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Facilitation of underplanted broadleaf trees by pine canopy under Mediterranean conditions depends on thinning intensity and type, not on species drought tolerance

José L. García-Pérez [a,c], Juan A. Oliet [a,*], Pedro Villar-Salvador [b], José Alfredo Bravo-Fernández [a]

[a] Departamento de Sistemas y Recursos Naturales. Escuela Técnica Superior de Ingeniería de Montes, Forestal y del Medio Natural, Universidad, Universidad Politécnica de Madrid, José Antonio Novais 10, Madrid 28040, Spain
[b] Universidad de Alcalá, Forest Ecology and Restoration Group (FORECO), Departamento de Ciencias de la Vida, Alcalá de Henares, Madrid 28805, Spain
[c] Campo Experimental La Campana. Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), Ctra, Chihuahua-Ojinaga, Km. 33.3, Aldama, Chihuahua 32910, Mexico

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ABSTRACT

Planted forests in dry Mediterranean regions are increasingly threatened by extreme climatic events, making adaptive management strategies such as thinning and underplanting essential. To apply these restoration practices at large scales, it is necessary to understand how different tree species respond to varying thinning intensities. This study evaluated the performance of seedlings from four late-successional, resprouting Mediterranean broadleaf species —*Acer monspessulanum* L., *Quercus pyrenaica* Willd *Sorbus torminalis* (L.) Crantz, and the evergreen *Quercus ilex* L. subsp. ballota (Desf.) Samp— underplanted along a canopy openness gradient created by thinning treatments in a 50-year-old *Pinus pinaster* plantation. Four thinning treatments were compared: no thinning (control), moderate thinning from below (20% basal area reduction), heavy thinning from below (35%), and heavy thinning from above (35%), leaving 28.7, 24.9 and 23.2 $m^2 \cdot ha^{-1}$ residual basal area, respectively. Thinning significantly increased light availability, throughfall, and soil moisture, with most improvements occurring under moderate thinning. Soil water availability increased at deeper soil layers in all thinned stands, while shallow soil moisture improved mainly under moderate thinning. After five years, seedling survival was high (>80%) across all species and generally increased with greater canopy openness. *Quercus pyrenaica* and *Q. ilex* showed the strongest positive response in survival to increased canopy opening, whereas *A. monspessulanum* and *S. torminalis* were less affected, likely due to differences in functional traits. Seedling growth was also enhanced by thinning, reaching maximum rates under moderate thinning, with *S. torminalis* exhibiting the highest growth and *A. monspessulanum* the lowest. Improved seedling performance under thinning was associated with reduced summer water stress and higher photochemical efficiency during dry periods. Overall, the study demonstrates that moderate thinning creates optimal environmental conditions for the facilitation of underplanted seedlings and provides guidelines for promoting structural and species diversification in Mediterranean pine plantations.

1. Introduction

Massive forest restoration was implemented during the 20th century in many regions of the world to address historical landscape degradation (Vallejo et al., 2012; Özcan and Çiçek, 2023). These restoration actions often increased forest area, reduced erosion, and restored hydrological functions (Chirino et al., 2006; Cruz-Alonso et al., 2019). Native pines were commonly used due to their fast growth and high colonization capacity (Vadell et al., 2016). However, many of these planted forests now have high stock levels, which hinders their progression into more diverse forests (Kelty, 2006) and increases the risk of stagnation, a specific stage in monospecific, non-differentiated and dense stands that provokes strong reductions of trees growth (Oliver and Larson, 1996). Stagnation is a dangerous stage of forest succession as stands become

* Corresponding author.
E-mail address: juan.oliet@upm.es (J.A. Oliet).

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susceptible to abiotic (drought, fire) and biotic (pests) disturbances, particularly in Mediterranean areas, which are under increasing pressure of climatic change (Vadell et al., 2016; Navarro-Cerrillo et al., 2019; Royo-Navascues et al., 2022).

Diversification of pine plantations using other woody species with different functional traits and reproductive strategies could help to accelerate progression from stagnation and increase ecological resilience and resistance (Pausas et al., 2004; Keskitalo, 2011; Puerta-Piñero et al., 2012). However, spontaneous diversification is often delayed or impeded due to various causes (Cruz-Alonso et al., 2019). In particular, the drought periods in Mediterranean areas, which are becoming longer and more intense (Miranda et al., 2023), preclude the natural regeneration of mid- and late-successional tree species (Mendoza et al., 2009). In addition, the landscapes surrounding many planted forests lack nearby sources of propagules due to the extirpation of former forests (Gómez-Aparicio et al., 2009; Kremer and Bauhus, 2020). Under these circumstances, active underplanting is a way to establish late successional species in the understory of plantations that could potentially become future sources of propagules (Corbin and Holl, 2012; Gavinet et al., 2016a; Lorente-Casalini et al., 2025).

Canopy of adult trees in Mediterranean plantations can compete with or facilitate underplanted seedlings depending on the interaction between climate, stocking levels, and stand structure (Gómez-Aparicio et al., 2009; Alem et al., 2015). Thinning reduces stand stocking levels, increases vertical and horizontal structural heterogeneity, and modifies canopy cover and the understory environment (Pretzsch, 2009; Lu et al., 2018). These changes have potential effects on underplanted species (Gómez-Aparicio, 2009; Helluy et al., 2021; Gavinet et al., 2015). Thinning can be characterized by its intensity and type (Nyland et al., 2016). In general, light to moderate thinning creates intermediate stocking levels that promote the facilitative role of the canopy by buffering extreme temperatures, reducing high radiation, and increasing throughfall (Aussenac, 2000; Gómez-Aparicio et al., 2005, 2008). This facilitative effect can increase the survival and growth of underplanted late successional tree species (Paquette et al., 2006; Löf et al., 2007; Lesko et al., 2024). In contrast, overstocked stands compete with the understory for water, nutrients, and light especially in dry climates (Maestre et al., 2003), reducing the establishment of planted seedlings (Prévosto et al., 2011). On the other hand, heavily thinned, understocked stands can reduce the facilitative capacity of the canopy under high radiation and extreme temperature conditions (Morcillo et al., 2022). These complex interactions likely explain why studies along aridity gradients in the Mediterranean have concluded that the optimum canopy openness varies with climate conditions (Gavinet et al., 2015). Finally, the type of thinning could also affect the performance of underplanted trees by affecting elements such as tree size heterogeneity, density and crown architecture, which in turn affect resource availability at fine scales (Hill et al., 2024). For instance, thinning from above −the removal of dominant or codominant crown classes to favor the best trees of the upper canopy classes, Nyland et al. (2016)− increases stand structural diversity and it is being considered a tool to diversify plantations (Schneider et al., 2021). In contrast, thinning from below, which removes trees from the lowest crown position, reduces structural diversity (Nyland et al., 2016). However, the viability and the effects of crown thinning in planted forests have been little studied (but see Cantiani and Marchi, 2016; Zhang et al., 2019).

Along with climate, the optimum canopy openness must also consider the functional characteristics of underplanted species. Functional traits such as shade and drought tolerance, leaf habit, specific leaf area (SLA), and phenotypic plasticity can influence the performance of planted species under varied stocking conditions (Gavinet et al., 2016a; Granados et al., 2016, Morcillo et al., 2022). For instance, compared to evergreen trees, deciduous trees are generally more sensitive to photoinhibition (Valladares, 2004; Sánchez-Gómez et al., 2006; Gavinet et al., 2015, 2016a) and show higher osmotic potential at the turgor loss point and SLA, which are surrogates of reduced drought tolerance (Bartlett et al., 2012; Greenwood et al., 2017). Previous studies testing artificial regeneration of late successional species under pine plantation understory have mainly focused on *Quercus* species (Rodríguez-Calcerrada et al., 2008; Padilla et al., 2009; Granados et al., 2016; Lesko et al., 2024). Understanding how the functional traits affect the performance of planted trees can provide guidance for species selection in underplanting. Due to the complex interactions between thinning characteristics and species functional traits, new experiments are needed to assess the relationships between canopy openness, specific functional traits, and underplanting response, in order to optimize silvicultural prescriptions for diversifying planted pine forests.

In this study, we evaluated the influence of canopy openness, as determined by different thinning intensities and types, in a *Pinus pinaster* Ait. ssp. *mesogeensis* plantation on understory environmental conditions and the performance of four late-successional broadleaf tree species: *Quercus ilex* L. subsp. ballota (Desf.) Samp, *Quercus pyrenaica* Willd, *Sorbus torminalis* (L.) Crantz and *Acer monspessulanum* L. All species are shade tolerant (Ruiz de la Torre, 2006), with small differences reflected in their similar root growth responses to shade (García-Pérez et al., 2021). They are resprouters species but differ in leaf habit and drought tolerance (Valladares, 2004; Quero et al., 2006). Thinning treatments were applied prior to underplanting in an experiment that tested two types of thinning (from below and from above) and two intensities (moderate and heavy). Our hypotheses were that, under our the environmental conditions: 1) Canopy openness increases soil moisture, light and air temperature and reduces air relative humidity, 2) Moderate thinning increases seedling performance more than no thinning and heavy thinning, as it increases resource availability while still buffering harsh abiotic conditions, and 3) Performance of underplanted species depend on their functional traits, with drought-tolerant species benefiting more from strong canopy opening.

2. Material and methods

2.1. Experimental site

The study is located at Jócar (40° 59" 43.42' N y 3° 10" 46.7′ W; Guadalajara, Central Spain), which has a typical continental Mediterranean climate. Mean annual temperature is 12.4 °C, ranging from 4.6 °C in January to 22.1 °C in July. Average annual rainfall is 640 mm (1961–2018, El Vado weather station, AEMET). Altitude is around 1070 m a.s.l. with northwest exposures and 10–15° slopes.

The main soil groups are Umbrisols and Alisols (FAO, 1988), 21–40 cm deep over clay parent material with quartzite stones. Soil texture is silty loam (sand 30%, silt 51%, clay 18%; n = 3). Bulk density is 1.45 g cm^{-3}, pH is 5.32, and electrical conductivity is 0.34 dS m^{-1}. Organic matter is 1.45%, nitrogen 0.07%, phosphorus 7.84 mg kg^{-1} and potassium 75.4 mg kg^{-1} (Oliet et al., 2022).

The dominant vegetation consists of *P. pinaster* reforestations planted in 1969 (2500 trees ha^{-1}) and thinned in 2005, removing 50% of the trees remaining (Serrada and Garrachón, 2001). The understory is composed of shrubs such as *Salvia rosmarinus* (L.), *Cistus ladanifer* L., *Cistus laurifolius* L., Schleid., *Juniperus oxycedrus* L, *Daphne gnidium* L., *Rosa* spp., *Crataegus monogyna* Jacq., and *Rubus ulmifolius* Schott. Juveniles of *Q. ilex*, *Quercus faginea* Lam., *A. monspessulanum*, and *Juniperus thurifera* L. occur in small numbers, together with grasses and legumes. The microtopography reflects former soil preparation at pine planting, with undisturbed slopes interspersed by furrows and mounds.

2.2. Experimental design and treatments

In November 2017 we established three experimental blocks (Fig. 1).

Prior to thinning, mean (±SE) pine height and diameter at breast height was 13.6 ± 0.5 m and 29.3 ± 0.6 cm, respectively, and mean basal area (BA) was 36.2 ± 0.8 $m^2 \cdot ha^{-1}$ (data from an inventory of all trees of the experimental plots, Figure S1, Oliet et al., 2022). Additional

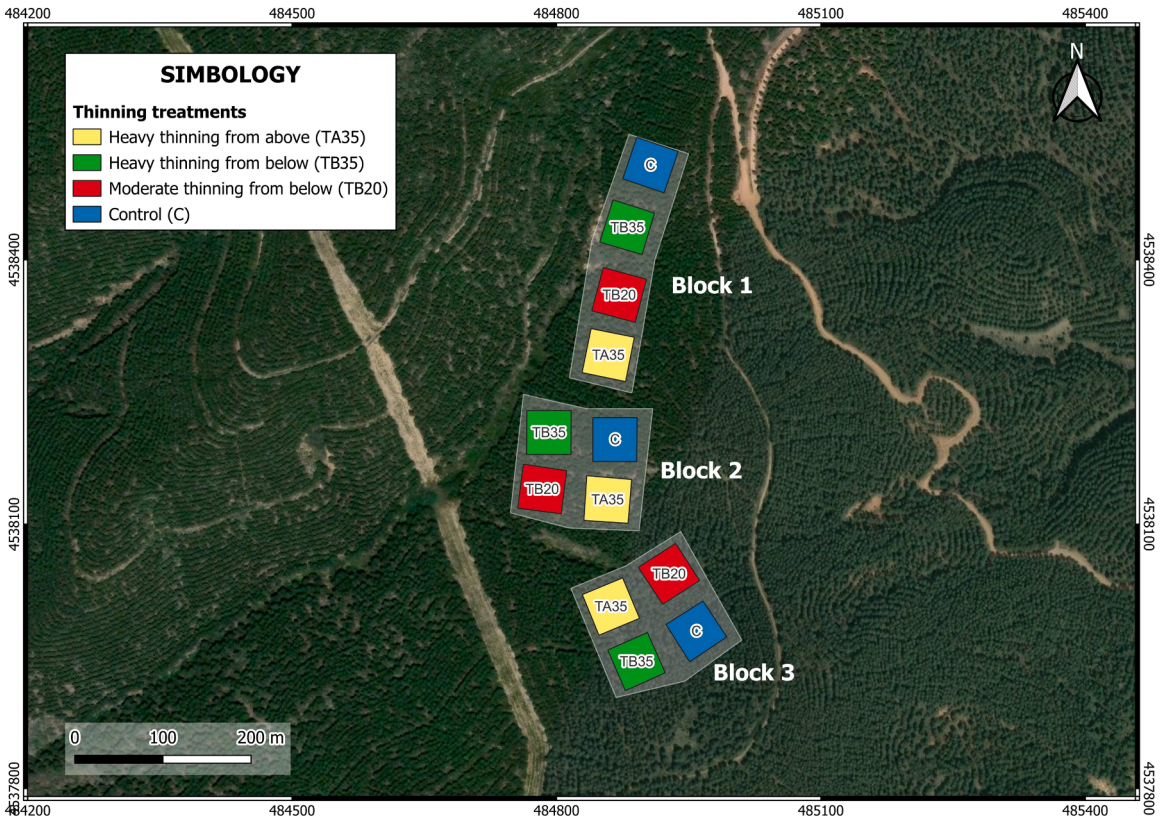


Fig. 1. Spatial distribution of the thinning treatments in the three blocks inside the *Pinus pinaster* plantation. In each thinning treatment, four tree species were randomly planted.

information of the stand can be found in Table S1. In each block, we randomly assigned four thinning treatments to four 50 × 50 m plots (plus a 10 m wide edge as a buffer strip). Thinning treatments differed in type and intensity: no thinning (Control), moderate thinning from below, in which 20% of the BA was removed (TB20); heavy thinning from below (TB35), in which 35% of the BA was removed; and heavy thinning from above (TA35), in which a 35% of BA was removed by cutting on average two codominant trees per each of the 100 crop trees reserved. Despite the stand was relatively young and uniform, crop trees could be selected among codominants and released to gain dominance in the midterm (Cantiani and Marchi, 2016). TA35 increased understory light heterogeneity, where shaded areas alternated with high light areas around the reserved tree.

Underplanted species differed strongly in drought tolerance and growth capacity traits (Table S2). *Quercus ilex*, the only evergreen species, showed a stress-tolerant syndrome, with low specific leaf area (SLA) and high wood density, coupled with the lowest osmotic potential at the turgor loss point and lowest xylem embolism vulnerability (P_{50}), indicating high drought tolerance (Knight and Ackerly, 2003; Reich, 2014; Greenwood et al., 2017; Maréchaux et al., 2015; Choat et al., 2018). In contrast, deciduous species showed higher SLA, osmotic potential at the turgor loss point, and P_{50}, and lower wood density, indicating faster growth but lower drought tolerance. Among them, *A. monspessulanum* had the lowest P_{50}, indicating comparatively high drought tolerance.

In March 2018, 15 one-year-old seedlings per tree species were planted in each experimental plot (60 seedlings plot^{-1}, 720 seedlings in the whole experiment). Seedlings were planted in new holes opened on the former furrows (1.5 m between seedlings within a furrow, 3.1 m between furrows). Holes were 30 cm in diameter and 60 cm deep and were drilled with an auger (BT 360 Sthil, Wailing, Germany). Cultivation procedure along the morphological and nutrient attributes of seedlings at planting are presented in Supplementary material and in Table S3, respectively.

One month after planting, some seedlings were predated by wild boar (*Sus scrofa)* and the resulting number of alive seedlings after predation was reduced by 4% in *A. monspessulanum,* 73% in *Q. pyrenaica,* 42% in *S. torminalis* and 58% in *Q. ilex*. Survival was calculated based on remaining plants. One year after planting, 23.5% of seedlings were browsed by deer (25% *A. monspessulanum,* 23% *Q. ilex*, 42% *Q. pyrenaica*, and 22% *S. torminalis*), which were excluded from the height growth analyses. Table S4 depicts sample size after wild boar predation.

2.3. Monitoring of environmental variables, understory vegetation cover and pine tree competition

Throughfall under the pine canopy was measured biweekly from July 2018 to December 2019 using three 12-cm rain gauges per plot (n = 9 per treatment) placed 1 m above the ground. Three additional rain gauges in a firebreak located < 200 m away from the experimental site measured the rain without canopy interception. Air temperature and relative humidity were recorded between June and September 2019 using one U23 Pro v2 data logger (Onset Computer Corporation, Inc. Southern MA, USA) placed 0.7 m above ground in the center of each plot (n = 3 per thinning treatment). Soil moisture was measured at two depths (0–20 cm and 30–40 cm) biweekly from July 2018 to December 2019 in three randomly selected planting holes per plot (n = 9 per thinning treatment). We used Time Domain Reflectometry (Field Scout 100, Spectrum Technologies, Inc., Painfield, IL ®) to measure soil moisture at 0–20 cm, vertically inserting two 20 cm long stainless-steel rods three months after planting. At the 30–40 cm depth, we used HS-10 sensors (ProCheck, Decagon Devices, Inc., Pullman, USA). The 10 cm rods of these sensors were inserted vertically after removing the top

30 cm with a soil probe. Both sensor types were previously calibrated and showed minimal differences.

Understory light environment was characterized by the Global Site Factor (GSF). GSF represents the proportion of global radiation around a point under the canopy relative to the global radiation in an open area and was estimated using hemispherical photography (Chianucci and Cutini, 2012). From October to December 2018 and 2019, photos were taken at every non predated by boar seedling in 2018 with a tripod 60 cm above the ground on overcast days with a digital camera (Nikon Coolpix 4500, Tokyo, Japan) using a fisheye lens (FC-E9 Nikon, Tokyo, Japan). Images were processed using Gap Light Analyzer 2.0 (Frazer et al., 1999), using site coordinates and considering a March to September growing season (Fournier et al., 2017).

Finally, as a proxy for competition, herb and shrub height and cover within 40 cm of each planted seedling were measured in autumn 2018, 2019, and 2023, as well as the distance to the nearest pine.

2.4. Seedling survival, growth, and physiological responses

To assess the response of seedling performance to the thinning treatments, we measured the survival, height, and diameter at the root collar at the end of the 2018, 2019 and 2023 growing seasons. Height was measured from root collar to the base of the terminal bud with a flexometer, while the diameter was measured with a digital caliper. To understand the ecophysiological basis of seedling performance differences, we measured simultaneously the water potential (ψ) and the maximum photochemical efficiency of photosystem II (F_v/F_m) during July, August, and September 2018, and again in July and September 2019.

Water potential was measured at predawn and mid-day in six plants per species and treatment. Excised leaves were bagged and stored in an icebox for immediate *in situ* measurement with a pressure chamber (PMS/1000, PMS Instruments, Corvallis, Oregon, USA). *Q. pyrenaica* was not measured in July 2018 due to the low number of available individuals.

F_v/F_m was measured in nine plants per species and treatment using a portable pulse-amplitude modulated fluorimeter (FMS2, Hansatech Instruments, Kings Lynne, UK). Leaves used for mid-day measurements were dark-adapted for at least 30 min prior to F_v/F_m measurements.

Two tears after planting, SLA was measured in six plants per species and treatment to assess acclimation to environmental changes after thinning (Lambers et al., 2008). Two leaves per plant were cut, wrapped in moist paper, bagged, placed in an icebox, transported to the laboratory, stored in a refrigerator at 4 ºC, and processed within 48 h. Leaves were scanned to measure their area using ImageJ version 1.52 (Schneider et al., 2012) and then oven-dried at 70 ºC for two days to determine their mass. SLA was calculated as the area-to-mass ratio.

2.5. Statistical analyses

We used ANOVA to test the effect of thinning treatments (main factor) on stand density, GSF, BA, and herb cover. Temperature and relative humidity data were used to calculate the vapor pressure deficit. Differences among thinning treatments in air relative humidity, temperature, and vapor pressure deficit, and the accumulated throughfall and soil moisture were assessed by linear mixed model. Thinning treatments, and soil depth were fixed factors, while the rain gauge, and air sensors were random factors.

Physiological variables were analyzed separately for each year using a linear mixed model. Fixed factors included sampling month, species, and thinning treatments, while time (predawn and midday, measured on the same individual) was a random factor. Individual seedlings were not included as a random factor because not all plants were measured consistently across every date.

Height and diameter increment after two and five years were analyzed separately by ANOVA with thinning treatment, species and their interactions as fixed factors.

Survival was analyzed through a generalized linear model with a binomial error distribution and a 'cloglog' link function, which is recommended for highly skewed datasets. The model was initially fitted with species, GSF, their interaction, and understory vegetation cover, and distance to the nearest pine tree.

Additionally, the relationship between seedling growth and GSF, understory vegetation cover, and distance to the nearest pine tree was analyzed using multiple linear regressions. Data were log-transformed when necessary to meet assumptions of normality and homoscedasticity.

Block was considered a fixed factor in all analyses due to the low number of replicates (Zuur et al., 2009). Analyses were performed with R, version 3.6., (R R Core Team, 2019) using the *lmer* function of the *lme4 package* (Bates et al., 2015) for linear mixed models, and *lm* and *glm* of the *stats package* to test linear and generalized linear models. Models are shown in Tables S5 and S6. Tukey's test (α=0.05) was used to assess differences between treatments using the *emmeans* package (Lenth, 2016).

3. Results

3.1. Thinning effects on the residual stand and understory environment

Compared to the control, stand density was reduced by 36% in the three thinning treatments without significant differences among them (Table 1). Density reduction, however, resulted in BA differences, with the TB20, TB35 and TA35 plots having on average 20, 30 and 35% lower BA than control plots, respectively. The lowest understory vegetation cover was observed in the unthinned control (Table 1).

Compared to 2019, spring 2018 was wetter, while the summer was drier and longer. In contrast, spring and early summer in 2019 were drier, but heavy late-summer rains relaxed drought earlier (Figure S2). Throughfall significatively increased with canopy openness ($F = 7.4$, $p < 0.001$). In the unthinned stands, throughfall reached 76% of open areas rainfall, increasing to 81% in TB stands (regardless of thinning intensity) and to 85% in the TA35 stands, which differed significantly from the unthinned stands (Fig. 2).

Thinning significantly affected GSF ($F = 264$ $p < 0.001$), although it did not vary linearly with changes in BA. TB20 increased GSF from 31.5% to 46.1%, while TB35, yielded only a further 7.2% increment despite resulting in an additional 15% of BA reduction. Thinning type (from below *versus* from above) did not affect mean GSF values, although TA35 showed higher variability according to box size in Fig. 3.

Neither air temperature nor relative humidity differed significantly among thinning treatments (Table S7). The only marginally significant difference ($p = 0.08$) in air temperature was observed between unthinned and thinned stands: minimum temperatures were ~0.5 °C lower and maximum temperatures ~1 °C higher under thinning (Table S7), leading to slightly higher vapor pressure deficit. Thinning intensity or type had no effect on temperature or relative humidity.

Soil moisture was significantly higher at deeper horizons (Figs. 4 and

Table 1
Characteristics of the stands and understory cover five years after thinning (means ± SE, n = 3 plots per treatment) and ANOVA results for comparisons among treatments (F-value and associated probability). Within a row, means with different letters indicate statistically significant differences.

	Control	Moderate low	Heavy low	Heavy above	F-value (P)
Stand density (trees ha^{-1})	537 ± 31 a	361 ± 19 b	332 ± 18 b	344.2 ± 21 b	63.1 (<0.001)
Basal area (m^2 ha^{-1})	35.7 ± 1.4 a	28.7 ± 1.6 b	24.9 ± 1.0c	23.2 ± 1.1 c	69.2 (<0.001)
Herb and shrub cover (%)	1.7 ± 0.7 b	12.6 ± 2.4 a	13.9 ± 1.9 a	8.5 ± 1.6 a	9.6 (<0.001)

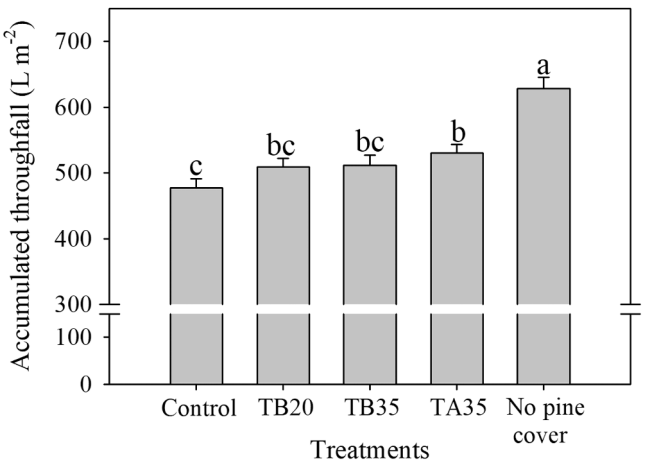


Fig. 2. Accumulated throughfall between July 2018 and December 2019 (mean ± 1 SE, n = 9) under the canopy of stands subjected to different thinning treatments and out of the stand (No pine cover). TB20 = Moderate thinning from below, 20% BA reduction; TB35 = Heavy thinning from below, 35% BA reduction; TA35 = Heavy thinning from above, 35% BA reduction. Distinct letters among treatments denote significant differences (α = 0.05), after Tukey's post hoc test.

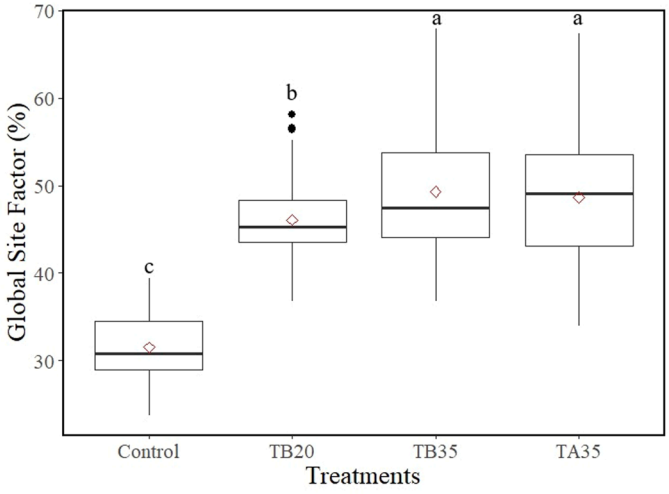


Fig. 3. Global Site Factor under the canopy of stands subjected to different thinning treatments (n = 77–138). TB20 = Moderate thinning from below, 20% BA reduction; TB35 = Heavy thinning from below, 35% BA reduction; TA35 = Heavy thinning from above, 35% BA reduction. Boxes are the 95th and 5th percentiles, while the solid line indicates the median, and red diamonds indicate the mean. Whisker represents the non-outlier minimum and maximum values. Distinct letters among treatments denote significant differences (α = 0.05), after Tukey's post hoc test.

S3). Thinning significantly increased soil moisture in both study years ($F = 4.87$, $p = 0.007$), although differences among thinning treatments varied with soil depth (thinning treatment × soil depth interaction, $F = 49.1$, $p < 0.001$). At 0–20 cm, TB20 showed the highest moisture, whereas at 30–40 cm all thinning treatments exceeded the unthinned stands (Fig. 4). Thinning type (TA35 v TB35) had no effect on soil moisture.

3.2. Survival

Overall, first year survival of intact seedlings (excluding those killed by wild boar immediately after planting) was 94 ± 3.0%. Species significantly differed in survival ($\chi^2 = 9.08$, $p = 0.028$) in the following order: *S. torminalis* > *A. monspessulanum* > *Q. pyrenaica* > *Q. ilex*. Survival significantly increased with GSF ($\chi^2 = 5.49$, $p = 0.019$) in all species, except for *A. monspessulanum*, which did not show any significant variation with this factor (interaction species × GSF, $\chi^2 = 9.61$, $p = 0.022$, data not shown). After the second year, overall survival dropped to 92 ± 2.3% and species differences vanished ($\chi^2 = 5.81$, $p = 0.12$). However, the positive effect of GSF on survival persisted ($\chi^2 = 6.05$, $p = 0.013$), while the species × GSF interaction shifted to an only marginally significant ($\chi^2 = 7.05$, $p = 0.071$, data not shown) value. After the fifth year, survival dropped to 81 ± 3.9% with species differences and the species × GSF interaction turning again to be significant ($\chi^2 = 13.92$, $p = 0.003$ and $\chi^2 = 13.60$, $p = 0.003$, respectively). By species, survival order changed to *S. torminalis* > *Q. pyrenaica* > *Q. ilex* > *A. monspessulanum*. Survival variation with GSF was similar to previous years, except for *S. torminalis*, which tended to be slightly negative with GSF (Fig. 5). No significant effects of distance to the closest pine or herb cover on survival were found (data not shown).

3.3. Growth and SLA

Two years after planting, thinning significantly increased diameter growth ($F = 3.2$, $p = 0.023$), but no height growth ($F = 2.1$, $p = 0.1$). After five years, thinning effects became more evident on both diameter ($F = 6.3$, $p < 0.001$) and height ($F = 19.7$, $p < 0.001$) growth, with TB20 seedlings showing the highest growth (Fig. 6). Species differed in height and diameter growth after two ($F = 173$, $p < 0.001$, $F = 37.3$, $p < 0.001$, respectively) and five years ($F = 58.1$, $p < 0.001$, $F = 6.5$, $p < 0.001$, respectively), with *S. torminalis* showing the highest and *A. monspessulanum* the lowest (Fig. 6). No significant thinning × species interaction was observed for height and diameter growth neither the second nor fifth year (ANOVA data not shown). Distance to the closest pine, or herb and shrub cover did not significantly influence the growth of planted seedlings (data not shown).

Thinning significantly affected SLA ($F=7.93$, $p = 0.001$) after two years. SLA was higher in TB20 and unthinned stands (154 ± 7.4 $cm^2 \cdot g^{-1}$) than in both heavy thinning treatments (135 ± 5.5 $cm^2 \cdot g^{-1}$). No significant interaction between thinning and planted species on SLA was observed ($F = 1.4$, $p = 0.17$). SLA significantly differed among species ($F = 161$, $p < 0.001$) in the following order: *S. torminalis* (195 ± 6.4 $cm^2\ g^{-1}$) > *A. monspessulanum* (167 ± 4.0 $cm^2\ g^{-1}$) = *Q. pyrenaica* (158 ± 6.2 $cm^2\ g^{-1}$) > *Q. ilex* (63 ± 2.0 $cm^2\ g^{-1}$).

3.4. Physiological response

Overall, seedling ψ was more negative in unthinned stands during both studied years, indicating higher water stress, with pattern differences within and between years. In 2018, TB20 showed the highest ψ (i.e., lowest water stress), both heavy thinning treatments (TB35 and TA35) showed intermediate values, and the unthinned treatment the lowest values. This pattern, however, varied across summer (Treatment × Month interaction, Table 2): differences among thinning treatments were negligible in July when soil water content was relatively high (Figure S3) but became apparent in the middle and at the end of the summer (Fig. 7). Similarly, species ψ differences occurred in August and September, but not in July (Species × Month interaction, Table 2), with the lowest ψ values in *S. torminalis* and the highest in *Q. ilex*. No significant species × thinning treatment interaction was found.

In 2019, interspecific patterns changed substantially. In July (the driest month in 2019), *A. monspessulanum* showed the lowest ψ, while *Q. pyrenaica* the highest. In September, species differences vanished and ψ was significantly higher than in July (Fig. 7). Additionally, there was a significant species × thinning treatment interaction (Table 2): *Q. pyrenaica, S. torminalis* and *Q. ilex* seedlings showed the lowest ψ (i.e. higher water stress) in the unthinned stands and the highest values in the TB20 stands, while *A. monspessulanum* showed no significant differences among thinning treatments although ψ tended to increase from the

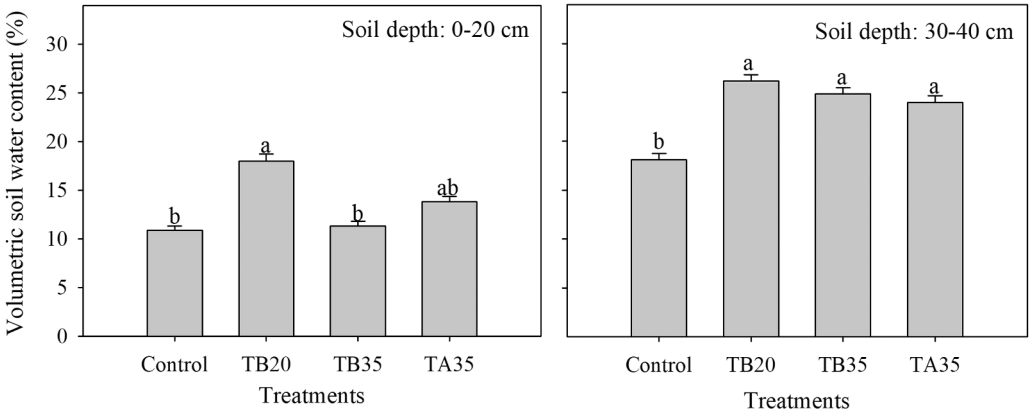


Fig. 4. Soil volumetric water content by thinning treatments (mean ± 1 SE) at shallow (0–20 cm, left) and deep (30–40 cm, right) soil layers in the four thinning treatments: Control (no thinning); TB20 = Low moderate thinning, 20% BA reduction; TB35 = low heavy thinning, 35% BA reduction; TA35 = Heavy thinning from above, 35% BA reduction). Distinct letters among treatments denote significant differences (α = 0.05), after Tukey's post hoc test.

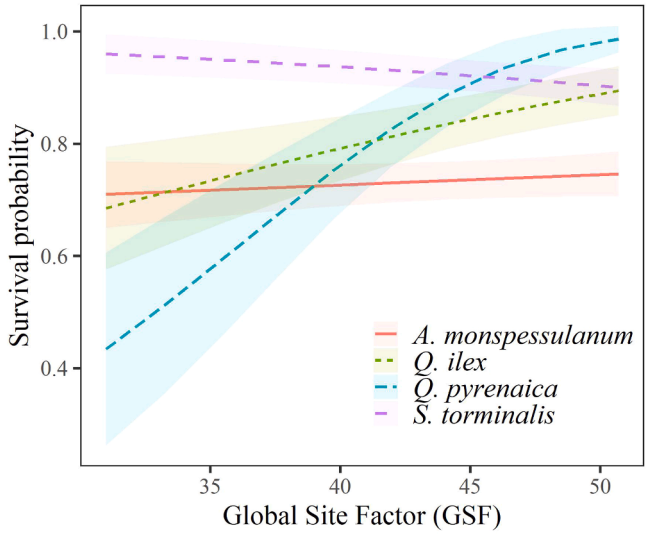


Fig. 5. Fifth year predicted survival probability of *A. monspessulanum, Q. pyrenaica, S. torminalis* and *Q. ilex* seedlings in relation to their GSF. Variation in GSF was achieved through different thinning treatments (see Material and Methods section for details). Shaded areas around the predictions represent ±1 SE.

unthinned to the TA35 stands (Fig. 7). As per 2018, a significant Treatment × Month interaction occurred in 2019 (Table 2), with minimum ψ values in the unthinned treatment in July, and thinning treatment differences vanishing after September rains (Table 2 and Fig. 7). Notably, ψ differences between the unthinned and thinned stands in July were large, averaging −1.2 MPa, with very low ψ values in the unthinned stands, averaging −5.1 MPa across species (Fig. 7).

In 2018, unthinned stands showed the highest F_v/F_m and TA35 stands the lowest in early summer, but treatment differences disappeared by late summer (Treatment × Month interaction, Table 2 and Figure S4). That year, *A. monspessulanum* showed the lowest F_v/F_m, while both oaks showed the highest values. In contrast, in July 2019, seedlings in the unthinned stands had significantly lower F_v/F_m than in the rest of thinning treatments. These differences, disappeared by September and F_v/F_m recovered to optimal values after summer storms.

4. Discussion

Our results demonstrate that thinning is a valid strategy for promoting specific diversification of *P. pinaster* stands through underplanting late successional tree species. Thinning improved water and light availability while increasing the short-term physiological performance of underplanted seedlings, and their mid-term growth and survival. However, responses differed among thinning treatment and species.

4.1. Canopy opening modifies soil water and light availability, but not air temperature and relative humidity of the understory

Canopy opening through thinning increased soil water and light availability in agreement with our first hypothesis. Soil water increase was mainly observed during spring, when underplanted seedlings are actively growing, and in summer when seedlings are exposed to drought. This result is in line with previous studies (Paquette et al., 2006; Tulod et al., 2019; Hill et al., 2024) and can be attributed to two factors. First, throughfall was reduced in the control (unthinned stand) compared to thinned stands, without any effect of thinning intensity or thinning type (Fig. 2). The difference in throughfall between the TA35 treatment and the control was 54 mm, which represented 12% of the total rainfall accumulated during the first two seasons after thinning. Similar throughfall values have been observed in thinned stands of *Pinus halepensis* Mill. (Granados et al., 2016). Despite those differences may not be large, small differences in water availability in water-stressed environments can have significant effects on seedling physiological performance (see following section). Second, stand density reduction can reduce pine root density and transpiration of adult trees and therefore competition for water with underplanted seedlings (Aussenac, 2000; Löf et al., 2007; Rose et al., 2020). Very interestingly, soil moisture varied differently with depth and thinning treatment. Shallow horizons (0–20 cm) showed a significant increase in soil water availability only under moderate thinning. This suggests that under intense thinning, the negative effect of evaporation on water availability in the upper soil layer could offset the benefits of increased throughfall and transpiration reduction. Therefore, a moderate opening of the stand fosters the facilitative effect of the pine canopy, at least in terms of soil water availability. In contrast, at deeper horizons (30–40 cm) the effects of thinning on soil moisture shifted: compared to the unthinned treatment, opening the canopy at any intensity and type increased similarly soil moisture (Fig. 4). These results suggest that at 30–40 cm, evaporation effect is no longer significant in comparison to increased throughfall and reduction of pine root density. Several studies in Mediterranean areas showed similar beneficial effects of thinning on soil moisture (Rodríguez-Calcerrada et al., 2008; Gavinet et al., 2015). This positive effect of thinning on soil moisture can modulate the morpho-physiological response of underplanted seedlings by alleviating drought stress especially during the driest months of the summer (see

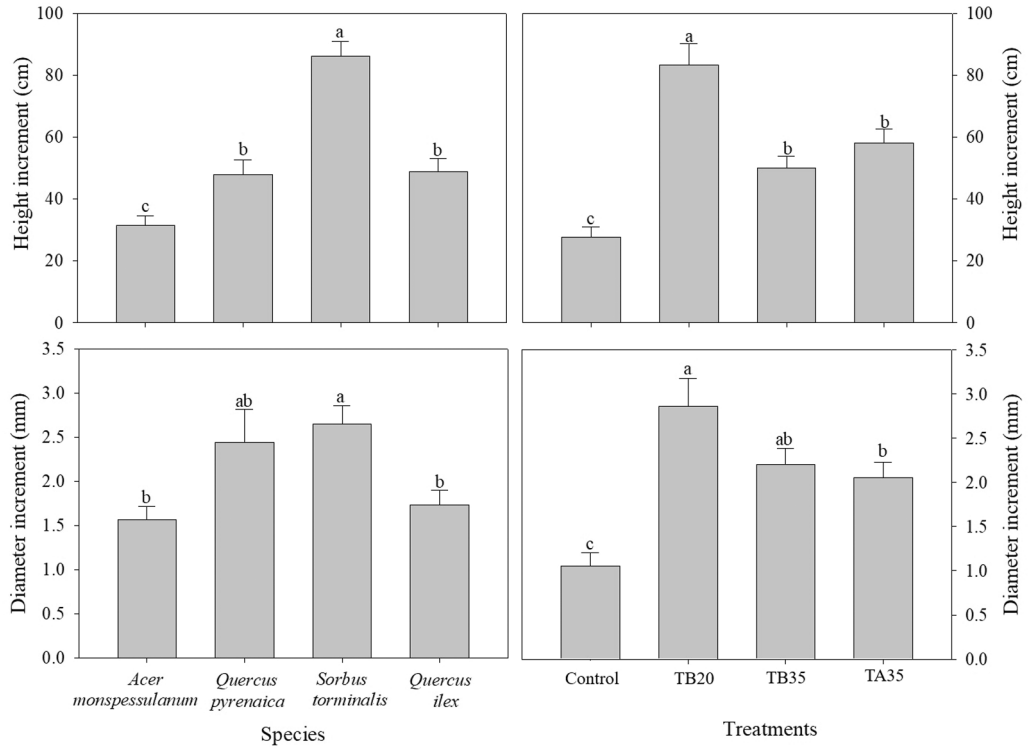


Fig. 6. Seedling height (upper subfigures) and basal stem diameter (lower subfigures) increment (mean ± 1 SE) five years after in four late successional tree species (left) planting in a *Pinus pinaster* plantation subjected to four thinning treatments (right): Unthinned; TB20 = Moderate thinning from below, 20% BA reduction; TB35 = Heavy thinning from below, 35% BA reduction; TA35 = Heavy thinning from above, 35% BA reduction. Distinct letters among treatments and species denote significant differences (α = 0.05), after Tukey's post hoc test.

Table 2
Statistical results for the water potential (ψ) and maximal photochemical efficiency of photosystem II (F_v/F_m) measured during various dates in the 2018 and 2019 summers in seedlings of four late successional species planted in a *Pinus pinaster* plantation subjected to four thinning treatments. F-values and associated probabilities in brackets are shown.

Year	Variable	Specie (S)	Thinning treatment (T)	Month (M)	T × S	T × M	S×M	T × S×M
2018	ψ	2.50 (0.016)	9.1 (<0.001)	90 (<0.001)	1.06 (0.39)	3.9 (0.024)	3.9 (<0.001)	1.46 (0.85)
	F_v/F_m	142 (<0.001)	7.1 (<0.001)	45.8 (<0.001)	0.92 (0.50)	4.4 (<0.001)	3.2 (0.003)	0.63 (0.87)
2019	ψ	0.10 (0.96)	21.21 (<0.001)	532 (<0.001)	4.1 (>0.001)	9.1 (<0.001)	7.0 (<0.001)	0.98 (0.45)
	F_v/F_m	63 (<0.001)	11.0 (<0.001)	270 (<0.001)	0.70 (0.71)	11.2 (<0.001)	0.42 (0.73)	0.89 (0.52)

next section, Granados et al., 2019 and Hill et al., 2024), in accordance with our first hypothesis.

Thinning increased light availability (Fig. 3), but it was not linear with BA reduction. Surprisingly, there were no significant differences in GSF between the two types of heavy thinning (thinning from below and from above), despite noticeable differences in gap structure of the canopy (Cantiani and Marchi, 2016). Contrary to our first hypothesis, thinning did not affect understory air temperature or relative humidity in summer, in contrast with other studies (Gavinet et al., 2016b; Granados et al., 2016; Thyroff et al., 2019; Hill et al., 2024) that show a mitigation of extreme high temperatures by the tree canopy with increasing stand density.

4.2. Species-specific performance of underplanted species to canopy openness

Overall, canopy opening increased survival and growth of underplanted trees, indicating that adult pines compete with establishing seedlings in highly stocked stands. However, contrary to our second hypothesis, moderate thinning only increased growth relative to heavy thinning, but not survival, which kept constant or augmented with GSF. In a similar thinning study at two Mediterranean locations with contrasting water availability, Gavinet et al. (2015) found a negative effect of thinning on seedling survival in the harsher location, but a positive effect of thinning in the milder location, consistent with our study. This suggests, according to the stress gradient theory (Bertness and Callaway, 1994), that facilitation effect of the canopy varies with abiotic stress, with a less positive or even negative effect of a dense canopy under mild stress sites such as in our study.

Seedling physiological responses to thinning largely reflected survival and growth responses and understory microenvironment, helping to unravel the main factors driving seedling response to thinning. Compared to thinned stands, seedlings in unthinned stands showed higher water stress and lower survival and growth (Figs. 5–7), likely due to reduced soil moisture. Seedling F_v/F_m was also lower in the unthinned stands, consistent with the reduced water potential, indicating higher seedling stress, especially during driest months of summer 2019 (Figure S4). The relationship between survival, growth, and physiological performance was, however, more complex across thinned stands and varied with thinning intensity. For most species, seedlings growth after five years was lower in the heavily thinned stands, consistent with higher water stress and our second hypothesis. Unexpectedly survival in most species also increased with canopy opening. Reduced growth and higher water stress of underplanted seedlings in heavily thinned stands

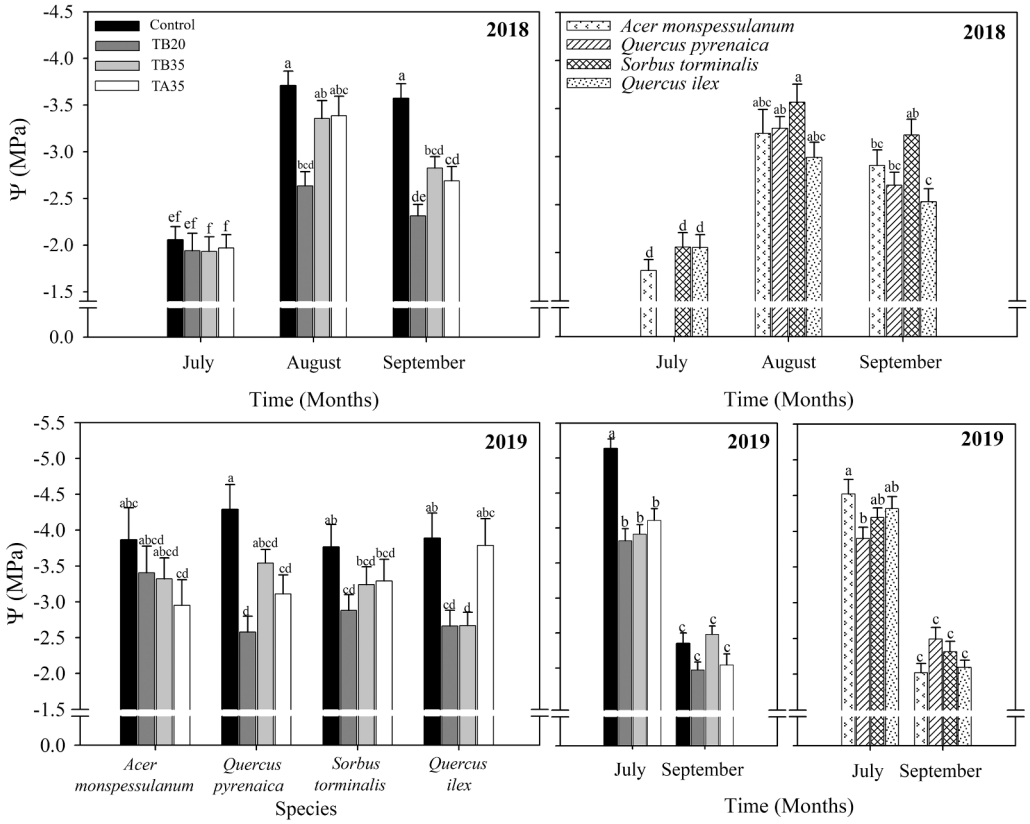


Fig. 7. Water potential (ψ; mean ± 1 SE) in the 2018 (top) and 2019 (down) summers in seedlings of four late successional tree species underplanted in a *Pinus pinaster* stand subjected to four thinning treatments: Unthinned; TB20 = Moderate thinning from below, 20% BA reduction; TB35 = Heavy thinning from below, 35% BA reduction; TA35 = Heavy thinning from above, 35% BA reduction. Distinct letters among treatments denote significant differences (α = 0.05), after Tukey's post hoc test.

could be explained by lower soil moisture at 0–20 cm (Fig. 4) and likely higher transpiration driven by increased light availability, which can further reduce seedling water potential (Aranda et al., 2005). Therefore, our water potential and soil moisture results suggest that a moderately opened canopy (20% BA reduction, reaching 28.7 $m^2 \cdot ha^{-1}$ and 46.1% GSF) ameliorates seedling stress and facilitates growth by increasing soil moisture, while a heavily opened canopy (35% BA reduction, reaching 23.2 $m^2 \cdot ha^{-1}$ and 53.3% GSF) is more effective at promoting or maintaining survival. The conflict between survival and growth results across thinned treatments may be explained by different physiological processes having different water stress thresholds. In heavily thinned stands, seedling water potentials were not low enough to compromise survival (the catastrophic embolism in Q. *ilex* occurs at water potentials < -7 MPa and in the rest of species at water potentials < -4 MPa (Martínez-Vilalta et al., 2002; Vilagrosa et al., 2012) but were low enough to limit growth. Fluorescence data also support this interpretation as the minimum F_v/F_m values were always > 0.7, indicating low to moderate levels of photochemical stress that do not compromise survival (Kalaji et al., 2014). In a similar pine plantation study, canopy openness significantly enhanced growth and photosynthesis rate but not survival (Lesko et al., 2024). On the contrary, the higher water stress of seedling in the unthinned stands was likely closer to damaging physiological limits, explaining the lower survival observed in highly stocked, unthinned stands. In summary, agreement between mid-term survival and growth and early physiological data indicates improved conditions for seedlings under open canopies, especially at moderate intensity (Granados et al., 2016; Helluy et al., 2021; Acevedo et al., 2024).

Compared to heavily thinned stands, seedlings in unthinned and moderately thinned stands showed higher SLA, an acclimation response to low light (Poorter et al., 2009). However, increased SLA is associated with lower stress tolerance (Knight and Ackerly, 2003; Valladares, 2004; Quero et al., 2006) and may have contributed to hinder survival and growth in the unthinned stands. Combined with water stress in summer, increased SLA is part of the *dry shade syndrome*, which reduces the performance of understory plants in dry, dense Mediterranean forests (Valladares, 2004).

Seedling survival response to canopy opening differed among species, suggesting species-specific functional and stress tolerance differences. However, support for our third hypothesis was weak, as no clear relationship was observed between survival responses and species drought-tolerance traits. For instance, *S. torminalis*, despite having lower stress-tolerance traits than *Q. ilex*, showed the highest survival and growth, with both performance traits unaffected by canopy opening. This indicates high tolerance to both dry-shade conditions under a dense canopy and harsher conditions in strongly thinned stands. A similar trend was also observed in *A. monspessulanum*. In contrast, survival of both oak species increased with canopy opening, hinting to low tolerance to dry-shade conditions, especially for *Q. pyrenaica*, which is less drought-tolerant than *Q. ilex*. Other factors associated with dense, unthinned stands, beyond drought and light stress, may therefore be more influential and merit further investigation.

5. Conclusions and practical implications

Our study reveals that canopy opening of pine plantations through thinning modifies the abiotic conditions of the understory with significant effects on the underplanted species. These effects change substantially with thinning intensity, response variable and the species, but not with the thinning type. A moderate canopy opening from below, achieved through a 20% reduction in BA, increases soil moisture and

reduces pine competition. These effects alleviate water and photosynthetic stress on underplanted seedlings, promoting growth of all the species. In addition, canopy opening affects survival in a different way depending on the species: *Quercus pyrenaica* and *Q. ilex* survival benefits the most with canopy opening, while *A. monspessulanum* and *S. torminalis* survival was unaffected by thinning. *Sorbus torminalis* showed the highest performance under understory conditions in both survival and growth. These responses are not necessary associated with specific traits such drought tolerance, evidencing the complexity of the interactions between environment and functional traits. Type of thinning (from below versus from above) had small effects in understory microenvironment and seedling physiological performance, but no effect on growth and survival after five years of planting. These results can be used to design silvicultural prescriptions for diversifying monospecific planted forests of inland meso-Mediterranean pine plantations, including thinning and species selection. Our study indicates that a minimum canopy openness involving 20% BA reduction, reaching 28.7 $m^2 \cdot ha^{-1}$ and 46.1% GSF residual values, is necessary to stimulate positive responses of underplantings. However, further mid- to long-term studies are needed to investigate potential interactions between stand stocking and planted species performance, which will provide the silvicultural basis for promoting the incorporation of the underplanting into the codominant crown class.

CRediT authorship contribution statement

García-Pérez José. L: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Oliet Juan A.:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Pedro Villar-Salvador:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **José Alfredo Bravo-Fernández:** Writing – review & editing, Project administration, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Key message

Canopy openness of pine plantations modulates environmental conditions of the understory and the performance of underplanted Mediterranean broadleaf seedlings.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123666.

Data availability

The data set will be provided upon request.

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