Universidad de Valladolid

Master on Forest Management based on Data Science
(DATAFOREST)

Monitoring *Quercus* seedling survival and growth beneath nurse shrubs and grazing exclusion in mine soils

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RESUMEN

Las interacciones facilitadoras entre plantas permiten a muchos individuos persistir en entornos estresantes. Sin embargo, su uso como técnica de restauración de la cubierta vegetal en ecosistemas degradados por el hombre requiere más conocimiento sobre su eficacia a largo plazo. Se diseñó un experimento de campo de 10 años se seguimiento para determinar si los arbustos colonizadores nativos (*Genista florida* y *Cytisus scoparius*), utilizados como plantas nodriza, mejoran la supervivencia y crecimiento de *Quercus petraea* y *Q. pyrenaica* en las minas de carbón a cielo abierto restauradas en el norte de España. Se plantaron 400 plántulas de cada especie de roble bajo cuatro tratamientos diferentes que combinaban la influencia de los arbustos y la valla sobre las plántulas de *Quercus*. Las parcelas cercadas dentro de este diseño experimental permiten la diferenciación de los dos principales efectos facilitadores ejercidos por los arbustos: la protección frente a presiones bióticas (herbivoría por ungulados) y abióticas (sequías de verano).

Los arbustos mejoraron la supervivencia de las plántulas en comparación con áreas sin ellos, particularmente para *Q. pyrenaica*. La mortalidad de plántulas en áreas sin arbustos ocurrió principalmente durante el primer año (90% vs. 11% bajo arbustos), mientras que bajo arbustos la mortalidad fue mayor el segundo año (93% fuera de arbustos vs. 50% bajo arbustos). Después, la supervivencia disminuyó gradualmente y, tras 10 años, la mortalidad alcanzó el 83% para *Q. petraea* y el 66% para *Q. pyrenaica* bajo arbustos, en comparación con el 96 y el 99%, respectivamente, fuera de la cubierta de arbustos. La herbivoría no parece ser una gran limitación para la supervivencia; un efecto marginal positivo de la valla se encontró solamente en años puntuales.

El crecimiento de las plántulas de *Quercus* depende del efecto positivo combinado del arbusto y la valla, siendo más importante para *Q. petraea*. La protección contra el estrés abiótico (sequías de verano) mediada por los arbustos puede ser más determinante del crecimiento de las plántulas de *Quercus* en la etapa temprana que la protección contra el estrés biótico (herbívoros), mientras que la valla gana protagonismo más tarde en áreas sin arbustos, especialmente para *Q. petraea*. Se encontraron pequeños incrementos de altura y diámetro de las plántulas de *Quercus* con el tiempo, más pronunciados para *Q. petraea*. Además, las diferencias en el crecimiento anual de las plántulas de *Quercus* entre áreas con y sin arbustos fueron menores en los años más estresantes.

Se concluye que en las minas de carbón restauradas para uso ganadero bajo un clima sub-Mediterráneo, donde los efectos de la sequía del verano se incrementan por las limitaciones de los suelos mineros, los arbustos colonizadores nativos, *Genista florida* y *Cytisus scoparius*, tienen un claro efecto facilitador sobre las plántulas de especies de *Quercus* ecológicamente contrastadas (*Q. pyrenaica* y *Q. petraeae*). El efecto facilitador se encontró sobre ambas especies, pero con diferente intensidad según la especie considerada y la variable medida (supervivencia o crecimiento). Aunque en nuestras condiciones de estudio, la restauración con arbustos nodriza tiene un efecto positivo sobre ambas variables, los mecanismos de facilitación involucrados no fueron los mismos para supervivencia y crecimiento.

Por lo tanto, el uso de arbustos como plantas nodriza para mejorar las condiciones ambientales puede tener un papel clave en la restauración de robledales degradados, especialmente para la especie eurosiberiana, en su límite bioclimático en áreas sub-Mediterráneas pastoreadas, resultando ser una técnica prometedora para la reintroducción efectiva de especies arbóreas sucesionales tardías, como *Q. petraea* y *Q. pyrenaica*, en minas sedel carbón rehabilitadas. La tolerancia al estrés de la especie objetivo, así como las condiciones más estresantes de años particulares, deben tenerse en cuenta para garantizar la eficacia de esta técnica de restauración.

Palabras clave: Facilitación, *Quercus* spp., arbustos nodriza, restauración forestal, herbivoría, supervivencia, crecimiento, minas de carbón.

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ABSTRACT

Facilitative interactions among plants enable plants to persist in stressful environments. However, its use as a restoration technique of plant cover in degraded man-made ecosystems requires more knowledge on the effectiveness of this technique in the long term. A 10-year field experiment was conducted to determine if native colonizer shrubs (*Genista florida* and *Cytisus scoparius*) used as nurse plants enhance *Quercus petraea* and *Quercus pyrenaica* survival and growth in reclaimed open-cast coal mines in Northern Spain. Of each tree species, 400 seedlings were planted under four different treatments combining the influence of nurse shrubs and fencing upon *Quercus* seedlings. Fenced plots within this experimental design allow the differentiation of the two main facilitator effects exerted by shrubs: the protection from biotic (herbivory by ungulates) and abiotic (summer droughts) stresses.

Shrubs enhanced seedling survival compared to areas without shrubs, particularly for *Q. pyrenaica*. Seedling mortality in areas without shrub cover occurred mostly during the first growing season (90% vs. 11% under shrubs), whereas under shrubs the highest mortality increment occurred during the second growing season (93% died outside shrubs vs. 50% died under shrubs). Afterwards, seedling survival decline gradually and, after 10 years, mortality reached 83% for *Q. petraea* and 66% for *Q.pyrenaica* under shrubs compared to 96 and 99%, respectively, outside the canopy of shrubs. Seedling herbivory did not seem to be a great limitation to survival; a marginally positive effect of the fence was found only in specific years.

Quercus seedling growth depended on the combined positive effect of shrub and fence, being more important for *Q. petraea*. The protection from abiotic stress (summer droughts) mediated by shrubs may be more determinant of the *Quercus* seedlings' growth at the early stage than the protection from biotic stress (herbivory), while the fence became more relevant later in areas without shrubs, especially for *Q.petraea.* Slow increments of *Quercus* seedling height and diameter over time were found, although both increments were more pronounced in *Q. petraea*. Moreover, the differences in *Quercus* seedling annual growth between areas with and without shrubs were lower in the most stressful years.

We conclude that in coal mines reclaimed for livestock use under a sub-Mediterranean climate where the summer drought effects are increased by the constraints of mine soils, the native colonizer shrubs, *Genista florida* and *Cytisus scoparius*, have a clear facilitative effect on seedlings of ecologically contrasted *Quercus* species (*Q. pyrenaica* and *Q. petraeae*). The facilitative effect was found for both *Quercus* species, but to a different degree depending on the species considered and the variable measured (survival or growth). Although in our study conditions, restoration with nurse shrubs does not confront survival against growth, the mechanisms of facilitation involved were not the same to enhance survival or growth.

Therefore, the use of shrubs as nurse plants to improve environmental conditions can have a key role in the restoration of degraded oak ecosystems, especially for the Eurosiberian species, under a bioclimatic limit in sub-Mediterranean grazed areas, resulting in a promising technique the effective reintroduction of late-successional tree species, such as *Q. petraea* and *Q. pyrenaica*, in reclaimed coal mines. The stress tolerance of the target species as well as the more stressful conditions in particular years should be taken in consideration in order to increase the effectiveness of this restoration technique.

Key words: facilitation, *Quercus* spp., nurse shrubs, forest restoration, herbivory, survival, growth, coal mine.

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1. INTRODUCTION

Over the last few decades, multiple theoretical and experimental works have revealed the capacity of some plant species, many of them shrubs, to modify the environment in such a way that favours the establishment of other species, mainly trees, through the facilitation process (Callaway, 1992; Pugnaire & Lázaro, 2000; Pugnaire & Luque, 2001; Callaway et al., 2002; Jordano et al., 2002; Alday et al., 2014). Facilitation is defined as a positive non-trophic interaction between species in which at least one of them benefits, but none of them is harmed (Callaway, 1997; Stachowicz, 2001; Brooker et al., 2008).

During plant-to-plant facilitation, some species benefit others by directly and positively modifying the microclimate (amount of light, temperature and air humidity; Moro et al., 1997a, b; Gómez-Aparicio et al., 2005, 2008; Prieto et al., 2011; Costa et al., 2017) and/or soil conditions (fertility, soil moisture, texture; Pugnaire et al., 1996a, 2004; Gómez-Aparicio et al., 2005; Prieto et al., 2011; Mihoč et al., 2016), and indirectly protecting against herbivores (Pugnaire, 2001; Rebollo et al., 2002; Gómez-Aparicio et al., 2008), attracting pollinators (Ghazoul, 2006), serving as a refuge/shelter against animals (Archer et al. 1988), inducing changes in the soil microbial community (Ezeokoli et al., 2020), edaphic fauna and mycorrhizal associations (Moora & Zobel, 2010; Casanova-Katny et al., 2011).

Positive interactions act simultaneously with negative interactions as competition, so the final balance depends on which mechanisms are more important in a given environment and/or time, resulting in positive or negative outcomes (Callaway & Walker, 1997; Holmgren et al., 1997; Pugnaire, 2001).

Facilitation seems to be more evident in stressful environments according to the stress gradient hypothesis (Bertness & Callaway, 1994), which postulates that positive interactions (e.g., facilitation) tend to be more important than negative ones (e.g., competition) in plant communities subjected to intense water stress or high herbivore pressure. The positive balance in plant-to-plant interactions has been observed and studied more often in harsh environments, also in the Iberian Peninsula (Greenlee & Callaway, 1996; Pugnaire et al., 1996a, b; Callaway 1997; Moro et al., 1997a, b; Brooker & Callaghan 1998; Pugnaire, 2001; Callaway et al., 2002; Brooker et al., 2008). Positive interactions are the rule under severe physical conditions (Callaway, 2007) or when consumer/herbivore pressure increases (García & Obeso, 2003; Baraza et al., 2006).

However, some researches show that both the net balance and the strength of the interactions may vary depending on other circumstances, such as extreme stress levels (Michalet et al., 2006), the abiotic stress factors involved (Maestre et al., 2009), the measurement of efficiency considered (Maestre et al., 2005; Costa et al., 2017), the facilitator species (Maestre et al., 2009; Rolo et al., 2013; Costa et al., 2017), the stress-tolerant/non-tolerant character of the species potentially benefited (Maestre et al., 2009; Madrigal-González et al., 2014) or the vital stage of the organisms interacting, among others (Bertness & Callaway, 1994). Therefore, although the stress gradient hypothesis is still considered a useful framework (Soliveres et al., 2015), it is not exempt from debate and has been more recently amended/reviewed (Maestre et al., 2005, 2009) because it has been found that, for instance, competition prevails again over facilitation in the most extreme conditions, so that the relationship between facilitation and stress is not linear (the greater the stress, the greater the facilitation) but U-shaped (the greater the facilitation is found in intermediate stress conditions).

Facilitation studies include research works on the "nurse" effect, by which a tree or shrub species facilitates the recruitment and survival of seedlings of other species (Callaway, 1992; Pugnaire et al., 1996b; Maestre et al., 2005; Smit et al., 2008; Gómez-Aparicio, 2008; Cuesta et al., 2010; Perea & Gil, 2014; Torroba-Balmori et al., 2015; Alday

et al., 2016; Costa et al., 2017; Cruz-Alonso et al., 2020; López- Marcos et al., 2020a; Díaz et al., 2021), resulting in the practical application of facilitation in degraded areas recovery (Padilla & Pugnaire, 2006; Brooker et al., 2008; Domínguez et al., 2015).

Shrubs' nurse effect is highlighted in several research works that assess their usefulness to restore degraded ecosystems in Mediterranean-climate areas of the Iberian Peninsula (Castro et al., 2002; Gómez-Aparicio et al., 2004; Gómez-Aparicio, 2008), and specifically in studies analysing the facilitating role of different shrub species promoting *Quercus* species establishment and growth (Pugnaire et al., 1996; Padilla & Pugnaire, 2006; Smit et al., 2008; Cuesta et al., 2010; Perea & Gil, 2014; Domínguez et al., 2015; Costa et al., 2017; Cruz-Alonso et al., 2020). Some studies directly propose facilitation as the new reforestation technique for the Mediterranean forest (Castro et al. 2002, 2004, 2021; Benayas & Camacho-Cruz, 2004; Gómez-Aparicio et al., 2004; Jordano et al., 2002). Nevertheless, few studies address the facilitating role of shrublands in the reforestation of environments drastically transformed such as those generated by coal mining (but see Torroba-Balmori et al., 2015; Alday et al., 2016). In these environments, the climate (summer drought), soil conditions (unstructured, poor soils and low water holding capacity) and herbivore pressure build a complex scenario that hinders the regeneration of late-successional species such as sessile oak (*Quercus petraea* (Matt.) Lieb.) and Pyrenean oak (*Quercus pyrenaica* Willd.).

Previous results derived from our studies in the coal mines of northwest Palencia show that plant-to-plant facilitation processes are key to explain the dynamics of woody plants natural colonization of restored coal mines and, in particular, oaks spreading from the surrounding forest (Milder et al., 2013; Martínez-Ruiz et al., 2021a). They support the idea of using shrubs as ecosystem engineering species to create a rapid and heterogeneous vegetation cover that provides favourable microsites for the establishment of late-successional species, such as *Quercus petraea* and *Q. pyrenaica* (Torroba-Balmori et al., 2015; Alday et al., 2016). Soil limitations (López-Marcos et al., 2020b) and herbivory (Sigcha et al., 2018) have been identified as some of the factors determining the successional dynamics of vegetation in mining sites.

Within this context, the possibility that shrubs have a positive effect on the establishment of woody trees in these highly degraded environments opens up great expectations for the forest regeneration of areas with similar limitations. Recent studies show that nurse plants positive effects can be very useful for forest restoration (Gómez-Aparicio, 2009; Rey et al., 2009; Castro et al., 2021). However, to contribute to forest expansion exploiting shrubs' facilitation potential as engineering species in forest restoration, it is necessary to identify and characterize the favourable microsites (microclimate, soil, physical barrier against herbivores), to determine under what circumstances positive interactions are more important on the environmental stress gradient, either climate aridity or low moisture retention capacity and poor-nutrient mining substrate (López-Marcos et al., 2020b), as well as herbivore pressure. It is also necessary to evaluate the nursing effect of native shrubs through several simultaneous performance measures (survival and growth), comparing species with contrasting ecological stress behaviours, and in years with different meteorological conditions (Costa et al., 2017). All this information will be very useful to promote precision forest restoration in which the chances of each plant becoming an adult tree while minimizing costs and disturbances effects (Castro et al., 2021).

Furthermore, taking into account that the species favoured by the facilitation process are often at the limit of their environmental tolerance (extremes of their potential ecological range), facilitation mechanisms could contribute to the expansion of their distribution areas, increasing the biological diversity of the community (Choler et al., 2001). This last aspect is especially interesting since several Eurosiberian temperate deciduous tree species such as *Quercus petraea*, which find their southern distribution limit (rear edge) in sub-Mediterranean mountain areas of the Spanish Iberian Peninsula (Gazol et

al., 2022), and whose forests are among the most threatened in our country as a result of climate change (Martínez-Ruiz et al., 2021b).

In this sense, it is of great interest to know whether the drought in the changing sub-Mediterranean environments shifts the sign of plant-to-plant interaction to facilitation or competition, as some works indicate (Maestre et al., 2005, 2009; Soliveres et al., 2015). Cuesta et al. (2010), for instance, points out to the improvement of the microclimate generated by *Retama sphaerocarpa* as factor contributing to *Quercus ilex* recruitment.

Based on these premises, in the present study we assessed the influence of nurse shrubs during ten years on reforested seedlings of two *Quercus* species (*Q. petraea* and *Q. pyrenaica*) in an open-cast coal mine reclaimed for livestock use in northern Spain. In these mining sites summer drought effects are increased by the lack of developed soil, and namely their low water holding capacity (López-Marcos et al., 2020b), limiting the development of *Quercus* species. Moreover, herbivory usually reduces the establishment success of these species (Gómez et al., 2001, 2003; Gómez-Aparicio et al., 2008; Rodríguez-Doce, 2010). Therefore, the use of shrubs as nurse plants might help to decrease these constrains but its effectivity might depend on the meteorological conditions of the different years.

Despite the long-standing recognition of the importance of positive plant-to-plant interactions in ecosystem functioning and in the restoration of degraded ecosystems (Whisenant, 1999; Pickett et al., 2001; Maestre et al., 2003), there are still few studies evaluating in field conditions their potential for the reintroduction of species of interest and for the restoration of biodiversity and ecosystem functions (Navarro-Cano et al., 2019). In a context of climate change, it is expected that the increase in aridity in sub-Mediterranean areas will further limit the natural recruitment capacity of *Quercus* species, alter their relative abundance in the community and enhance shrub facilitating role as a key element for the establishment of their seedlings (Pérez-Ramos, 2014).

Therefore, the knowledge derived from this study can contribute to optimize oak (*Quercus petraea* and *Q. pyrenaica*) forest regeneration in coal mining areas, promoting natural processes such as shrub-tree facilitation. Facilitation is an important structuring force in natural plant communities that could be used as restoration tool, especially in severe and chronically disturbed environments (Brooker et al., 2008).

In this study we consider four key limiting factors for forest regeneration in general in the Iberian Peninsula (Martínez-Muñoz et al., 2019; Martínez-Ruiz et al., 2021a): i) poorly developed soils, ii) summer drought, iii) high herbivore pressure, and iv) interannual variability in meteorological conditions. Therefore, the conclusions obtained can be easily extrapolated to similar areas in which the three factors act individually or simultaneously.

2. OBJECTIVES

The aim of this experiment was to quantify the medium-term effectiveness of using native colonizer shrubs as nurse plants to reintroduce the two main tree species present before the mining operations. Thus, we assessed the influence of native nurse shrubs (*Genista florida* (L.) Link and *Cytisus scoparius* L.), during ten years, on survival and growth of planted seedlings of two *Quercus* species (*Q. petraea* and *Q. pyrenaica*) in an open-cast coal mine reclaimed for livestock use in northern Palencia, and we tried to relate growth to climate during the monitoring period (2011-2021).

Our specific objectives are to:

1) quantify shrub facilitation effects on *Quercus* species seedlings' survival, structural characteristics and growth through their protection against herbivores,
2) prove the role of shrubs as engineering species that generate suitable conditions for trees growth in restored mines,
3) model/determine shifting from shrub facilitation to competition in meteorologically harsh years,
4) quantify shrub facilitation effects on tree species with different ecological requirements and drought tolerance.

Under our objectives above, our hypotheses were, as follows: (1) the effect of shrubs is positive for the medium-term survival of the two *Quercus* species seedlings; (2) shrubs are also be beneficial for medium-term seedling growth and their structural characteristics; (3) a shift in the sign of the interaction occurs in meteorologically harsh years from facilitation to competition or neutral balance; and (4) different patterns between species for the studied parameters exist according to their different ecological requirements.

3. MATERIAL AND METHODS

3.1. Site description and mine restoration treatment

The experiment site was located in a 17 ha reclaimed open-cast coal mine near Guardo, Palencia, Northern Spain (latitude 42º 48' N, longitude 4º 52' W, ca. 1200 m a.s.l.; Figure 1a), in the 'Montaña Palentina' area on predominantly limestone of Paleozoic age, with the presence of clay and to a lesser degree of sand (Milder et al., 2013).
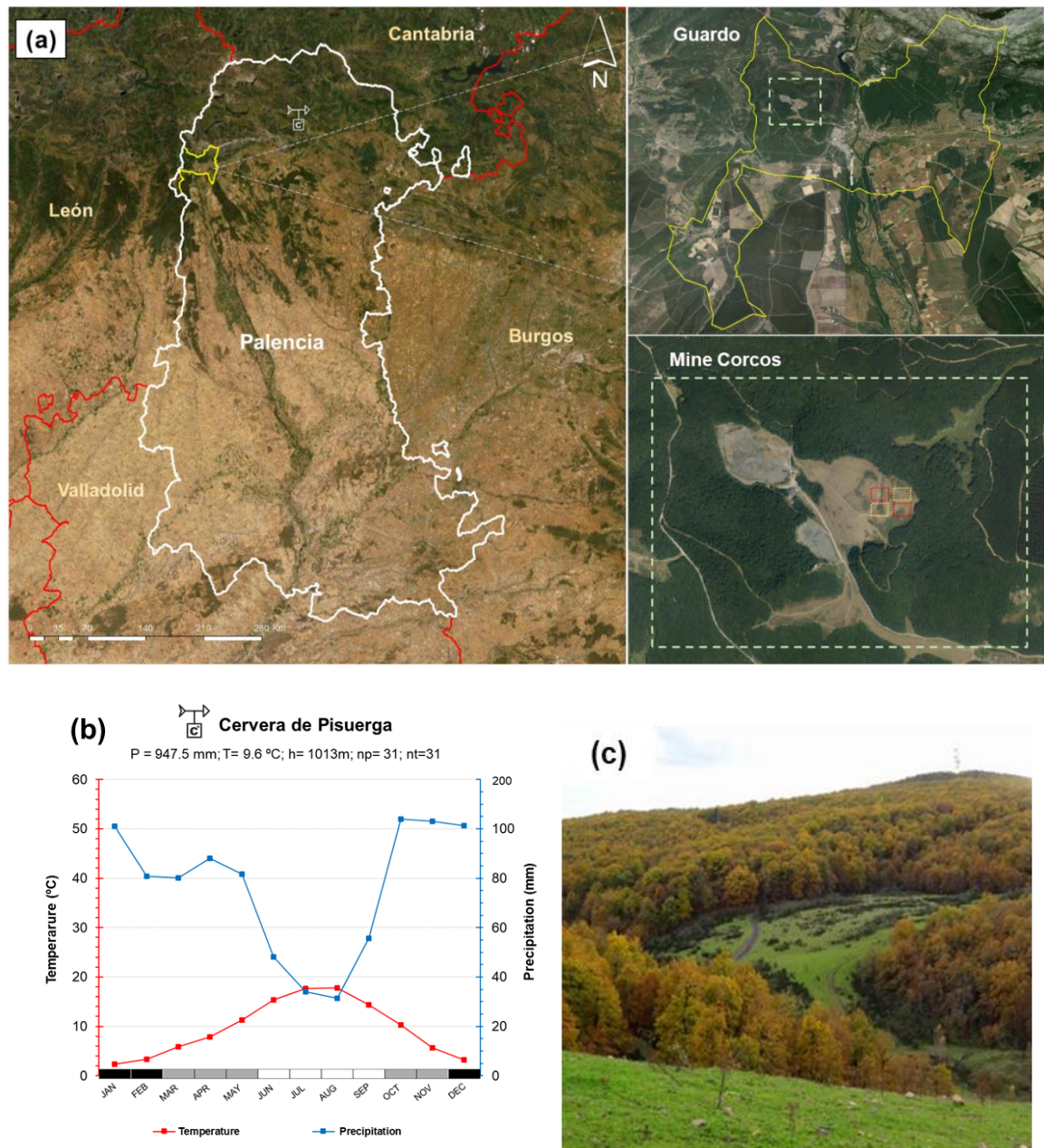
Figure 1: (a) Location of Corcos mine study area in northern Palencia, near Guardo, and position of the four plots use in the experiment set-up (two fenced plots in yellow, and two non-fenced plots in red). **(b)** Bioclimatic diagram of Walter & Lieth (1960) including frost periods (▬ sure frost; ▨ probable frost; □ no frost) of the meteorological station of Cervera de Pisuerga-2234 (1991-2021), the closest to the study area with data available to date (latitude 42º 51' N, longitude 4º 30' W, 1013 m a.s.l.). **(c)** Ecosystems surrounding the mine.

The climate is sub-humid Mediterranean (MAPA, 1991), with an annual mean temperature of 9.6 ºC and average annual precipitation of 947.5 mm (period: 1991–2021;

data provided by the Spanish Meteorological National Agency, AEMET, from the Meteorological Station at Cervera de Pisuerga 2234). Rainfall is not distributed regularly throughout the year, there is a rainy season in autumn and spring and a dry season in summer (July and August) with less than 4% of total annual rainfall (Figure 1b). The mean minimum in the coldest month (January) is –1.9 ºC, and the mean maximum in the warmest month (July/August) is 25.5 ºC. Precipitations and temperatures of the study years (2011-2020) were rather different (see Annex A).

The ecosystems surrounding the mine consists of temperate broad-leaved deciduous woodlands dominated by *Quercus pyrenaica* Willd. and *Quercus petraea* (Matt.) Liebl., and some shrubs such as *Cytisus scoparius* (L.) Link and *Genista florida* L. (Figure 1c), considered to be nonpalatable and even of some toxicity to ungulates (Ammar et al., 2004). The soil of the natural forest that surrounds this mine responds to a Typic Dystroudept (Soil Survey Staff, 2014) with a fine texture known as sandy clay loam with an acid pH (4.3−4.8) without evidence of carbonates, high organic matter content, and low content in available phosphorous (López-Marcos et al., 2020b).

The opencast mine was reclaimed in October 2000, using a combination of topsoiling and hydroseeding after filling the open pit with coal wastes from nearby mines (Torroba-Balmori et al., 2015). The opencast pit surface was regraded to the original contour and covered with fine-textured materials amended with cattle manure that contained a very poor seed bank (González-Alday et al., 2009). The fine-textured topsoiling material used was a mixture of topsoil and sediments from deeper parts of the neighbouring opencast pits (Martínez-Ruiz et al., 2021a). This mixture had a clay loam texture, with a pH of 6.5, electrical conductivity of 114.3 mS/cm, easily oxidizable carbon of 19.8 g/kg, available phosphorous of 9.7 mg/kg and an effective depth of 10–15 cm (López-Marcos et al., 2020b). These soils are classified as Lithic Udorthents (sensu Soil-Survey-Staff, 2014) and they have a very low water-holding capacity compared to the natural soil in the forest (1.0–3.4 vs.19.87±1.52 g/cm^2; López-Marcos et al., 2020b).

After topsoiling, the mine was revegetated with a grassland perennial species mixture (more details in Alday et al., 2011). The reclaimed area has been colonized by native shrubs species from the surrounding forest, mainly *Cytisus scoparius* and *Genista florida* (Martínez-Ruiz et al., 2021b), and grazed by wild ungulates (deer, roe deer, and wild boar), and livestock (cattle and horses) (Milder et al., 2013).

3.2. Experimental design and data collection

The experimental set-up used in this work, with fenced and non-fenced plots, was already used in previous studies, in which were only investigated the short-term effects (two first growing seasons) of nurse shrubs and herbivory exclusion on *Quercus* spp. seedling survival and annual growth (Torroba-Balmori et al., 2015). Now, we explore and quantify both the combined short and medium-term effects on seedling survival, annual growth, height and diameter and its relation to drought dynamics during the period of study (2011-2020). We get deeper on the differentiation of the main facilitation vias: protection against herbivores and generation of microclimate, and the impact of the local conditions on the strength of facilitation processes amongst species over time.

The enclosures consisted of wire mesh fence (2m high, mesh hole: 5cm width x 15cm length) fixed through poles and were constructed to prevent ungulates grazing (Torroba-Balmori et al., 2015). Fenced plots within this experimental design allow the differentiation of the two main facilitator effects exerted by shrubs: the protection from biotic (herbivory by ungulates) and abiotic (summer droughts) stresses.

The nurse shrubs species used were the two natural mine sites colonizers, *C. scoparius* and *G. florida*, with similar vertical structures in the mine (mean height 222±6.6 cm). Both species are non-thorny leguminous shrubs, capable of actively fixing the

atmospheric nitrogen (Talavera et al., 1999). Also, they share common characteristics (i.e., structure and leaf phenology) and they usually co-exist in mine areas where their regeneration in mixed stands. Both species are considered alike species within the same functional group and therefore they were not differentiated during the experiment, based on the methodology carried out in studies using similar functional group species (e.g., Gómez-Aparicio et al., 2004).

The experimental set-up consisted of four plots (30m x 30m) established in a flat area of the mine in February 2011: two fenced plots and two non-fenced plots, with sub-plots with and without shrubs into each one to assess the combined influence of nurse shrubs and grazing upon *Quercus* seedlings (Figure 2). The treatments were: (a) no-grazing and no-shrubs (fenced areas with no shrub cover, FN); (b) no-grazing and shrub cover (fenced areas under shrubs, FS); (c) grazing and no-shrubs (non-fenced areas with no shrub cover NN); (d) grazing and shrub cover (non-fenced areas under shrubs, NS).

Within each plot, 10 sub-plots (5 with shrubs and 5 without shrubs) were allocated randomly ca. 4 m apart from each other (each sub-plot ca. 2 x 2 m; when subplots were under shrubs, they gathered 2-3 shrubs). For instance, in a fenced main-plot, 5 FN sub-plots and 5 FS sub-plots were located, whereas in a non-fenced main plot 5 NN sub-plots and 5 NS sub-plots were set. A total of 40 sub-plots were established, ten per treatment (Figure 2).
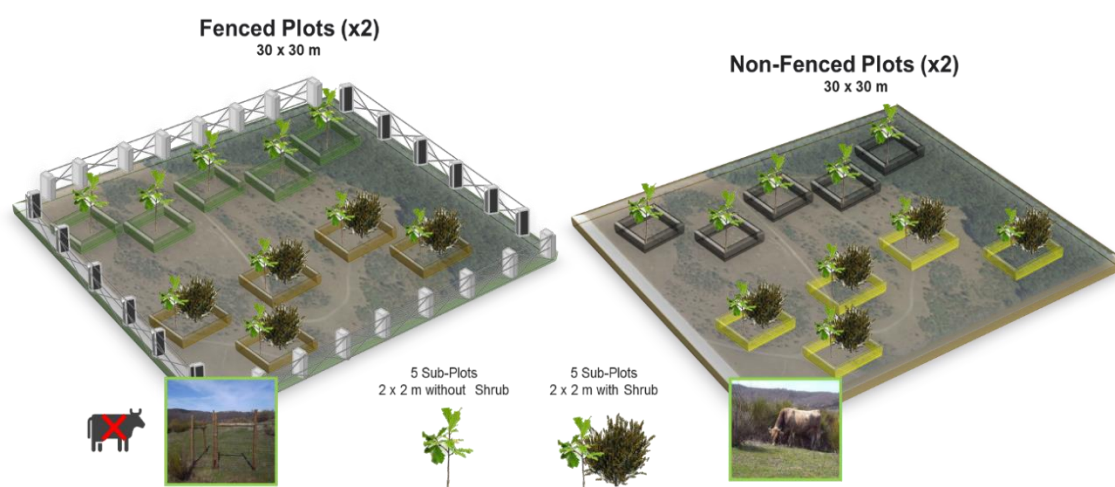
Figure 2: Experimental set-up in the mine "Corcos" near Guardo, northern Spain.

In each sub-plot 10 tagged seedlings (one-year-old) of each species (400 seedlings of *Q. petraea* and *Q. pyren*aica in total) were planted in March 2011. Seedlings (Cordillera Cantábrica Provenance), grown in cylindrical pots (type: S.L 35, 235 cm^3,16 cm deep x 5 cm wide) filled with peat, were provided by the central nursery of Junta de Castilla y León. They were placed separated from each other by 30 cm, in two rows when they were planted in open areas and in one row around the shrub stem, 20 cm far from it, when they were planted under shrubs (see Torroba-Balmori et al., 2015). When the lowest branches of the shrub prevented the seedlings to be placed at that distance, seedlings were planted as near to the stem as possible (ca. 30 cm). Planting was carried out using a small auger (20 cm x 6 cm) to minimize the damage to the shrub roots and soil structure disturbance. In all the cases, the soil was returned to the holes and firmed around the root collar of the seedlings.

Before plantation, initial seedling dimensions, height of leader stem (cm) and diameter at root collar (mm), were measured (see 4.1. Results). One month after plantation, post-plantation survival success was checked through seedling survival evaluation, considering them as dead when stems were dry and no chlorophyll was visible (99.8% of seedlings survived; Torroba-Balmori et al., 2015). After this first survival

evaluation, seedlings were monitored for ten consecutive years (2011–2020). Every autumn, we recorded survival, height and annual growth of the main stem (cm), diameter at root collar (mm) of each individual. Survival was corrected through time for those seedlings that were apparently dead and resprouted in the next surveys.

3.3. Temporal evaluation of climate conditions

The overall climate conditions were analyzed for the last 30-year normal climate period and the last 10 years, matching the length of the field experiment. Several climate variables were used besides monthly data provided by Cervera de Pisuerga Meteorological Station, such as minimum, mean and maximum temperature and precipitation. The potential evapotranspiration index of Thornthwaite –PET– (1948), the water balance and the Standardized Precipitation Evapotranspiration Index (SPEI) were calculated using SPEI package (version 1.7; Vicente-Serrano et al., 2010; Beguería et al., 2014) that uses the Thornthwaite index for estimating the reference evapotranspiration (PET). The SPEI was used as a drought indicator during the study (2011-2020) and Thornthwaite PET as water requirements.

The SPEI is a multi-scaler probabilistic index that allows monitoring of drought conditions at various timescales (Musei et al., 2021). Here, we calculate the SPEI at 1- , 6- , and 12-months for the last 31 years (1991-2021) as well as for our monitoring period (2011-2021).

The SPEI overcomes the disadvantages of other drought indices such as the Palmer drought severity index (PDSI) and the standardized precipitation index (SPI) (Li et al., 2019). It is based on precipitation and temperature and therefore combines the sensitivity of the PDSI to changes in evaporation demand with the simplicity of calculation and the multi-temporal nature of the SPI (Musei et al., 2021). Thus, there has been an increase in the use of the SPEI index in climatology and hydrology studies and is one of the most used drought indices in Europe (Bezdan et al., 2019). The SPEI is based on the difference between precipitation (P) and potential evapotranspiration (PET) accumulated in a certain period (Zhang et al., 2015).

3.4. Establishment limitations and facilitation analysis

All statistical analyses were implemented in the R software environment (4.1.2; R Development Core Team, 2021). Seedling survival was analysed using lme4 package for generalized linear mixed models (GLMM; Bates et al., 2013). Annual growth, height and diameter analyses were carried out with nlme package for linear mixed models (LMM; 3,1-137; Pinheiro et al., 2018). The effect of initial seedling dimensions on survival and annual growth were analysed by GLM or LMM (Pinheiro & Bates, 2000), respectively, considering the initial dimensions (height or diameter) as covariables in the models.

First, we checked the differences between *Quercus* species for the initial dimensions (height and diameter) of planted seedlings using Linear Mixed Models (LMM) with the Restricted Maximum Likelihood method (REML; Richards, 2005). Since they were significant, we looked for differences between treatments/microhabitats for each *Quercus* species separately. Working over the model matrix, multiple pairwise comparisons were calculated to test differences between fixed factor levels (Pinheiro & Bates, 2000). Consequently, the Bonferroni correction was used to adjust for the significance level for each t test (Sokal & Rohlf, 1995). Finally, we assessed, for each species separately, the effect of the initial differences in the dimensions of the seedlings on survival and growth, considering the initial height or diameter as covariable in the models (GLMM for survival and LMM for growth). Since the initial dimensions of planted seedlings didn't have an effect on survival or annual growth, they were not considered in the final models.

Second, the roles that shrubs, fenced areas, planted species and time played in seedling survival were analysed, using GLMMs. In model construction we started with the full model including the interaction between presence/absence of shrubs and fence, species and time as fixed effects. In these models, random effects accounting for spatial and temporal pseudoreplication were included (main-plot, sub-plot and time; Pinheiro & Bates, 2000). The survival data, having a binary response (live or not), were analyzed by logit-link binomial models.

Third, to assess the effect of shrub, fence, species and time on seedlings annual growth, height and diameter we used LMM. *Quercus* species, year and presence/absence of shrubs and fence were included as fixed factors and main-plot, sub-plot, individual and year as random factors. In all analyses, model simplification guidelines followed Crawley (2013) using the Akaike information criterion (AIC; Pinheiro & Bates, 2000). Starting from the full model, the minimal adequate LMM was obtained by sequential removal of non-significant model terms until no further reduction in AIC was observed, and the analysis of the variance of the best model was obtained.

Fourth, the causes of the annual growth were investigated. Based on the best model selected to explain seedlings' annual growth of *Quercus* species along time, as a result of the fence and shrub influence, we explored the annual growth as a response of the annual climate (precipitation, mean temperature water balance, PET, 1-, 6- and 12-month SPEI). Monthly climate variables were aggregated to get annual statistics with several alternative functions (minimum, mean, maximum, sum) for different periods: a) the January-December 12-month period, as in the usual calendar year basis, b) the October-September 12-month period, and c) the April-September 6-month period.

After assessing all the possible models through AIC, multicollinearity, and residuals behaviour, the final model included, as fixed factor, $SPEI_{Oct-Sept}$ and $PET_{April-Sept}$ which could help us to explain the influence of meteorologically harsh years on seedlings' annual growth. The model heteroskedasticity was introduced using Varident variance function structure (Pinheiro & Bates, 2000).
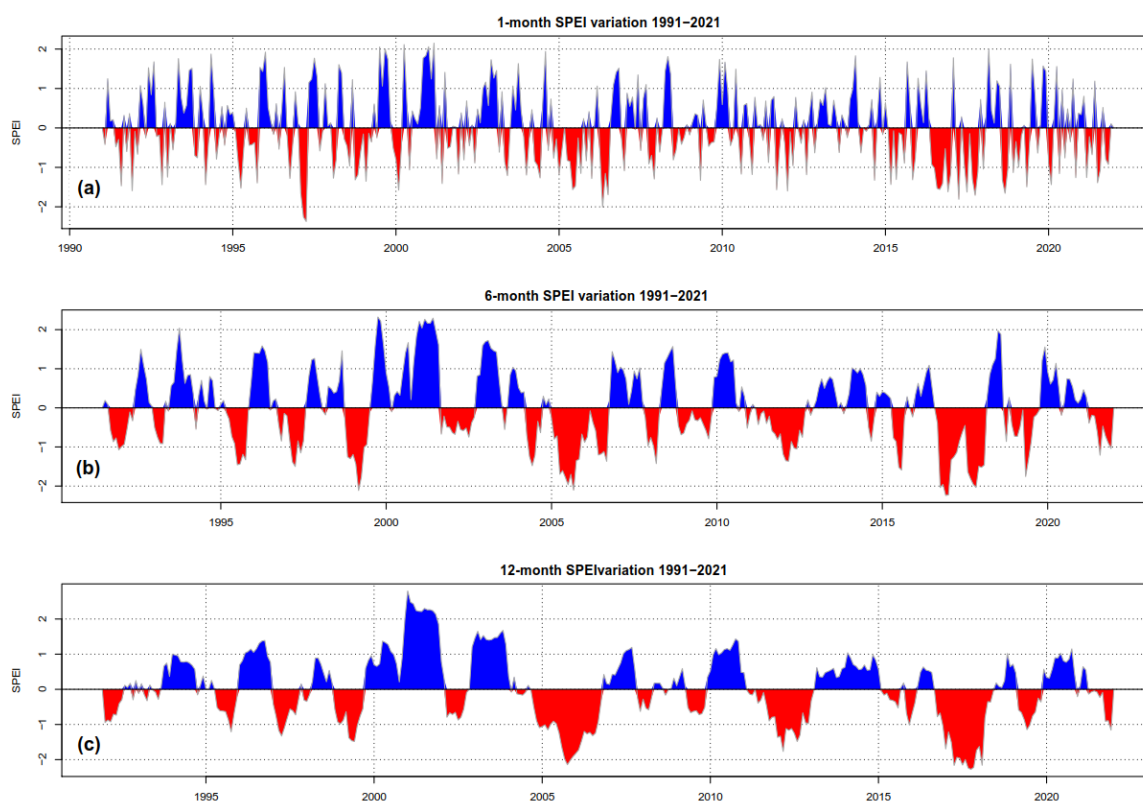
4. RESULTS

4.1. Temporal evaluation of climate conditions

The results of the drought analysis based on the SPEI climate index for the last 31 years (1991-2021) showed a high frequency of drought and short-lived wet periods on the short timescales (1-, 6-months; Figure 3a, b, respectively), whereas on a longer timescale (12-months) drought periods were longer and less frequent (Figure 3c).

The 1-month SPEI (Figure 3a) showed low autocorrelation in the monthly values for short periods, despite winters tend to have positive SPEI values the alternance between positive and negative SPEI was extremely frequent.

The 6-months SPEI (Figure 3b) showed more consistent periodic trends, since it tends to have consistent negative values during summer and positive values during winter. Nevertheless, low intensity and short-length summer negative values periods were common to many years. The 12-months SPEI (Figure 3c) revealed high interannual variability, with many years not having either negative or positive SPEI values. Despite the periodicity the 1-month, 6-months and 12-months SPEI did not show trend over the last normal period.


Figure 3: Variation of calendar year SPEI with time (period: 1991-2021) at different timescales: 1-month **(a)**; 6-months **(b)** and 12-months **(c)**, for the meteorological station of 'Cervera de Pisuerga'.

The results of the drought analysis based on the SPEI climate index for the monitoring period (2011-2021) showed that the longest and most severe droughts were recorded during 2012 (SPEI = -1.11) and 2017 (SPEI = -1.69), whereas wettest periods were recorded in 2014 (1.01) and 2020 (0.89; Figure 4).
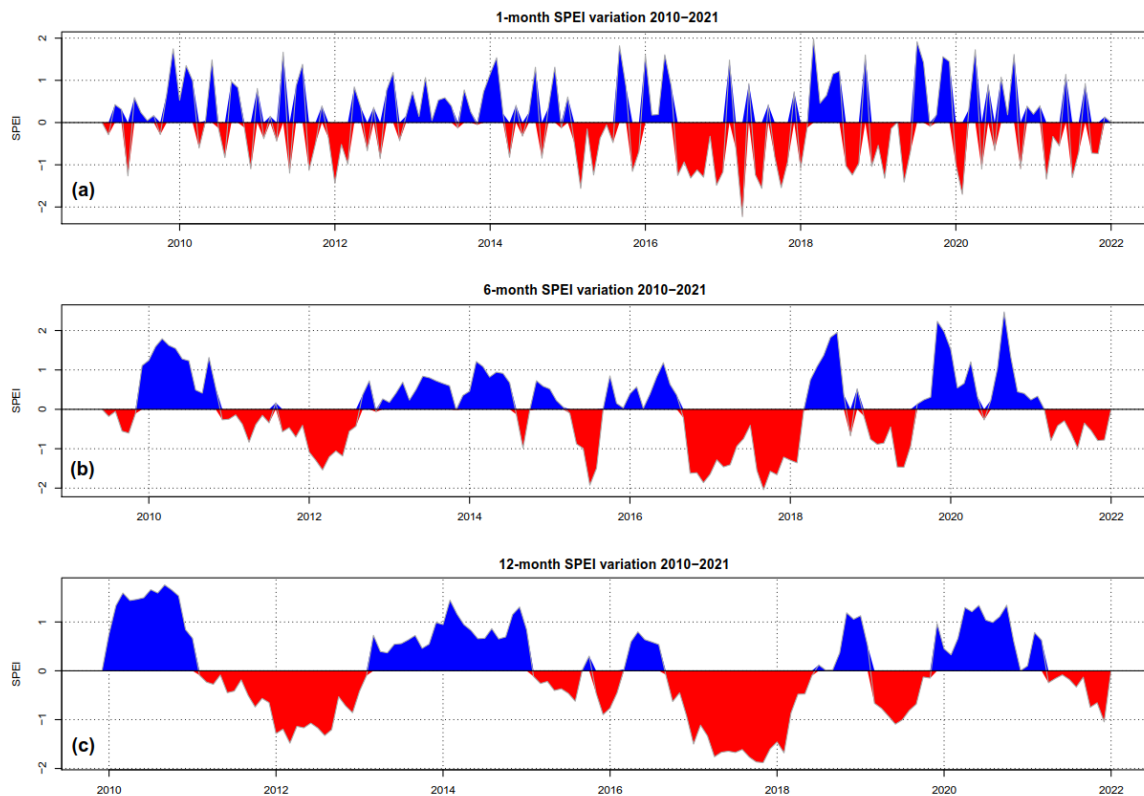
Figure 4: Variation of calendar year SPEI with time (period: 2011-2021) at different timescales: 1-mounth **(a)**, 6-months **(b)**, and 12-months **(c)** for the meteorological station of 'Cervera de Pisuerga'.

The distribution of the SPEI annual values during the monitoring period (2011-2021) was shifted to the left compared to the distribution for the period of the last 31 years (Figure 5a), indicating drier conditions for plants during the 10-year monitoring period. Contrary to SPEI, the distribution of the PET values during the monitoring period (2011-2021) was shifted to the right compared to the distribution for the period of the last 31 years (Figure 5b), indicating an increase in the potential evapotranspiration during the 10-year monitoring period.
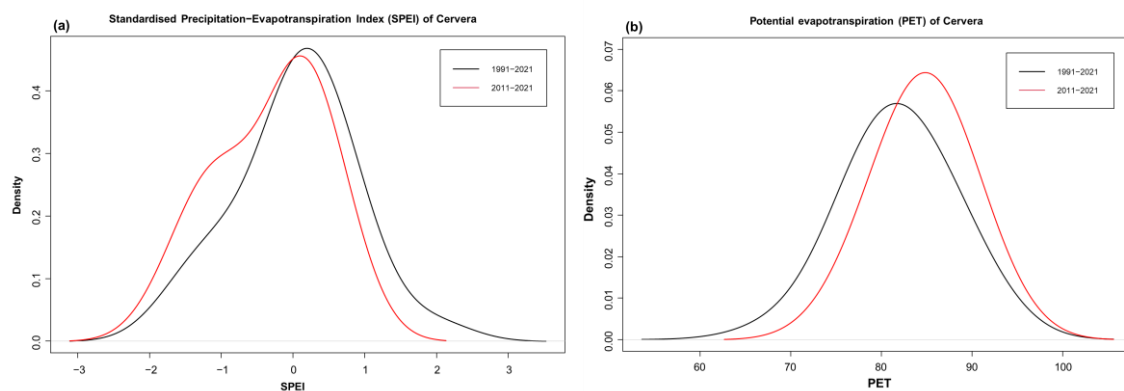
Figure 5: (a) 12-months SPEI **and (b)** 12-months PET distributions for the monitoring period (2011-2021) in comparison with the last 31 years (1991-2021).

These results suggest an increase in water stress for plants in the last 10 years compared to previous periods. Indeed, the SPEI mean annual value for the period 1991-2021 was 0.01, whereas for the period of 2011-2021 its variability increased and reached an average value of -0.13 (see Table 1). The PET also shifted to more water-demanding

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conditions during the same periods. The PET mean annual value for the period 1991-2021 was 51.31 and for the period of 2011-2021 reached an average value of 53.06 (see Table 1).

Table 1: Mean values of SPEI and PET calculated at different timescales for both periods (the last 31 years, 1991-2021, and the 10 years of monitoring, 2011-2021). T = monthly mean temperature (ºC) and P = monthly mean precipitation (mm).

	SPEI$_{(Oct-Sep)}$	SPEI$_{12}$	PET$_{(Apr-Sept)}$	PET$_{12-months}$	T (º)	P (mm)
Last 31 years	0.04	0.01	81.60	51.31	9.59	78.96
Last 10 years	-0.08	-0.13	83.50	53.06	10.18	76.48

The average SPEI for the time scale of 12-months calculated from October$_{(year-1)}$ to September$_{(current year)}$ followed the same trend as when calculated with the 12-months of the calendar year: it decreased from 0.04 for the period 1991-2021 to -0.08 for the period of 2011-2021 (Table 1). The average PET for the time scale of 12-months calculated from April to September of every year followed the same trend as when calculated with the 12 months of the calendar year: it increased from 81.6 for the period 1991-2021 to 83.5 mm for the period of 2011-2021 (Table 1).

The decrease in SPEI and the increase in PET suffered in the last 10 years are associated with an increase in the average annual temperature by 0.59 ºC, which increases the difference between PET$_{Ap-Sept}$ and the average monthly precipitation by 2.6 times (see table 1). SPEI and PET values for each year of the monitoring period are summarized in table 2. The year with the greatest SPEI value occurred in 2014 (SPEI=0.91) and the lowest value occurred in 2017 (SPEI=-1.38) when PET reached the highest value (PET=89.49) representing an average increase of 6.59 mm with respect to the other years of the period analyzed (Table 2).

Table 2: Mean values of SPEI from October$_{(year-1)}$ to September$_{(current year)}$, and PET from April to September for the monitoring period (2011-2021).

year	PET$_{(April-Sept)}$	SPEI$_{(Oct-Sep)}$
2011	83.38	0.23
2012	78.82	-1.10
2013	76.53	0.14
2014	81.79	0.91
2015	86.86	0.16
2016	84.08	0.10
2017	89.49	-1.38
2018	84.70	-0.86
2019	83.16	-0.12
2020	87.80	0.79
2021	81.91	0.23

4.2. Seedling initial dimensions and their potential effect on survival and growth

The lineal mixed models showed significant differences between *Quercus* species in seedling dimensions. *Q. pyrenaica* seedlings were smaller than *Q. petraea* seedlings in height (Qpy: 14.6±0.73 vs. Qpt: 23.0±1.15; F=201.66, p<0.0001) and diameter (Qpy: 3.7±0.18 vs. Qpt: 4.2±0.21; F=67.82, p<0.0001).

Also, there was a shrub by fence interaction on the seedling diameter of both *Quercus* species (Qpy: F=8.87, p<0.0053; Qpt: F=8.58, p<0.006), and on the height of *Q. pyrenaica* seedlings (F=5.52, p<0.0248), being the largest values for seedlings planted outside shrubs in the fenced areas (FN; Table 3).

Table 3: Mean ± SE of initial dimensions of *Quercus* seedlings planted in the different micro-habitats when they differed. Different letters indicate differences between pairs of micro-habitats (p<0.05). Qpy: *Quercus pyrenaica*; Qpt: *Q. petraea*.

	Dimensions	FS	FN	NS	NN
Qpy	Height	13.1 ± 1.32 b	16.5 ± 1.66 a	15.6 ± 1.57 ab	13.2 ± 1.33 b
	Diameter	3.5 ± 0.35 b	4.0 ± 0.40 a	3.8 ± 0.38 ac	3.5 ± 0.35 bc
Qpt	Diameter	3.98 ± 0.40 b	4.42 ± 0.44 a	4.26 ± 0.43 ab	4.01 ± 0.40 b

However, initial differences in the height of *Q. pyrenaica* seedlings did not influence survival (see Table B1.a in Annex B) or growth over time (t=0.049, p=0.825; see Table B2.a in Annex B). The initial differences detected in the diameter of the *Q. pyrenaica* seedlings did not influence survival over time (see Table B1.b) but did influence growth (t=3.998, p<0.001; see Tables B2.b in Annex B) over time and first-year growth (t=3.589, p<0.001; see Table B2.c in Annex B).

Concerning *Q. petraea* seedlings, no relationship was found between the initial diameter of the seedlings and survival over time (see Table B3 in Annex B), but between the initial diameter of the plants and growth over time (t=4.182, p<0.001; see Table B4.a in Annex B) and first year growth (t=4.936, p<0.001; see Table B4.b in Annex B). Since the initial height of *Q. petraea* seedlings was similar we didn't explore for its effect on survival and growth over time.
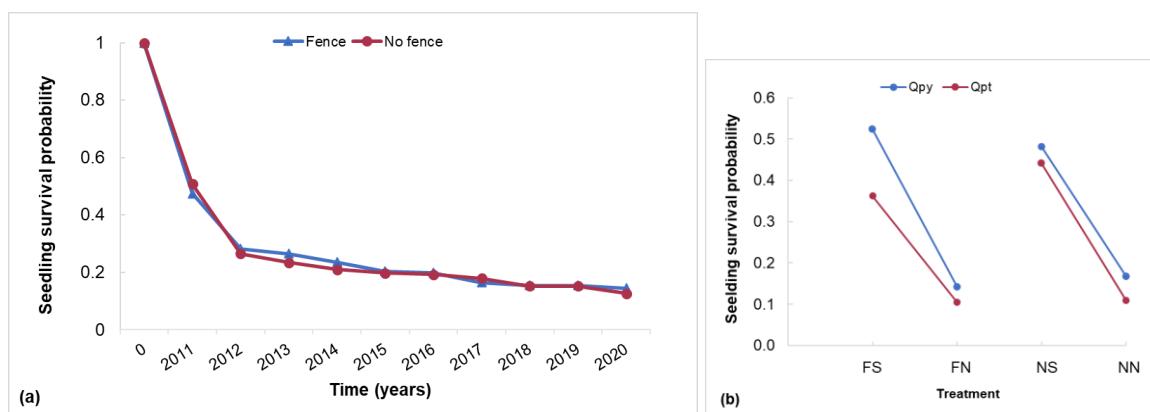
4.3. Seedling survival

The GLMM detected significant main effects of shrub, time, in years after plantation, and species on seedling survival (Table 4). The GLMM showed a marginal effect of the fence on seedling survival (Table 4) through the fence x time interaction (p<0.07) and the shrub x fence x *Quercus* spp. interaction (p<0.064). The fence affected seedling survival depending on the year (fence x time interaction; Figure 6a), and increased differences between *Quercus* species in seedling survival under shrubs (shrub x fence x *Quercus* spp. interaction; Figure 6b).

There was also a significant shrub x *Quercus* spp. x time interaction (Table 4). Seedling survival descended significantly through time for both the species, being greater under shrubs than outside shrubs, and being *Q. pyrenaica* survival always greater than *Q. petraea* survival, except for the first year after planting under shrubs (Figure 7).

The seedling mortality in areas without shrub cover occurred mostly during the first growing season (after the first dry season; Figure 7), whereas mortality under shrubs occurred more gradually during the first growing season and the highest mortality increment occurred during the second growing season (i.e., after the second dry season). Thus, in the first autumn (October 2011, 6th month after plantation), survival under shrubs was much greater than in areas without shrub cover (Qpy=91.0%, Qpt=90.7% vs. Qpy=17.0%, Qpt=5.5%), whereas in the second autumn (October 2012, 18th month after plantation) the seedling survival had decreased in both areas but more sharply under shrubs (under shrubs: Qpy=54.5%, Qpt=45.7%; in open areas: Qpy=12.0%, Qpt=2.5%). Afterwards, seedling survival continued to decline gradually and, in general, stabilised around 2017 (under shrubs: Qpy=34.5%, Qpt=28.0%; in open areas: Qpy=5.0%, Qpt=0.5%).

Table 4: Model parameters estimates derived from the GLMM models for seedling survival. The intercept is *Q. petraea* in non-fenced and no-shrub areas.

Fixed effects	Estimate ± SE	Z-value	p-value
Intercept	-0.07±0.75	-0.10	0.921
shrub	2.78±1.00	2.79	0.005
fence	-0.80±1.05	-0.76	0.448
Quercus spp.	0.52±0.42	1.25	0.211
time	-1.48±0.18	-8.36	<0.001
shrub x fence	0.06±1.38	0.04	0.968
shrub x *Quercus* spp.	-0.94±0.49	-1.93	0.054
fence x *Quercus* spp.	-0.14±0.56	-0.26	0.797
shrub x time	0.88±0.19	4.66	<0.001
fence x time	0.40±0.22	1.81	0.070
Quercus spp. x time	0.46±0.15	3.02	0.003
shrub x fence x *Quercus* spp.	1.23±0.66	1.85	0.064
shrub x fence x time	-0.32±0.24	-1.33	0.184
shrub x *Quercus* spp. x time	-0.33±0.16	-2.09	0.037
fence x *Quercus* spp. x time	-0.20±0.18	-1.07	0.284
shrub x fence x *Quercus* spp. x time	0.08±0.19	0.40	0.693

Figure 6: (a) Seedling survival (mean of both *Quercus* spp.) in fenced and non-fenced areas through time (fence x time interaction). **(b)** Seedling survival for *Q. pyrenaica* (Qpy) *and Q. petraea* (Qpt) species in the four treatments for the whole period. FS: fenced areas under shrubs; FN: fenced areas without shrubs; NS: non-fenced areas under shrubs; NN: non-fenced areas without shrubs.
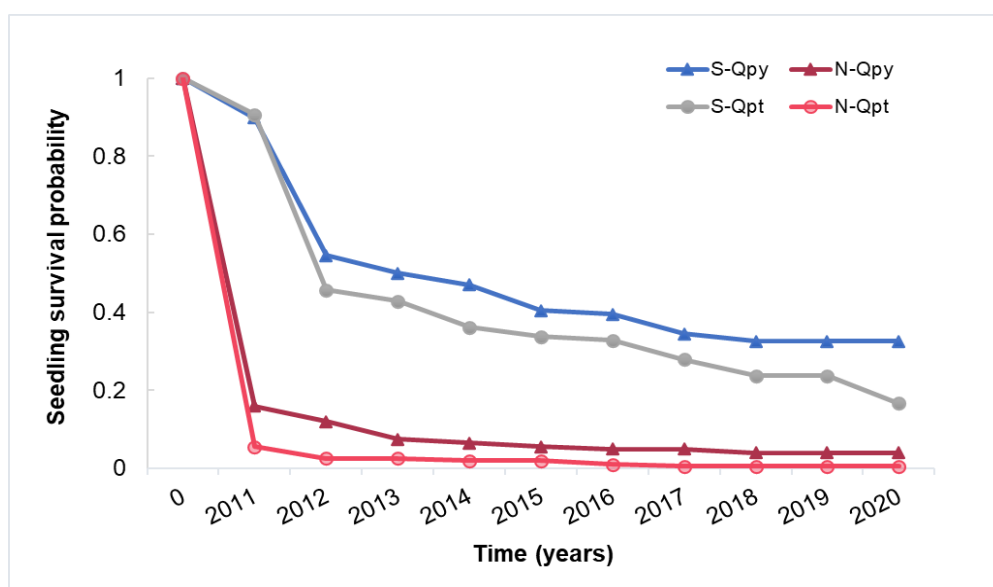
Figure 7: Seedling survival for *Q. pyrenaica* and *Q. petraea* species with and without shrubs through time. S-Qpy: *Q. pyrenaica* under shrubs; N-Qpy: *Q. pyrenaica* without shrubs; S-Qpt: *Q. petraea* under shrubs; N-Qpt: *Q. petraea* without shrubs.

4.4. Seedling height

The LMM showed significant main effects of the *Quercus* species, shrub, fence, and time, in years, after plantation on seedling height, as well as several two-way and all the three-way interactions, which were also very significant (Table 5; Figure 8).

Table 5: Model parameters estimates derived from LMM models for seedling height, and results of the ANOVA. The intercept is *Q. petraea* in non-fenced and no-shrub areas.

| Fixed effects	Estimate ± SE	F-value	p-value
Intercept	21.35±3.01	1551.15	<0.0001
Quercus spp.	-9.47±1.63	274.70	<0.0001
shrub	7.09±3.54	13.81	0.0003
fence	-5.48±4.38	94.46	<0.0001
time	-3.17±1.25	131.43	<0.0001
Quercus spp. x shrub	2.49±2.01	3.20	0.0739
Quercus spp. x fence	2.48±2.31	20.34	<0.0001
shrub x fence	-2.07±5.11	14.14	0.0002
Quercus spp. x time	-2.27±1.10	0.10	0.7524
shrub x time	3.01±1.30	7.73	0.0059
fence x time	9.17±1.53	126.48	<0.0001
Quercus spp. x shrub x fence	-3.83±2.84	21.58	<0.0001
Quercus spp. x shrub x time	-1.60±1.29	14.89	0.0001
Quercus spp. x fence x time	0.49±1.32	17.77	<0.0001
shrub x fence x time	-3.89±1.61	25.69	<0.0001
Quercus spp. x shrub x fence x time	-1.89±1.37	1.92	0.1659
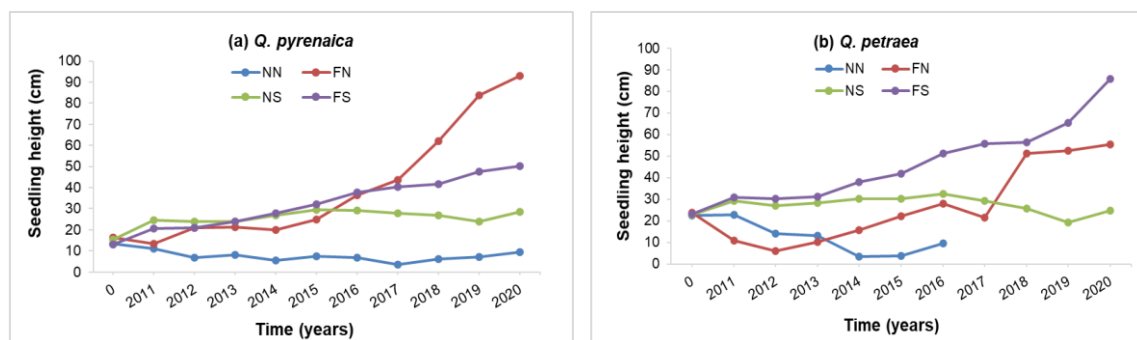
Figure 8: **(a)** Seedling height for *Q. pyrenaica* (Qpy) and **(b)** *Q. petraea* (Qpt) species through time in the four treatments. FS: fenced areas under shrubs; FN: fenced areas without shrubs; NS: non-fenced areas under shrubs; NN: non-fenced areas without shrubs.

In general, a similar increasing trend of seedling height over time was observed for both species (*Quercus* spp. x time interaction was not significant; see Table 5); the height of *Q. petraea* seedlings being always higher than *Q. pyrenaica* seedlings. The *Q. pyrenaica* seedling height tripled in ten years (from 14.6±0.73 cm at plantation to 45.4±11.29 cm ten years later), and the *Q. petraea* seedling height increased 2.4 times in ten years (from 23.0±1.15 cm to 55.3±6.27 cm).

The shrub had a positive effect on increasing the seedlings height of both species, while without shrubs the seedling height was maintained (Qpy) or even decreased (Qpt) until 2014 and increased afterward, being the increase more pronounced from 2017 particularly for Qpt. Thus, the height trend over time reversed and the seedlings height under shrub became lower than outside shrub from 2018 (*Quercus* spp. x shrub x time interaction; Figure 9a).

The fence also had a positive effect on increasing the height of the seedlings of both species, while without a fence the seedling height hardly changed over time. In addition, the seedling height differences between fence and non-fenced sites increased with time, being that difference greater for *Q. pyrenaica* (*Quercus* spp. x fence x time interaction; Figure 9b).
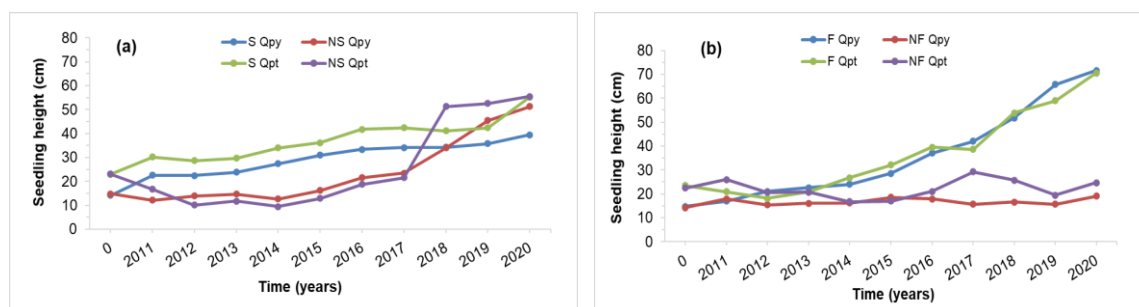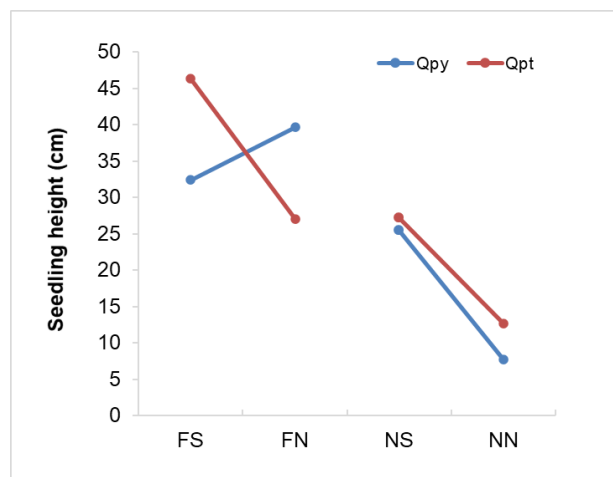

Figure 9: Seedling height for *Q. pyrenaica* (Qpy) and *Q. petraea* (Qpt) species through time under shrub (S) versus outside shrub (N) sites **(a)**, and in fenced (F) versus non-fenced (N) sites **(b)**.

There was also a combined effect of shrub and fence on seedling height over time (shrub x fence x time interaction; Figure 10). In fenced sites, seedlings height increased over time, being greater under shrub until 2018 and afterward the trend reversed. However, in non-fence sites, seedlings height barely increased over time, being always greater under shrub. Thus, the differences in height between seedlings planted under shrub in fenced areas (FS) compared to those planted in non-fenced areas without shrub (NN) increased with time.
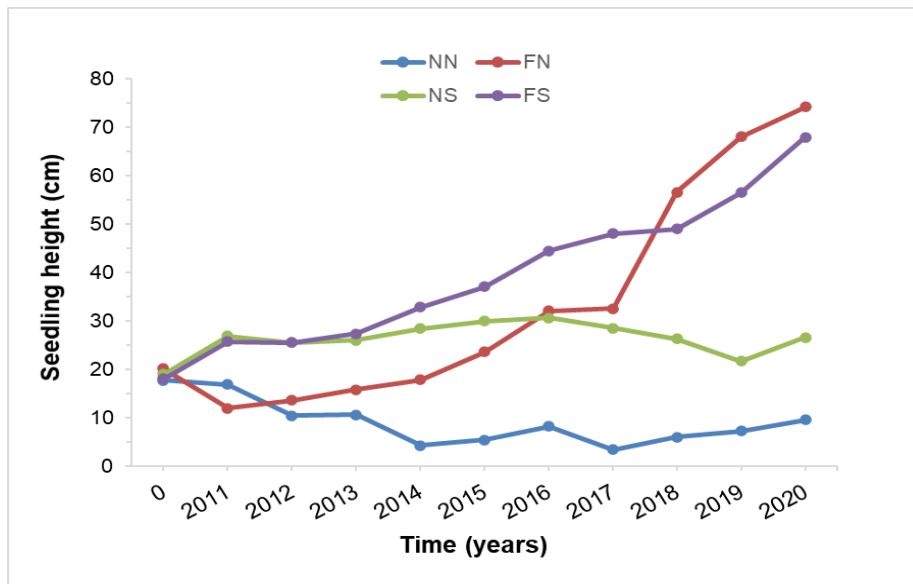
Figure 10: Seedling height through time in the four treatments regardless of *Quercus* species. FS: fenced areas under shrubs; FN: fenced areas without shrubs; NS: non-fenced areas under shrubs; NN: non-fenced areas without shrubs.

The height of *Q. petraea* seedlings was higher under shrub than outside shrub both in fenced and non-fenced areas. However, the height of *Q. pyrenaica* seedlings showed opposite trends depending on the presence or not of the fence, being height higher under shrubs than outside shrubs in non-fenced areas and vice versa in fenced areas. The fence also accentuated the height differences between *Quercus* species, both under and outside shrubs (*Quercus* spp. x shrub x fence interaction, Figure 11).

Figure 11: Seedling height for *Q. pyrenaica* (Qpy) and *Q. petraea* (Qpt) species in the four treatments for the whole period. FS: fenced areas under shrubs; FN: fenced areas without shrubs; NS: non-fenced areas under shrubs; NN: non-fenced areas without shrubs.
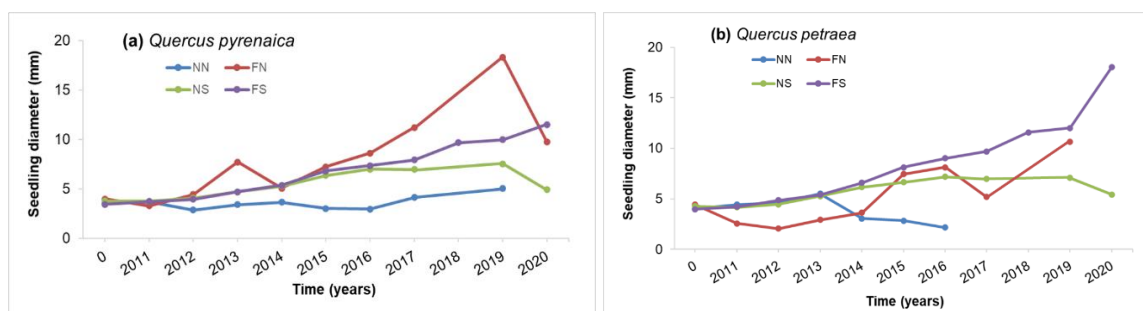
4.5. Seedling diameter

The LMM showed a significant main effect of the *Quercus* species on seedling diameter (Table 6; Figure 12). Seedling diameter also depended on the shrub presence, even though shrub main effect is masked by all their interactions with the other factors in the model, that, similarly to *Quercus* spp. x shrub interaction, tend to be highly significant. The main effects of the fence, year and time were significant, so all the interactions in the model did. Thus, the LMM showed a significant four-way interaction (*Quercus* spp. x shrub

x fence x time; p=0.026). There was also a significant effect of the fence presence and time on diameter, being all the two-way and three-way interactions significant (Table 6).

Table 6: Model parameters estimates derived from LMM models for seedling diameter, and results of the ANOVA. The intercept is *Q. petraea* in non-fenced and no-shrub areas.

| Fixed effects	Estimate ± SE	F-value	p-value
Intercept	3.84±0.62	1352.58	<0.001
Quercus spp.	-0.52±0.22	125.92	<0.001
shrub	0.41±0.76	1.79	0.182
fence	-0.71±0.88	37.71	<0.001
time	-0.04±0.23	183.36	<0.001
Quercus spp. x shrub	-0.06±0.28	13.27	<0.001
Quercus spp. x fence	0.21±0.32	10.29	0.001
Quercus spp. x time	0.09±0.15	37.56	<0.001
shrub x fence	-0.68±1.08	11.96	<0.001
shrub x time	0.43±0.24	8.32	0.004
fence x time	1.50±0.29	53.20	<0.001
Quercus spp. x shrub x fence	0.17±0.39	8.11	0.004
Quercus spp. x shrub x time	-0.08±0.16	11.99	<0.001
Quercus spp. x fence x time	0.12±0.20	27.37	<0.001
shrub x fence x time	-0.78±0.32	20.17	<0.001
Quercus spp. x shrub x fence x time	-0.46±0.21	4.94	0.026

Figure 12: (a) Seedling diameter for *Q. pyrenaica* (Qpy) and **(b)** *Q. petraea* (Qpt) species through time in the four treatments. FS: fenced areas under shrubs; FN: fenced areas without shrubs; NS: non-fenced areas under shrubs; NN: non-fenced areas without shrubs.

Seedling diameter increased significantly through time for both the species, being, in general, the diameter of *Q. petraea* seedlings greater than the diameter *Q. pyrenaica* seedlings (Figure 13). The *Q. pyrenaica* seedling diameter increased 2.4 times in ten years (from 3.7±0.18 mm at plantation to 8.7±1.95 mm ten years later), and the *Q. petraea* seedling height increased 2.8 times in ten years (from 4.2±0.21 mm to 11.7±1.17 mm).
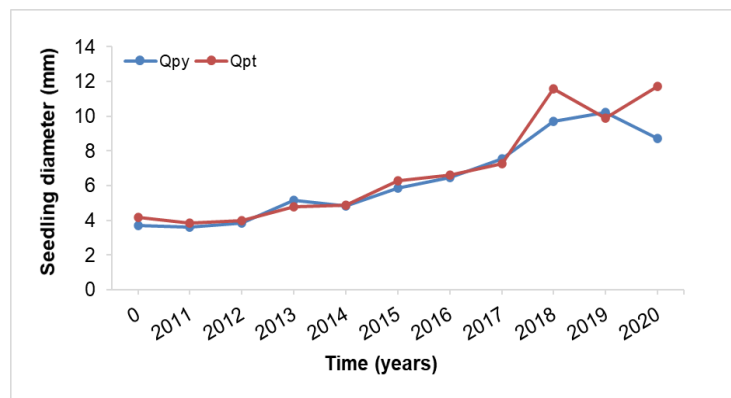
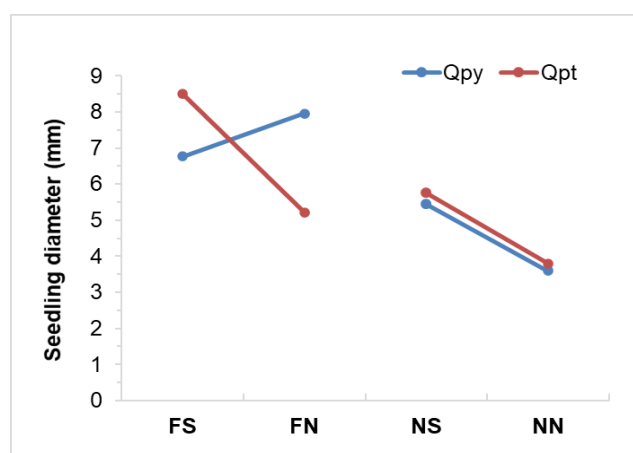**Figure 13:** Seedling diameter for *Q. pyrenaica* (Qpy) and *Q. petraea* (Qpt) species through time.

There was always a significant positive effect of the shrub on *Q. petraea* seedling diameter (Figure 14c) whereas on *Q. pyrenaica* seedling diameter the shrub's positive effect varied with the years (Figure 14a). The fence had also a positive effect on the *Q. pyrenaica* seedling diameter along time (Figure 14b) whereas on the *Q. petraea* seedling diameter the fence positive effect appeared later (2015-2020; Figure 14d).
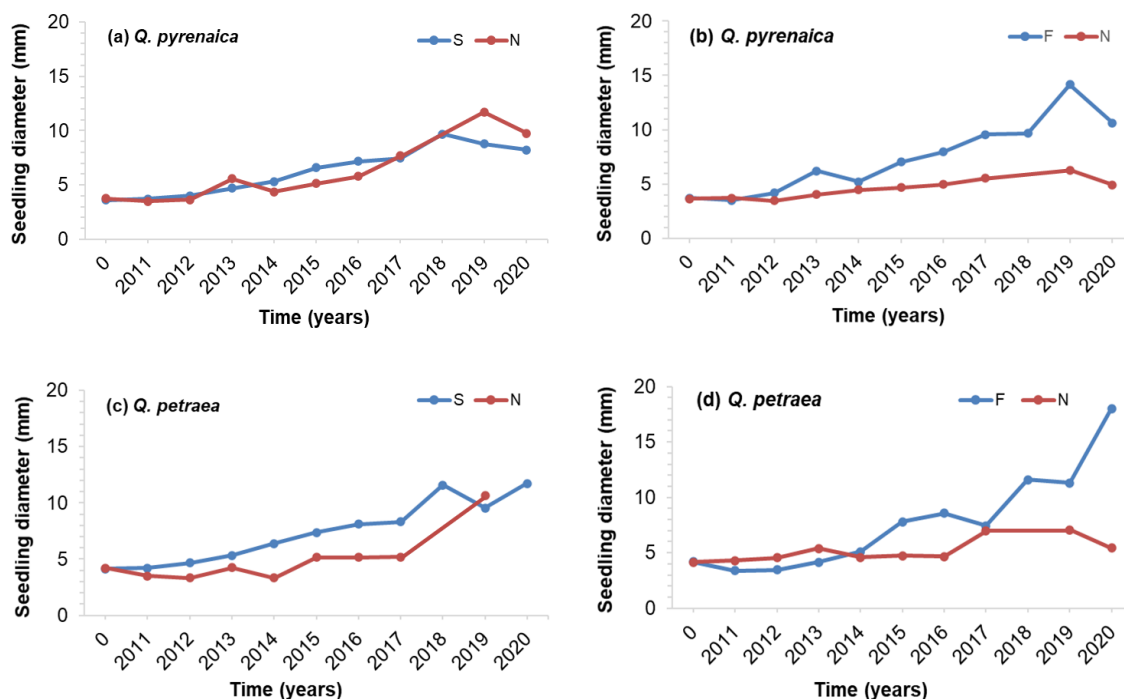
Figure 14: Seedling diameter for *Q. pyrenaica* (Qpy) and *Q. petraea* (Qpt) species through time under shrub (S) versus outside shrub (N) sites (a and c), and in fenced (F) versus non-fenced (N) sites (b and d).

For *Q. petraea* seedlings, the diameter was higher under shrub than outside shrub both in fenced and non-fenced areas, although the difference was greater in fenced areas. However, for *Q. pyrenaica* seedlings, the diameter was higher under shrub than outside shrubs in non-fenced areas whereas in fenced areas the trend is reversed (*Quercus* spp. x shrub x fence interaction, Figure 15). The fence also accentuated the differences in diameter between *Quercus* species, both under and outside shrubs.
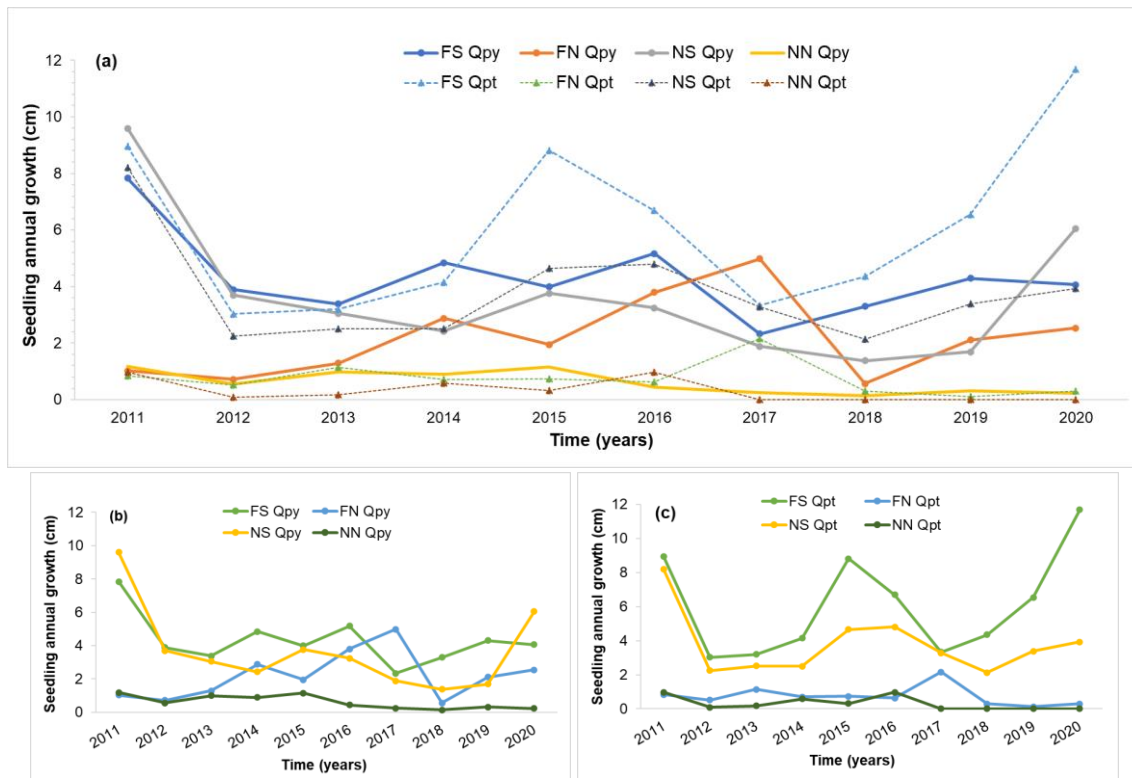
Figure 15: Seedling diameter for *Q. pyrenaica* (Qpy) and *Q. petraea* (Qpt) species in the four treatments for the whole period. FS: fenced areas under shrubs; FN: fenced areas without shrubs; NS: non-fenced areas under shrubs; NN: non-fenced areas without shrubs.

4.6. Seedling annual growth

The LMM showed a significant main effect of the fence on seedling annual growth (Table 7; Figure 16), although it also depended on the year (fence x time interaction), the shrub presence (fence x shrub interaction), and the *Quercus* species involved (fence x *Quercus* spp. and *Quercus* spp. x time interactions). The LMM also detected a marginal four-way interaction (fence x shrub x *Quercus* species x time; p=0.085; Figure 16).

Table 7: Model parameters estimates derived from LMM models for seedling annual growth, and results of the ANOVA. The intercept is *Q. petraea* in non-fenced and no-shrub areas**.**

Fixed effects	Estimate ± SE	F-value	p-value
Intercept	-0.93±2.42	85.36	<0.0001
fence	6.26±2.99	27.16	<0.0001
shrub	5.45±2.09	1.97	0.1616
Quercus spp.	3.25±2.09	0.02	0.8976
time	0.76±0.66	0.17	0.6945
fence x shrub	-5.99±2.95	20.11	<0.0001
fence x *Quercus* spp.	-3.56±3.00	12.99	0.0003
shrub x *Quercus* spp.	-1.78±2.16	3.02	0.0826
fence x time	-0.53±0.75	6.60	0.0158
shrub x time	-0.86±0.63	3.88	0.0505
Quercus spp. x time	-0.72±0.63	9.93	0.0017
fence x shrub x *Quercus* spp.	2.69±3.09	1.85	0.1735
fence x shrub x time	1.03±0.75	0.02	0.8792
fence x *Quercus* spp. x time	1.16±0.75	0.50	0.4781
shrub x *Quercus* spp. x time	0.56±0.64	1.09	0.2970
fence x shrub x *Quercus* spp. x time	-1.32±0.77	2.96	0.0853

Figure 16: (a) Seedling annual growth for *Q. pyrenaica* (Qpy) *and Q. petraea* (Qpt) species through time in the four treatments, and for each *Quercus* species separately, **(b)** for *Q. pyrenaica* and **(c)** for *Q. petraea*. FS: fenced areas under shrubs; FN: fenced areas without shrubs; NS: non-fenced areas under shrubs; NN: non-fenced areas without shrubs.

The annual mean growth recorded in the experimental plots was more intense under shrubs canopy. Indeed, mean growth without shrub protection tends to be lower than 2 cm per year while mean growth under shrubs' canopy is around 4 cm per year. The shrub x time interaction (Figure 17) showed that the intensity of the positive shrub effect on *Quercus* seedling growth depended on the year. The differences in growth between areas with and without shrubs were much greater in 2011 (Qpy= 8.65±0.07 cm vs. Qpt=1.00±0.10 cm) and 2020 (Qpy= 6.43±1.37 cm vs. Qpt=0.77±0.62 cm), whereas considerably reduced in 2012 vs. 2011 or 2017 vs. 2016.
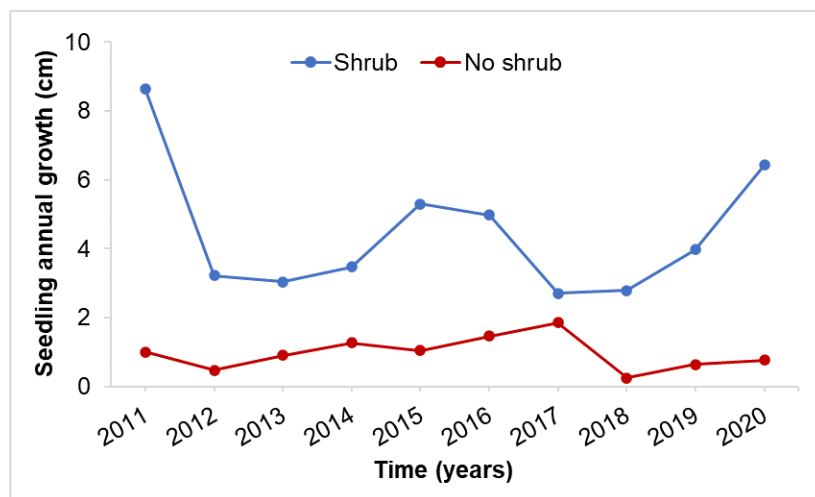
Figure 17: Seedling annual growth (mean value for both *Quercus* spp.) in areas with and without shrubs through time.

The fence positively increased seedling growth from the second year after plantation (Figure 18a). For the monitoring period, the average growth of seedlings in fenced areas was 3.3±0.18 cm compared to 2.1±0.19 cm without fence, regardless of the *Quercus* species and the shrub presence.

The fence also increased differences in seedling growth between sites under and outside shrubs' canopy, particularly for *Q. petraea* (Figure 18b). Thus, in fenced areas, *Q. petraea* seedling growth under shrubs was higher than *Q. pyrenaica* seedling growth (Qpt=6.07±0.68 cm vs. Qpy=4.31±0.34 cm) contrary to found outside shrubs (Qpt=0.75±0.13 cm vs. Qpy=2.19±0.32 cm).

Figure 18: (a) Seedling annual growth (mean of both *Quercus* spp.) in fenced and non-fenced areas through time (fence x time interaction). **(b)** Seedling annual growth for *Q. pyrenaica* (Qpy) *and Q. petraea* (Qpt) species in the four treatments for the whole period. FS: fenced areas under shrubs; FN: fenced areas without shrubs; NS: no-fenced areas under shrubs; NN: non-fenced areas without shrubs.
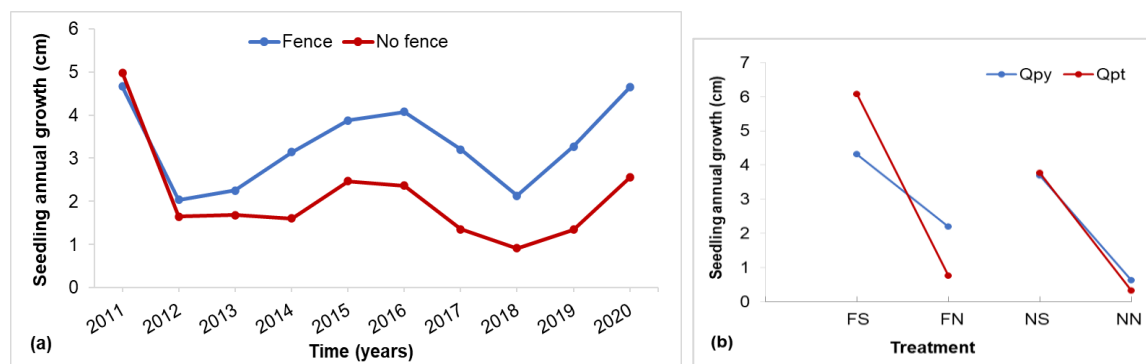
There was also a significant *Quercus* spp. x time interaction (Table 7, Figure 19) since seedling annual growth didn't differ between *Quercus* species for some years (2011, 2016, and 2017), whereas others the *Q. pyrenaica* annual growth was higher than *Q. petraea* seedling growth (2012-2014) or vice-versa (2018-2020). It is noteworthy to mention the highest annual growth raised for both species the first year after planting (Qpy= 4.91±2.57 cm vs. Qpt=4.74±2.95 cm). The next highest growth values were reached in 2020 (Qpt= 3.98±1.61 cm vs. Qpy=3.22±2.46 cm).
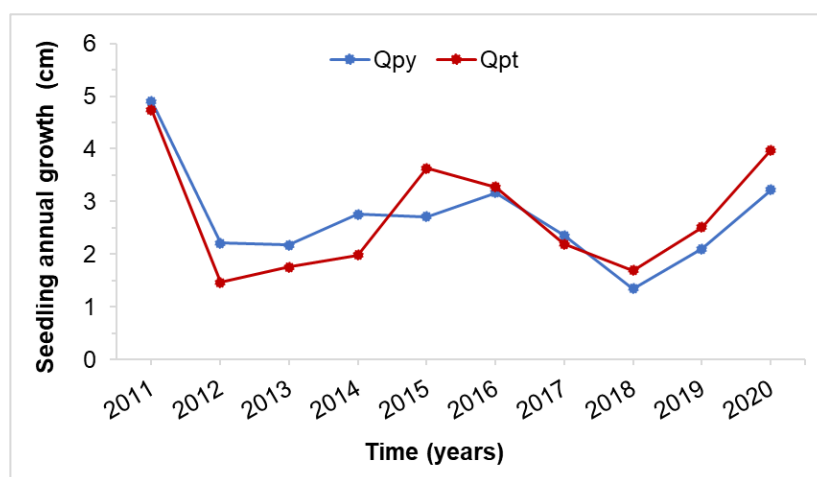
Figure 19: Seedling annual growth for *Q. pyrenaica* (Qpy) *and Q. petraea* (Qpt) species through time (*Quercus* species x time interaction).

4.7. Relating annual growth to drought

The LMM showed significant main effects of the shrub, *Quercus* species, $SPEI_{O-S}$ (standardized precipitation evapotranspiration index), and PET_{Ap-S} (potential evapotranspiration) on seedling annual growth, as well as an effect of the fence by interaction with other factors (Table 8).

Table 8: Model parameters estimates derived from LMM models for seedling annual growth considering climate parameters ($SPEI_{O-S}$, PET_{Ap-S}), and results of the ANOVA. The intercept is *Q. petraea* in fenced areas under shrub.

| Fixed effects	Estimate + SE	F-value	p-value
Intercept	-42.16 ± 5.02	706.29	<0.0001
fence	16.34 ± 6.34	15.61	0.0585
shrub	34.24 ± 25.78	64.93	<0.0001
Quercus spp.	29.89 ± 6.74	21.20	<0.0001
SPEI	-25.39 ± 5.36	100.73	<0.0001
PET	0.60 ± 0.06	71.06	<0.0001
fence x shrub	-23.19 ± 28.73	6.38	0.0196
fence x *Quercus* spp.	-27.84 + 8.81	1.88	0.1709
shrub x *Quercus* spp.	-25.49 ± 31.83	2.49	0.1152
fence x SPEI	19.44 ± 6.65	3.87	0.0492
shrub x SPEI	63.99 ± 32.17	20.25	<0.0001
Quercus spp. x SPEI	11,.0 ± 7.37	14.21	0.0002
fence x PET	-0.21 ± 0.08	3.09	0.0790
shrub x PET	-0.43 ± 0.31	11.33	0.0008
Quercus spp. x PET	-0.37 ± 0.08	12.14	0.0005
SPEI x PET	0.33 ± 0.07	29.48	<0.0001
fence x shrub x *Quercus* spp.	44.90 ± 35.36	0.08	0.7742
fence x shrub x SPEI	-2.97 ± 44.35	2.08	0.1493
fence x *Quercus* spp. x SPEI	-27.29 ± 9.52	4.52	0.0337
shrub x *Quercus* spp. x SPEI	4.41 ± 37.71	1.62	0.2033
fence x shrub x PET	0.26 ± 0.35	1.40	0.2377
fence x *Quercus* spp. x PET	0.36 ± 0.11	3.11	0.0779
shrub x *Quercus* spp. x PET	0.34 ± 0.39	11.81	0.0006
fence x SPEI x PET	-0.25 ± 0.08	2.26	0.1331
shrub x SPEI x PET	-0.81 + 0.39	25.54	<0.0001
Quercus spp. x SPEI x PET	-0.15 ± 0.09	2.67	0.1027
fence x shrub x *Quercus* spp. x SPEI	-33.93 ± 49.13	4.07	0.0438
fence x shrub x *Quercus* spp. x PET	-0.58 ± 0.43	2.06	0.1517
fence x shrub x SPEI x PET	0.04 ± 0.55	5.91	0.0152
fence x *Quercus* spp. x SPEI x PET	0.34 ± 0.11	10.21	0.0014
shrub x *Quercus* spp. x SPEI x PET	0.00 ± 0.46	0.56	0.4530
fence x shrub x *Quercus* spp. x SPEI x PET	0.4 ± 0.6	0.44	0.5097

There was also a significant fence x shrub interaction suggesting a greater shrub effect on seedling growth in fenced sites, as mentioned before in Figure 18b. The remaining significant interactions point out to the indirect influence of the climate (SPEI and/or PET) through its effects on other components of the experimental design, e.g., enclosure, and their potential interactions.

The annual growth of *Q. petraea* seedlings increased as the SPEI increased only under shrubs, particularly in the fenced sites, whereas outside the shrubs improving the SPEI was not enough to increase seedling annual growth (Figure 20). The annual growth of *Q. pyrenaica* seedlings, higher under shrubs in both fenced and non-fenced sites, increased in the four microhabitats as the SPEI increased.
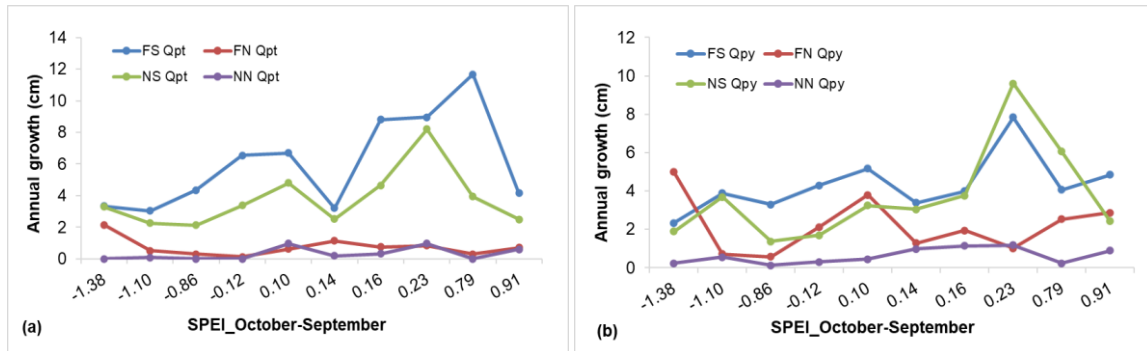
Figure 20: Seedling annual growth for *Q. petraea* **(a)** and *Q. pyrenaica* **(b)** in the four microhabitats in relation to the SPEI values for the period October$_{(year-1)}$-September$_{(year)}$. F: fenced areas; NF: non-fenced areas S: under shrubs; NS: without shrubs.

Without shrubs, the annual growth of *Q. pyrenaica* seedlings was higher than *Q. petraea* seedlings' annual growth, regardless the PET value. However, under shrubs, *Q. pyrenaica* seedlings' annual growth was higher than *Q. petraea* seedlings annual growth for PET values below 82 and lower for PET values above 82 (shrub x *Quercus* spp. x PET interaction; Figure 21).
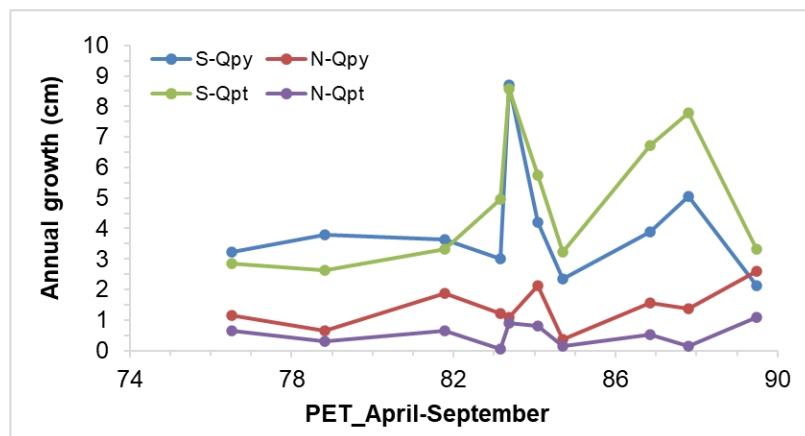
Figure 21: Seedling annual growth for *Q. petraea* and *Q. pyrenaica* in sites with and without shrubs in relation to the PET values for the period April-September (the growing season).

5. DISCUSSION

5.1. Temporal evaluation of climate conditions

According to the dominant trend in Mediterranean areas (Moreno et al., 2005; Kelley et al., 2012; IPCC, 2021), our results suggest that the climate in northern Palencia Province is gradually changing. Previous studies (e.g., Moreno et al., 2005) point out to the mediterraneization of the ecosystems in the Iberian Peninsula as a consequence of climate change, being that process driven by drought. Indeed, it has been largely demonstrated that SPEI index is increasing at least since 1990, revealing the occurrence of progressively longer and more severe drought episodes in the Iberian Peninsula (e.g., Salinas-Sole et al., 2018). Our results agree with such a trend in the study area at the different time scales analysed (1-, 6-, and 12-months). We also found the existence of longer and more frequent drought periods for the meteorological station of Cervera de Pisuerga during the 10-year monitoring period (1991-2021).

The analysis of the SPEI and PET demonstrates the reduction in water balance and the increase in potential evapotranspiration, associated with the increase in the average annual temperature by 0.59 ⁰C, during the 10-year monitoring period. Water supply by precipitation has not been sufficient to compensate the demand, as in Vicente-Serrano et al., 2014), resulting in the increase in water stress for plants in the last 10 years compared to largest periods.

The rising evapotranspiration (Salinas-Sole et al., 2018), changes in the main sources of moisture in Atlantic or Mediterranean water bodies (Gimeno et al., 2010), and the interannual rainfall variability of Mediterranean climates (Cubillo & De Castro, 2007) are some of the causes of such drying trend, which is the thermodynamic consequence of the rising concentrations of greenhouse gases (Kelley et al., 2012). Indeed, the evolution of temperature and precipitation is linked to global and local factors (González-Hidalgo et al., 2011; 2017) among which are the different mechanisms of atmospheric circulation according to the hemisphere, or more local factors such as land-use changes.

5.2. Seedling survival

The results of the 10-year monitorization of the growth of the two *Quercus* seedlings beneath shrub canopy and in open field conditions showed that native shrubs, *Genista florida* and *Cytisus scoparius*, enhanced *Quercus pyrenaica* and *Q. petraea* seedling survival compared to areas without shrubs. A positive effect on seedling survival exists when seedlings are planted beneath shrub canopies in this 'Corcos mine' site. Our medium-term establishment results, obtained during the experiment, are in agreement with the existence of neighbour effects among woody species, especially facilitating effects when the neighbour species are shrubs and the species of interest species are trees (Gómez-Aparicio, 2009). The positive effect of other leguminous shrub species on *Quercus* seedling survival has also been described recently: *Retama sphaerocarpa* (Rolo et al., 2013), *Genista hirsuta* Vahl (Smit et al., 2007, 2008), *Cytisus multiflorus* (L'Hér.) Sweet (Costa et al., 2017). This result supports the idea of using shrubs as ecosystem engineers to improve late-successional species establishment in mined sites (Alday et al., 2014; Bradshaw, 1997).

The effect of shrubs on microclimate amelioration (Gomez-Aparicio et al., 2005, 2008; Smit et al. 2008; Muhamed et al., 2013) and the improvement of soil properties (e.g., fertility, water holding capacity; Pugnaire et al., 2004; Costa et al., 2017; López-Marcos et al., 2020b), as a whole, may help to reduce the water stress in seedlings under shrubs compared with seedlings in areas without shrubs, favoring their survival. We will have identified soon, in the study area, the importance of microclimatic amelioration induced by shrub canopy on seedling survival and growth with the help of a complementary

experiment being carried out by our research group (unpublished data). However, we can anticipate that there is a clear soil improvement under the canopy of these native shrubs in the study area, especially relevant in grazed mine sites (Muñoz-Cerro et al., 2022).

As expected in Mediterranean systems, the first summer after plantation is a critical period for seedling survival (Navarro-Cerrillo et al., 2005; Castro et al., 2006; Costa et al., 2017); here 50% of seedlings died in the first summer (2011). However, the most affected individuals were those located outside shrubs, whereas most of the seedlings beneath shrub canopies survived after that period (89% died outside shrubs vs. 10% died under shrubs). These results pointed out the positive effect of shrubs on seedling survival when conditions became demanding. Alternatively, seedlings mortality under shrubs increased during the second year after plantation (93% died outside shrubs vs. 50% died under shrubs), probably because of the lower precipitations during the second growing season (see Table A1, Annex A) that might have reduced the soil water availability in the mine. This dry period generated very hard conditions for seedling survival in the mine, especially considering that the water holding capacity of mine soil is lower than in the nearby natural forest soil ($1–3.5$ g/cm^2 vs. 19.8 g/cm^2; López-Marcos et al., 2020b). Therefore, the amelioration of environmental conditions by shrubs was not and might not be enough to satisfy the water requirements of studied seedlings during most stressful periods, especially if they occur early after planting. After the first two dry seasons, seedling survival under shrubs decreased more slowly; after 10 years mortality rate beneath shrubs reached 83% for *Q. petraea* and 66% for *Q.pyrenaica* compared to 96 and 99%, respectively, outside the canopy of shrubs. Similar studies have documented that extreme environmental severity prevents a significant effect of facilitation (Brooker et al., 2008), whereas studies in arid and semi-arid environments have also found a shift from positive to negative outcomes between plants when water resources decrease, possibly because the facilitator cannot compensate for its own resource competition or rain interception (Maestre & Cortina, 2004).

Although *Quercus* species are not very attractive for some herbivores, like cattle, due to their high tannin concentrations (Rodríguez-Doce, 2010), ungulates in general could destroy seedlings by trampling or pulling up without consumption affecting their survival. In non-fenced areas shrubs as a protective mechanical barrier, even in the case of non-spiny plants (Gómez et al., 2001), could prevent seedling damage by ungulates and might hide the enclosure effect on *Quercus* seedling survival. However, contrary to studies in other areas of Spain (Gómez et al., 2003), enclosures did not significantly enhance *Quercus* seedling survival, suggesting that ungulate browsing is not a major problem for *Quercus* regeneration in the study area. Indeed, in areas without shrubs enclosures did not have a positive effect on seedling survival either, as found by Costa et al. (2017) in open oak woodlands of central-western Spain. Therefore, the most limiting factor for seedling survival in this mine seems to be summer drought, and the most important effect of shrubs is the amelioration of abiotic conditions in agreement with Costa et al. (2017).

The different survival patterns of both species can be due to their different traits in response to the environment. *Q. petraea* is adapted to environments where resources are abundant, and it hardly endures stressful conditions such as high radiation, water deficit, or above-ground disturbances, whereas *Q. pyrenaica* presents traits related to a stress tolerance strategy such as a higher self-shading, root to shoot ratio, sprouting habit, and a more conservative growth strategy than *Q. petraea* (Rodríguez-Calcerrada et al., 2008). Those differences may explain why in our experiment *Q. pyrenaica* has shown higher survival throughout time compared with *Q. petraea*, as it happens in other drought-prone habitats (Rodríguez-Calcerrada et al., 2010). Moreover, the higher self-shading in *Q. pyrenaica* seedlings (Rodríguez-Calcerrada et al., 2008) minimizes the leaf area exposed to high-intensity radiation, thus maintaining water balance by reducing transpiration at the plant level and avoiding the probability of suffering severe photoinhibition and overheating outside the shrub canopies (Bragg & Westoby, 2002).

Therefore, it is necessary to consider the ecological requirements and characteristics of species of interest to select the most adapted species to the main site constraints before using shrubs as nurse plants. This selection will determine the success of tree reintroduction and their self-maintenance, as in the future those species also will influence the nutritional and microbial properties of the mine soil (Mukhopadhyay et al., 2013).

5.3. Seedling height and stem diameter growth

Our results showed rather slow increments of *Quercus* seedling height and diameter over time, although both increments were more pronounced in *Q. petraea*. This species tripled its height in 10 years and its diameter increased only 2.8 times, whereas *Q. pyrenaica* seedling height and diameter increased only 2.4 times. Indeed, the *Q. petraea* height and diameter were higher than those of *Q. pyrenaica* seedlings at the beginning of the experiment. These results are consistent with the very slow growth of *Quercus* seedlings that can be found in Mediterranean areas, as reported by Costa et al. (2017) in open oak woodlands of central-western Spain, especially when conditions of the first dry season are stressful (Navarro-Cerrillo et al. 2005). The more pronounced height and diameter increments over time in *Q. petraea* than in *Q. pyrenaica* found in our study are consistent with that found by Rodríguez-Calcerrada et al. (2008) in an experiment studying the response to light of both *Quercus* species, showing contrasting ecology at the seedling stage.

Quercus seedlings' height and diameter depended on shrub and fence combined effects. The positive relationship of the seedling growth (height and diameter) of both *Quercus* species with the presence of shrubs was stronger in non-fenced areas: for *Q. pyrenaica* seedlings' height and diameter, and for *Q. petraea* seedling height from the beginning, and later (from 2014) for *Q. petraea* seedling diameter. In the fenced areas, however, this positive relationship remained over time for *Q. petraea* seedlings (although differences in seedling height with and without shrubs were reduced over time), whereas for *Q. pyrenaica* seedlings height remained higher under shrubs only until 2017 and diameter was higher only for particular years, when it seems that the positive effect of the fence on seedling height became stronger in areas without shrubs. The height and diameter increments in *Quercus pyrenaica* and *Q. petraea* seedlings were very slow or practically non-existing in non-fenced areas without shrubs.

These results confirm that nurse shrubs already facilitate *Quercus* species through two mechanisms: a) the modification of the microclimate and b) the protection against herbivores. They also suggest that the initial protection from abiotic stress (summer droughts) mediated by shrubs may be more determinant of the (height and diameter) growth of *Quercus* spp. than the protection from biotic stress (herbivory). Even though first year growth was intense notwithstanding the protection against herbivores, such protection gained importance over time and thus the fence became more relevant later in areas without shrub. This explains why we didn't find a significant effect of the fence on seedling growth of both *Quercus* species in the study area when we considered only the first two years of monitoring (Torroba-Balmori et al., 2015). Other studies also find a defensive late effect of the enclosures on the growth of *Quercus* species, which becomes more relevant when saplings are larger (Zamora et al., 2001; Baraza 2004; Gómez-Aparicio et al., 2008).

The positive combined effect of shrub and fence on seedling height and diameter was more important for *Q. petraea*, pointing out the higher stress undergone by *Q. petraea* compared with *Q. pyrenaica* in this reclaimed site (Torroba-Balmori et al., 2015). Indeed, the fence accentuated the differences in height and diameter between *Quercus* species, particularly outside the canopy of shrubs because the seedlings here do not benefit from shrub facilitating effects.

The higher seedling growth found beneath shrub canopies in comparison with areas outside shrubs is probably promoted by less stressful light conditions, and better soil properties and water status under shrubs (López-Marcos et al., 2020b). These results contrast with other studies (Gómez-Aparicio et al., 2005; Marañón et al., 2004), where despite finding higher seedling survival in shady habitats, under neighbour plants the seedling growth decreased or did not improve compared with areas outside shrubs. Neutral or negative interactions among nurse species and target species are usually found in facilitation studies when growth is considered, in contrast to the generally positive effects upon survival (Gómez-Aparicio, 2009), but sometimes stem elongation can be higher in shaded microsites than outside shrubs (Pérez-Ramos et al., 2010). In addition, although *Quercus* seedlings under shade conditions may grow less than those under full light, the shortage of water may also reduce their growth, so the equilibrium between both factors determines the final response (Baraza et al., 2004; Marañón et al., 2004). In our study conditions, restoration with nurse shrubs does not confront survival against growth, but favours both, as found in open oak woodlands in central-western Spain (Costa et al., 2017), resulting in a promising technique for *Quercus* reintroduction in mine sites.

5.4. Seedling annual growth and its relation to climate

The fence had a significant positive effect on the medium-term annual growth of both *Quercus* species, contrary to what was observed on survival for which only a marginally positive effect of the fence was found in specific years. However, the positive effect of the fence on annual seedling growth found in our study became evident from the second year after the plantation. That explains why in previous studies when we only investigated the short-term fence effects (first two years after planting), we did not find a significant effect of the fence on *Quercus* seedling growth (Torroba-Balmori et al., 2015). Other studies also find a defensive late effect of the enclosures on the growth of *Quercus* species (Zamora et al., 2001; Baraza 2004; Gómez-Aparicio et al., 2008).

The fence also increased differences in seedling growth between sites with and without shrubs (fence x shrub interaction), particularly for *Q. petraea*, suggesting a bigger vulnerability of *Q. petraea* seedlings to herbivory. Thus, although the positive relationship of the seedling annual growth of both *Quercus* species with the presence of shrubs was clear from the beginning in the non-fenced areas, this positive effect is intensified for *Q. petraea* in fenced areas. It is long known the impact of physical damages caused by ungulates during *Quercus* species establishment (Ramírez-Marcial et al., 1996; Bonfil & Soberón, 1999, 2000) or other tree species (Sánchez-Velásquez et al., 2011) in different ecosystems around the world. Herbivory by ungulates has influenced vegetation patterns throughout the Mediterranean Basin for thousands of years (Callaway & Pugnaire, 1999; Zamora et al., 2000).

Our results go further and support the hypothesis that, initially, protection from abiotic stress (summer droughts) mediated by shrubs is more determinant of the *Quercus* seedling's annual growth than the protection from biotic stress (herbivory). Later, protection against ungulates' herbivory gain importance. Fence protection against ungulates became more relevant, adding to the defensive effect of the shrub, especially on *Q. petraea*, pointing out the higher pressure undergone by *Q. petraea* compared with *Q. pyrenaica* in this reclaimed site (Torroba-Balmori et al., 2015). In any case, the seedling annual growth in non-fenced areas without shrubs was extremely low for both *Quercus* species.

Our results also showed a different seedling annual growth of both *Quercus* species depending on the year (*Quercus* species x time interaction), which translates into different patterns over time: annual growth being similar for both *Quercus* species in some years (2011, 2016, and 2017), higher for *Q. pyrenaica* (2012-2014) or *Q. petraea* (2018-2020) in others. Previous studies on seedling growth (Rodríguez-Calcerrada et al., 2008) found

that when there was no water shortage, *Q. petraea* seedlings grow more than those of *Q. pyrenaica* in greater light conditions, being those differences minimal when both species were in shade. In contrast, in our study, *Q. pyrenaica* annual growth was greater in all conditions (under and outside shrubs regardless of the fence) at the beginning (see Torroba et al., 2015), pointing out the higher stress initially undergone by *Q. petraea* compared with *Q. pyrenaica* in this reclaimed site. The limiting conditions of the summer drought in the study area probably affected more *Q. petraea*, with more drought-sensitive features, than *Q. pyrenaica*, better adapted to water stress (Rodríguez-Calcerrada et al., 2008), reducing initially its growth and the effectiveness of its reintroduction in these mined sites compared with *Q. pyrenaica*. However, with time, the established *Q. petraea* seedlings manage to grow more than *Q. pyrenaica* seedlings and the trend is reversed.

Moreover, the intensity of the positive shrub effect on *Quercus* seedling's annual growth depended on the year (shrub x time interaction). Thus, in more stressful years, such as 2012 and 2017, the differences in *Quercus* seedling annual growth between areas with and without shrubs were lower. Then, as previously mentioned, the amelioration of environmental conditions by shrubs was not enough to satisfy the water requirements of studied seedlings during most stressful periods. Thus, although seedlings survive better beneath the shrub canopies, under more extreme dry seasons shrub cover is not enough to prevent the seedling death as well as to enhance growth. However, we did not find a negative effect of shrub cover on the *Quercus* seedling annual growth in our study. Moreover, in our study conditions, restoration with nurse shrubs does not confront survival against growth, but favours both, as found in open oak woodlands in central-western Spain (Costa et al., 2017), confirming that the use of shrub as engineering species is a suitable technique for *Quercus* reintroduction in mine sites.

However, the evaluation of meteorological conditions during the 10-year monitoring period showed different patterns of annual growth for both *Quercus* species, according to the climate conditions. The annual growth of *Q. pyrenaica* seedlings increased in the four microhabitats as the standardized precipitation evapotranspiration index (SPEI) increased, being higher without shrubs in the fenced sites and under shrubs in the non-fenced sites. These opposite tendencies suggest stronger shrub protection from biotic factors (herbivory) on the *Q. pyrenaica* seedlings' annual growth in grazed areas whereas whether the fence is responsible for protection from herbivory the *Q. pyrenaica* seedlings may compete more with shrubs for resources and, as a result, the annual growth became higher outside the shrub canopy.

In a similar study conducted in Sierra Nevada, Gomez-Aparicio et al. (2008) observed that under-canopy conditions reduced the aerial biomass of seedlings and the mass fraction of the leaves of *Q. pyrenaica* because the canopy intercepts rain during the growing season and, therefore, shading can also cause drought, so *Q. pyrenaica* seedlings growing in open areas could be favored in humid years, even though this species is tolerant to shade in the early stages of life (Quero et al., 2006).

On the other side, high PET also tend to favour *Q. pyrenaica* seedlings' growth likely through its relationships not with higher water demand but with high spring temperatures, when low temperature, not drought, tends to limit growth, thus extending the growing season.

Contrary to what happens with *Q. pyrenaica*, the annual growth of *Q. petraea* seedlings increased as the SPEI increased only under shrubs, particularly in the fenced sites. Outside the shrub canopy, the SPEI improvement seems not to be enough to increase seedling annual growth, which was always higher in the fenced sites. These results emphasize again the greater relevance of fence protection from biotic stress for *Q. petraea* seedlings, adding to the defensive effect of the shrub, pointing out the higher pressure undergone by *Q. petraea* compared with *Q. pyrenaica* in this reclaimed site (Torroba-Balmori et al., 2015).

On the other hand, our results showed a greater positive shrub effect on *Q. petraea* seedling annual growth as the water stress for plants increases (higher potential evapotranspiration, PET), whereas without shrubs, the annual growth of *Q. pyrenaica* seedlings was always higher than *Q. petraea* seedlings' annual growth, regardless the PET value. This result points out again the higher water stress undergone by *Q. petraea* compared with *Q. pyrenaica* in this reclaimed site (Torroba-Balmori et al., 2015).

It is known that Q. petraea was not able to spread over open areas and under the forest canopy the increase in measurable saplings was lower compared to the increase of Q. pyrenaica (Rodríguez-Calcerrada et al., 2008). Future warming and severity of droughts will likely accelerate the reduction of suitable regeneration niches for this and likely many other temperate trees near the southern edge of the distribution, increasing the probability of extinction of such populations (Willi et al., 2006).

6. CONCLUSIONS

We conclude that in coal mines reclaimed for livestock use under a sub-Mediterranean climate where the summer drought effects are increased by the constraints of mine soils, the native colonizer shrubs, *Genista florida* and *Cytisus scoparius*, have a clear facilitative effect on seedlings of ecologically contrasted *Quercus* species (*Q. pyrenaica* and *Q. petraeae*). The facilitative effect was found for both *Quercus* species, but to a different degree depending on the species considered and the variable measured (survival or growth). Although in our study conditions, restoration with nurse shrubs does not confront survival against growth, the mechanisms of facilitation involved were not the same to enhance survival or growth.

In terms of survival, both Quercus species were favoured by shrubs, although the Mediterranean species (Q. pyrenaica) showed higher survival throughout time compared with the Eurosiberian species (Q. petraea). Native shrubs appear to play a more important role in modifying abiotic conditions (soil improvement has been tested in complementary studies) than in protection against large herbivores (a marginally positive effect of the fence was found only in specific years). The shrub positive effect was particularly important the first summer after plantation and decrease with time, particularly under more extreme and frequent dry seasons.

However, in terms of growth, a positive combined effect of shrub and fence on *Quercus* seedling exists, being more important for *Q. petraea*. The protection from abiotic stress (summer droughts) mediated by shrubs may be more determinant of the *Quercus* seedlings' growth at the early stage than the protection from biotic stress (herbivory), while the fence became more relevant later in areas without shrubs, where the effect of wild ungulates and/or livestock browsing on the growth of taller seedlings became a major constrain, especially for *Q. petraea*. Slow increments of *Quercus* seedling height and diameter over time were found, although both increments were more pronounced in *Q. petraea*. In addition, shifting from shrub facilitation to competition might not occur in meteorologically harsh years in sub-humid Mediterranean restored mines.

Therefore, the native nurse shrubs, *Genista florida* and *Cytisus scoparius*, can have a key role in the restoration of degraded oak ecosystems, especially for the Eurosiberian species, under a bioclimatic limit in sub-Mediterranean grazed areas, resulting in a promising technique the effective reintroduction of late-successional tree species, such as *Q. petraea* and *Q. pyrenaica*, in reclaimed coal mines. However, two key parameters should be taken into consideration; (i) the stress tolerance strategy of the selected species; i.e. the success being greater if the species is less sensitive to the main constraints in the area; and (ii) the previsions of climate change that indicate a decrease in the water balance and an increase in the potential evapotranspiration in the study area during the 10-year monitoring period compared to previous periods, indicating an increase in water stress for

plants. Thus, although seedlings of both *Quercus* species survive and grow, in general, better beneath the shrub canopies, under more extreme dry seasons, shrub cover may not enough to prevent the seedling death as well as to enhance growth, especially in the case of *Q. petraea*.

7. ACKNOWLEDGEMENTS

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9. ANNEXES

Annex A.

Table A1: Precipitation (mm) during the monitoring years. Data provided by the Spanish Meteorological National Agency from the Meteorological Station at Cervera del Pisuerga.

MONTHS	Precipitation (mm)										
	2010	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**
January	92.20	146.40	7.00	128.00	132.20	95.20	193.40	27.00	33.40	61.40	45.20
February	188.40	50.00	55.80	78.80	148.40	63.00	97.40	217.80	74.80	33.80	18.40
March	114.00	54.00	17.20	136.00	71.00	10.00	64.00	33.40	260.00	49.20	67.40
April	42.60	64.20	98.40	72.00	51.80	81.00	184.20	17.60	97.80	68.60	190.80
May	58.80	116.90	76.60	48.00	64.20	31.40	83.60	98.40	80.00	39.40	52.00
June	91.40	16.60	39.60	50.00	37.60	51.80	17.20	31.80	91.60	37.20	78.50
July	27.80	36.60	24.00	41.80	21.20	45.40	19.40	9.00	40.80	104.40	20.00
August	0.40	50.70	5.40	13.20	55.40	9.40	0.80	22.20	0.00	42.40	43.20
September	72.80	7.60	61.00	60.00	16.00	127.80	10.20	7.00	9.40	31.60	42.40
October	151.80	75.40	157.20	130.20	131.00	141.60	19.00	4.00	39.80	127.20	219.40
November	86.10	119.60	58.00	77.20	170.30	56.80	66.40	46.30	259.90	230.60	48.20
December	179.03	62.40	91.40	139.00	76.40	56.40	11.20	139.00	27.50	243.00	95.20
P (year)	**1105.33**	**800.40**	**691.60**	**974.20**	**975.50**	**769.80**	**766.80**	**653.50**	**1015.00**	**1068.80**	**920.70**
P (Jan-Sept)	688.40	543.00	385.00	627.80	597.80	515.00	670.20	464.20	687.80	468.00	557.90
P (Jl-Aug)	28.20	87.30	29.40	55.00	76.60	54.80	20.20	31.20	40.80	146.80	63.20
P (Oct$_{(y-1)}$-Sept$_y$)		959.93	642.40	934.40	944.20	892.70	925.00	560.80	877.10	795.20	1158.70

Table A2: Temperatures (ºC) during the monitoring years. Data provided by the Spanish Meteorological National Agency from the Meteorological Station at Cervera del Pisuerga.

MONTHS	Mean Temperature (ºC)											
	2010	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**
January	1.1	2.8	3.8	3.8	4.0	3.3	4.3	3.6	3.6	3.6	4.6	2.6
February	4.3	5.0	2.5	2.4	2.7	1.8	3.8	5.4	1.6	7.4	7.9	6.2
March	4.3	5.8	8.0	4.9	6.7	7.0	4.2	7.8	3.7	6.6	7.2	7.2
April	9.0	11.6	5.6	6.9	10.4	9.6	6.5	10.2	9.0	7.8	10.3	8.3
May	9.5	13.3	12.4	8.2	10.3	12.4	11.2	13.8	11.5	11.2	14.3	11.4
June	14.0	14.5	16.0	13.4	14.9	17.0	15.4	18.0	15.6	15.7	14.7	15.2
July	18.4	15.5	17.0	19.6	16.8	20.0	18.9	19.1	18.0	18.8	19.5	17.7
August	18.1	18.0	19.2	17.6	17.0	18.4	19.8	18.9	19.1	18.6	18.7	19.2
September	14.9	17.3	15.4	16.3	16.3	13.5	17.4	14.9	18.5	15.9	15.8	16.2
October	9.6	13.4	10.6	11.3	14.6	10.8	12.4	14.9	11.4	12.1	10.0	12.4
November	4.4	7.6	5.6	5.1	6.9	8.7	6.1	7.1	6.0	5.1	8.9	5.3
December	2.5	4.1	3.9	3.9	4.2	6.6	6.4	3.6	5.9	5.9	3.2	6.6
T (year)	**9.18**	**10.74**	**10.00**	**9.45**	**10.40**	**10.76**	**10.53**	**11.44**	**10.33**	**10.73**	**11.26**	**10.69**
T (Jan-Sept)	10.40	11.53	11.10	10.34	11.01	11.44	11.28	12.41	11.18	11.73	12.56	11.56
T (Jl-Aug)	18.25	16.75	18.10	18.60	16.90	19.20	19.35	19.00	18.55	18.70	19.10	18.45
T (Oct$_{(y-1)}$-Sept$_y$)		10.03	10.42	9.43	9.95	10.73	10.63	11.38	10.52	10.74	11.34	10.51

Annex B.

Table B1: Model parameters estimates derived from the generalized linear mixed models (GLMM) to assess the effect of **(a)** the initial **height** or **(b) diameter** (covariables) of *Quercus pyrenaica* seedlings on their **survival** over time.

(a) height	estimate±SE	z-value	p
intercept	3.381±0.778	4.347	<0.001
shrub	-1.012±0.899	-1.126	0.260
fence	0.083±0.971	0.086	0.932
time	-5.598±1.238	-4.520	<0.001
height	**0.016±0.013**	**1.176**	**0.239**
shrub*fence	0.106±1.214	0.088	0.930
shrub*time	4.697±1.528	3.074	0.002
fence*time	-1.462±1.684	-0.688	0.385
time*height	**-0.0003±0.002**	**-0.128**	**0.898**
shrub*fence*time	1.539±2.120	0.726	0.468
(b) diameter			
intercept	3.479±0.876	3.970	<0.001
shrub	-1.020±0.904	-1.129	0.259
fence	0.053±0.967	0.054	0.957
time	-5.591±1.250	-4.471	<0.001
diameter	**0.037±0.123**	**0.299**	**0.765**
shrub*fence	0.134±1.212	0.110	0.912
shrub*time	4.758±1.541	3.088	0.002
fence*time	-1.385±1.682	-0.824	0.411
time*diameter	**-0.167±0.024**	**-0.712**	**0.477**
shrub*fence*time	1.423±2.125	0.670	0.503

Table B2: Model parameters estimates derived from linear mixed models (LMM) to evaluate the effect of **(a)** the initial **height** or **(b)** **diameter** (covariables) of ***Quercus pyrenaica*** seedlings on **growth over time** and **(c)** the initial diameter on the **first-year growth**.

(a) height	estimate±SE	t-value	p
intercept	2.593±1.598	1.622	0.105
shrub	3.592±1.117	3.215	0.002
fence	3.021±2.106	1.435	0.163
time	0.070±0.292	0.239	0.817
height	**-0.006±0.032**	**-0.179**	**0.858**
shrub*fence	-3.302±1.912	-1.727	0.086
shrub*time	-0.234±0.222	-1.054	0.294
fence*time	0.724±0.380	1.906	0.067
time*height	**-0.004±0.006**	**-0.752**	**0.453**
shrub*fence*time	-0.509±0.357	-1.423	0.157
(b) diameter on growth over time			
intercept	-1.596±1.844	-0.865	0.387
shrub	3.000±1.085	2.766	0.006
fence	1.312±2.059	0.637	0.529
time	0.787±0.344	2.286	0.052
diameter	**1.257±0.314**	**3.998**	**<0.001**
shrub*fence	-1.224±1.861	-0.658	0.512
shrub*time	-0.158±0.215	-0.735	0.463
fence*time	0.944±0.370	2.549	0.017
time*diameter	**-0.229±0.059**	**-3.856**	**<0.001**
shrub*fence*time	-0.792±0.349	-2.268	0.025
(c) diameter on first-year growth (2011)			
intercept	-3.149±2.335	-1.348	0.181
shrub	5.658±1.537	3.681	0.002
fence	0.515±2.822	0.183	0.872
diameter	**1.827±0.509**	**3.589**	**<0.001**
shrub*fence	-1.269±2.746	-0.462	0.650

Table B3: Model parameters estimates derived from the generalized linear mixed models (GLMM) models to assess the effect of initial **diameter** of *Quercus petraea* seedlings (covariable) on the **survival** over time.

	estimate±SE	z-value	p
intercept	0.517±1.596	0.324	0.746
shrub	4.636±0.557	8.322	<0.001
fence	0.847±0.649	-1.304	0.192
time	0.874±0.279	-3.131	0.002
diameter	**-0.151±0.137**	**-1.100**	**0.271**
shrub*fence	0.215±0.752	0.286	0.775
shrub*time	-0.063±0.119	-0.524	0.600
fence*time	0.178±0.139	1.286	0.198
time*diameter	**0.032±0.024**	**1.339**	**0.181**
shrub*fence*time	-0.081±0.152	-0.532	0.595

Table B4: Model parameters estimates derived from the linear mixed models (LMM) to assess the effect of initial **diameter** of *Quercus petraea* seedlings (covariable) on **(a)** the **growth over time** and **(b)** the **first-year growth**.

(a) growth over time	estimate±SE	t-value	p
intercept	-8.090±3.000	-2.696	0.007
shrub	5.988±2.141	2.797	0.006
fence	5.965±3.049	1.956	0.061
time	2.140±0.579	2.821	0.022
diameter	**1.546±0.370**	**4.182**	**<0.001**
shrub*fence	-5.819±3.014	-1.931	0.055
shrub*time	-1.240±0.654	-1.898	0.060
fence*time	-0.907±0.766	-1.184	0.246
time*diameter	**-0.233±0.077**	**-3.043**	**0.002**
shrub*fence*time	1.451±0.763	1.901	0.059
(b) diameter on first-year growth (2011)			
intercept	-10.788±3.993	-2.702	0.009
shrub	6.002±2.216	1.866	0.480
fence	4.214±4.897	0.861	0.480
diameter	**3.115±0.631**	**4.936**	**<0.001**
shrub*fence	-3.729±4.892	-0.762	0.459