	**4.3** **	**6.1** **

954

955 Table 5. Results of type III ANOVA and associated P values testing for the effects of competition (C),
956 canopy opening (O), hydric conditions (H) and their interaction on *Q. pubescens* morphological and
957 physiological traits. (Notes: * for P < 0.5, ** for P < 0.01 and *** for P < 0.005)

	Competition (C)	Canopy Opening (O)	Hydric conditions (H)	C × O	C × H	O × H	C × O × H
Aboveground biomass (g)	131.3***	64.5***	20.4***	48.1***	5.6*	21.6***	1.2^{ns}
Underground biomass (g)	23.2***	43.7***	4.1*	5.6*	1.4^{ns}	7.9**	0.3^{ns}
Aboveground/underground	65.5***	1.6^{ns}	13.2***	34.5***	3.1^{ns}	6.2*	5.0*
Fine roots biomass (g)	19.5***	46.1***	2.3^{ns}	17.6***	3.2^{ns}	3.2^{ns}	1.8^{ns}
Primary roots biomass (g)	25.2***	37.2***	5.4*	4.2*	0.7^{ns}	10.1**	1.0^{ns}
Leaf biomass (g)	173.3***	95.8***	43.2***	89.2***	15.3***	36.3***	11.1**
Stem biomass (g)	84.8***	46.9***	14.0***	28.4***	8.2**	19.1***	2.2^{ns}
SLA (mm^2/mg)	14.0**	1.7^{ns}	10.0**	1.6^{ns}	0.5^{ns}	7.1*	2.9^{ns}
Leaf surface (mm^2)	2.9^{ns}	5.3*	0.1^{ns}	1.5^{ns}	0.04^{ns}	1.3^{ns}	0.1^{ns}
Number of leaves	27.1***	46.0***	5.7*	13.4***	2.0^{ns}	6.1*	3.1^{ns}
Fungal abundance (µg/g)	32.5***	3.9^{ns}	6.6*	12.3***	0.7^{ns}	0.3^{ns}	0.03^{ns}
SQI (Seegling Quality Index)	11.7**	20.7***	2.9^{ns}	0.4^{ns}	0.003^{ns}	3.3^{ns}	3.4^{ns}

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