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ORIGINAL PAPER

Hardwood seedling establishment below Aleppo pine depends on thinning intensity in two Mediterranean sites

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Abstract

- ***Key message*** **Aleppo pine stands can be made more resilient to disturbances such as forest fires, by introducing native and resprouting hardwood species. Pine density impacts seedling establishment by modifying resource availability and abiotic stress. Under Mediterranean conditions, moderate thinning (15–20 m^2/ha) was the most effective in promoting the establishment and growth of a number of hardwood species.**
- ***Context*** Developing silvicultural methods to help Mediterranean forests adapt to climate change is of high importance. Introducing resprouting hardwood species below pine stands is expected to promote diversity and resilience of these stands, particularly to forest fires.
- ***Aims*** The aim of this study was to examine how the intensity of pine thinning influences understory microenvironment and the establishment of various hardwood seedlings in two Mediterranean sites.
- ***Methods*** Aleppo pine stands were thinned down to three levels of basal area (uncut 30 m^2/ha, moderate thinning 13–20 m^2/ha, heavy thinning 7–10 m^2/ha) at two Mediterranean sites (South-East France and South-East Spain). Seedlings of six hardwood species were introduced in the understory, and their survival and growth were monitored and related to changes in microenvironment induced by thinning.
- ***Results*** At both sites, thinning improved light availability and seedling diameter increment of all target species. Thinning increased extreme temperature and evaporative demand. Heavy thinning increased summer soil moisture in SE Spain but not in SE France. The worst conditions for seedling survival were reached under uncut stands in SE France and low-density stands in SE Spain.
- ***Conclusion*** Thinning in pine stands accelerated seedling growth, but excessive thinning worsened summer drought and affected seedling survival. Moderate thinning (15–

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Contribution of the co-authors AV, EC, VRV, and BP were involved in the design of the experiment. All authors participated to field data collection and writing the manuscript. JG wrote the first version of the manuscript and, together with AV, analyzed the data. VRV in Spain and BP in France designed and supervised the experiment implementation and coordinated the work.

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20 m^2/ha) seems to be the best option in support of the introduction of hardwoods in the understory, which can improve forest diversity and resilience in the future.

Keywords Ecological restoration · Tree shelter · Microclimate · Shade–drought interaction · Soil moisture · Underplanting oak

1 Introduction

Forest fires, drought, extreme events, and pest outbreaks are all predicted to increase in the Mediterranean Basin (Kovats et al. 2014; Moriondo et al. 2006). In this context, it is vital to develop silvicultural methods that increase the resistance and resilience of Mediterranean forests to environmental perturbations (Lindner et al. 2008).

Over the last few decades, Mediterranean forests have experienced a rapid expansion of pioneer conifer stands, driven by natural colonization after land abandonment in SE France (Barbero et al. 1990) or afforestation efforts in SE Spain (Ortuño 1990). This expansion process is particularly visible in Aleppo pine (*Pinus halepensis*), forming dense monospecific stands that are highly flammable and facilitate the spread of large fires (Pausas et al. 2004, 2008). The capacity of this species to regenerate after a fire hinges on its canopy-stored seed bank; so, any fire interval shorter than its age to maturity (i.e., 10–20 years, Ne'eman et al. 2004) is likely to cause a regeneration failure (Daskalakou and Thanos 1996; Pausas et al. 2008). In contrast, hardwood species are mostly resprouters: they have the ability to regrow from dormant buds and belowground reserves after a fire, which promotes faster vegetation recovery and makes them less vulnerable to high fire frequencies (Pausas et al. 2004; Schelhaas et al. 2010). Resprouter species can thus be considered keystone species for fire-resilient forests (Puerta-Piñero et al. 2012). Furthermore, monospecific Aleppo pine stands have been shown to be highly sensitive to insect attacks (Maestre and Cortina 2004) and to reduce plant species richness and diversity in the understory (Chirino et al. 2006), whereas mixed pine–hardwood stands are shown to be less sensitive to pest outbreaks and herbivory (Jactel and Brockerhoff 2007), to potentially host greater biodiversity (Cavard et al. 2011), and to be more resilient to disturbances and changing environmental conditions for a number of ecosystem processes (Jactel et al. 2009; Yachi and Loreau 1999). Promoting mixed pine–hardwood stands is therefore increasingly advocated as a strategy to enhance forest resilience (Pausas et al. 2004; Keskitalo 2011).

Mixed stands can be created by introducing hardwood species into pine stands to overcome seed limitations, but the operation proves delicate in Mediterranean conditions where seedling survival in summer is a major demographic bottleneck. Successful seedling introduction hinges on selecting species adapted to local conditions (Padilla et al. 2009; Vallejo et al. 2012). Reducing tree density by thinning has also been shown to be a critical factor for seedling establishment in forest understory (Paquette et al. 2006). Thinning increases light availability in the understory but also affects the water balance in a more complex way (Aussenac 2000), with potentially important implications for seedling survival in water-limited areas. Forest managers need information on suitable management methods to enhance forest diversity and resilience; yet, few studies have investigated the effect of thinning on understory microclimate and seedling performance under Mediterranean conditions.

Here, we examined the effect of Aleppo pine thinning at three intensities in two different experimental sites—one in South-East Spain and one in South-East France. In each site, we assessed the effect of thinning on understory microclimate and the establishment (survival and growth) of six resprouter hardwood species. The applied objective was to help assess whether overstory thinning help hardwood species establishment for increasing biodiversity and resilience in Aleppo pine stands.

2 Material and methods

2.1 Experimental sites

Experiments were conducted at two sites in SE Spain and SE France (see map in Online Resource 1). In Spain, the experiment was located in the forest of La Hunde, Ayora, province of Valencia (hereafter "Ayora") on a flat area at a mean altitude of 800 m (30° 7′ N; 1° 13′ W to 39° 6′ N; 1° 11′ W). In France, the experimental site was located at Saint-Mitre-les-Remparts in the Bouches-du-Rhône département (hereafter "St Mitre") in a flat area adjacent to the Mediterranean Sea at a mean altitude of 130 m (43° 4′ N; 5° 0′ W). Both sites are covered by Aleppo pine forest forming closed stands aged 40–60 years old 32 m^2/ha, originating from afforestation at Ayora and from natural colonization of abandoned land at St Mitre.

At Ayora, Aleppo pines were used to afforest former almond fields, and they are dominant in an area spanning over 1500 ha, with a sparse understory composed mainly of dwarf scrubs (*Thymus* sp.) and medium shrubs (*Rosmarinus officinalis*, *Ulex parviflorus*) and scattered adult *Quercus ilex ballota*. Soils are calcareous with a sandy-loam texture, stoniness in the range 27–49 %, and a mean depth of 35 cm. At St Mitre, the forest is located on old fields divided up by stone walls ("terraces") over an area of about 150 ha surrounded by a mosaic of agricultural areas with sparse oak trees, shrublands, other Aleppo pine forests, and urban areas. The understory is composed of scattered *Quercus ilex* trees and a spatially heterogeneous shrub layer (main species, *Quercus coccifera*). Soils are calcareous with a sandy-loam texture, low stoniness, and a mean depth of 40 cm.

The climate is quite similar between the two sites. Historical records (1961–1990, Online Resource 2) show a dry season of 3 months and a mean temperature of 14 °C in both sites but a lower average annual rainfall at Ayora (480 mm) than at St Mitre (570 mm) mainly due to wetter autumns. During the experiment (2009–2014), annual rainfall at Ayora was 527±48 mm with July–August rainfall of 14±6 mm and annual rainfall at St Mitre was 561±154 mm with July–August rainfall of 20±3 mm except in 2011 (71 mm).

2.2 Thinning treatments and pine stand characteristics

At each site, three thinning treatments were tested: (i) unthinned, (ii) moderate thinning, and (iii) heavy thinning. At Ayora, the tinning treatments were applied in 2002 and removed about 50 and 75 % of initial basal area. Each treatment was replicated in three 30 m×30 m plots (9 plots in total). At St Mitre, the tinning treatments were applied in 2006 and removed 30 % (moderate regime) and 60 % (heavy regime) of initial basal area. Each treatment was replicated in four 25 m×25 m plots (12 plots in total). Before seedling introduction, each plot was inventoried by measuring the DBH of each tree >1.30 m high. The resulting stand characteristics for each treatment are shown in Table 1.

2.3 Selection and introduction of hardwood species

At each site, we selected 6 native species occurring in the surroundings (Table 2), with the exception of the thermophilous *Ceratonia siliqua* in France (subnatural and present at few locations along the Mediterranean coast). The two oak species are the main late-successional dominant species of hardwood forests: the evergreen oak *Quercus ilex* at both sites, and the deciduous oaks *Quercus faginea* at Ayora and *Quercus pubescens* at St Mitre. Seeds were collected in the region local to each experimental site at different locations with similar ecological conditions, using different trees for each species in order to account for intraspecific variability. *Q. ilex* and *Q. pubescens* at St Mitre were directly sown in November 2007 by introducing 3 acorns in 50 sowing points per plot. Other hardwood seedlings were cultivated in nurseries and transplanted into the field at 1 year old, in November 2009 at St Mitre and in November 2010 at Ayora. At Ayora, 15 seedlings per species and per plot were planted in holes dug by a backhoe. At St Mitre, 18 seedlings per species and per plot were planted in holes dug manually. Plots were fenced to avoid predation by large herbivores. Herbivory by insects may still have occurred, but although not specifically recorded, we did not notice important events and assume that herbivory pressure was similar between thinning treatments.

2.4 Monitoring of environmental factors

Light transmission, soil moisture, air temperature, and air humidity were monitored at both sites. Solar photosynthetically active radiation (PAR) transmission was calculated in each plot as the ratio of photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) in the plot to the PPFD at a nearby open site in July. At Ayora, 10 PPFD measures were taken in each plot and in the open every 3 h from 6 a.m. to 6 p.m., using a ceptometer (Sunfleck, Decagon devices, USA). At St Mitre, PPFD was recorded every minute for 24 h using 5 sensors per plot (SKP 215, Skye Instruments, UK).

Soil water content was measured at two depths: top layer (0–10 cm) and at 30-cm depth. At Ayora, soil water content in the top layer was recorded on a monthly basis using 7 TDR probes per plot (TDR100, Campbell Scientific) placed in randomly selected plantation holes. Soil moisture at 30-cm depth was simultaneously recorded on a subsample of 3 randomly selected plantation holes per plot using an HS-10 volumetric water content sensor (ProCheck, Decagon Devices, USA). At St Mitre, soil moisture in the top layer was measured monthly with a portable TDR probe (Wet2, Delta-T Devices, UK) at 9–15 measurement points, and soil moisture at 30-cm depth was recorded hourly by 12 TDR probes per treatment distributed in two randomly selected plots (EC-5, Decagon Device). Measurements were taken in two consecutive years in each site, i.e., 2011–2012 at Ayora and 2013–2014 at St Mitre.

Air temperature and humidity were monitored hourly using 3–5 sensors per treatment, distributed in the same plots as the TDR probes. Sensors (HOBO sensors at Ayora and Hygrochron iButton DS1923 sensors at St Mitre) were installed at an aboveground height of about 30 cm in small shelters to protect them from direct radiation and rainfall. From temperature and air humidity, we calculated the vapor pressure deficit (VPD), which is closely related to plant evapotranspiration (FAO 1998). The data was then used to calculate daily mean, maximum and minimum temperature, and VPD.

2.5 Seedlings and understory vegetation monitoring

Each seedlings was individually tagged. Survivorship, basal diameter, and height were measured yearly. For oaks sown in St Mitre, all emerged acorns were measured, and the mean of the sowing-point seedling dimensions was used to avoid pseudoreplication. Growth measurements were used to compile a relative growth rate (RGR) in basal diameter and height for 3-year-old seedlings, as follows (Hoffmann and Poorter 2002):

$$\mathrm{RGR} = \frac{\ln(\mathrm{Xi}) - \ln(\mathrm{X0})}{\mathrm{ti} - \mathrm{t0}}$$

Table 1 Stand characteristics (means±standard error) after applying the thinning treatments

	Ayora (Spain)			St Mitre (France)		
	Uncut	Moderate thinning	Heavy thinning	Uncut	Moderate thinning	Heavy thinning
Tree density (number/ha)	1067±244	344±32	165±43	1644±448	576±29	196±63
Basal area (m^2/ha)	31.7±2.2	12.4±2.7	7.5±1.8	32.0±3.9	19.2±0.7	10.2±0.9

Tree density and basal area were measured just before seedling introduction

where X_i is the performance indicator (height or diameter) at the last measurement date t_i and X_0 is the same indicator at the first measurement date t_0 (first year after sowing for *Quercus* species sown at St Mitre, outplanting for other species).

Three years after seedling introduction, understory shrub and herb covers were visually assessed, and shrub height was recorded using 3 to 10 transects per plot.

2.6 Data analysis

As the two site conditions differed on several factors such as history, species introduced, and intensity of thinning treatments, the statistical analyses were conducted separately for each site. Effects of thinning on light transmission and mean seasonal soil water content were tested by one-way ANOVA. Effects of thinning on other environmental factors were analyzed using linear mixed models, with treatment and date as fixed factor and measurement sites (probes) as random factor. Thinning treatments and species differences in survival over time were tested by comparing Kaplan-Meier estimates of the survival function (Kaplan and Meier 1958) with a Mantel-Cox log-rank test. Effect of treatment and species identity on final seedling RGR was tested using two-way ANOVA after first transforming the variables (if necessary) to satisfy the conditions of normality and homoscedasticity of residuals. Post hoc Tukey tests evaluated between-treatment differences for each species. All statistical analyses were performed using R software (3.1.0).

3 Results

3.1 Understory microclimate and vegetation development

At both sites, mean light transmission, maximum daily temperature, and VPD increased with canopy openness (Table 3). Maximum PPFD in the open was about 2300 μmol m^{-2} s^{-1} at both sites. Light transmission reached higher values at Ayora but decreased with basal area as a negative exponential relationship and in a consistent way between the two sites (Online Resource 3). The increase in maximum temperature and VPD with canopy openness was particularly pronounced in summer, where temperature increase reached 13 % increase in both sites and VPD increase reached 14 % (Ayora) to 40 % (St Mitre) in the heavy thinning treatment.

Thinning did not affect soil water content in the upper layer in either site (Online Resource 4). In the deeper layer, soil water content was higher in the heavy thinning treatment at Ayora ($p=0.01$, Fig. 1). This difference persisted all year long, although it was higher in the rainy seasons (winter and spring, +23 %) than in the dry seasons (summer and early autumn, +

Table 2 Resprouting hardwood species introduced under a pine canopy at the two sites

Site	Species	Life-form	Leaf habit
Ayora and St Mitre	*Arbutus unedo* L. (Au)	Shrub	Evergreen
Ayora and St Mitre	*Fraxinus ornus* L. (Fo)	Tree	Deciduous
Ayora	*Quercus ilex ballota* Desf. (Qib)	Tree	Evergreen
Ayora	*Quercus faginea* Lam. (Qf)	Tree	Deciduous
Ayora	*Rhamnus alaternus* L. (Ra)	Shrub	Evergreen
Ayora	*Acer opalus granatense* Boiss. (Ag)	Tree	Deciduous
St Mitre	*Quercus ilex ilex* L. (Qii)	Tree	Evergreen
St Mitre	*Quercus pubescens* Willd. (Qp)	Tree	Deciduous
St Mitre	*Ceratonia siliqua* L. (Cs)	Tree	Evergreen
St Mitre	*Sorbus domestica* L. (Sd)	Tree	Deciduous

Table 3 Effect of thinning on microclimatic variables and understory development

	Ayora (Spain)			St Mitre (France)		
	Uncut	Moderate thinning	Heavy thinning	Uncut	Moderate thinning	Heavy thinning
Light (PAR) transmission (%)	14.7±2.1 *A*	35.6±3.9 *B*	62.9±6.9 *C*	10.4±0.5 *a*	19.4±3.7 *b*	37.9±3.6 *c*
Summer[1] daily mean temperature (°C)	25.0±0.1 *A*	25.2±0.2 *A*	25.3±0.3 *A*	24.3±0.1 *a*	24.5±0.1 *a*	24.5±0.1 *a*
Summer[1] daily maximum temperature (°C)	34.0±0.2 *A*	35.8±0.5 *B*	36.0±0.1 *B*	30.8±0.1 *a*	33.0±0.4 *b*	34.8±0.4 *c*
Summer[1] daily mean Vapour Pressure Deficit (kPa)	2.08±0.02 *A*	2.16±0.05 *B*	2.20±0.06 *B*	1.31±0.01 *a*	1.36±0.02 *a*	1.41±0.02 *b*
Summer[1] daily maximum Vapour Pressure Deficit (kPa)	4.34±0.06 *A*	4.84±0.16 *B*	4.93±0.05 *B*	2.77±0.02 *a*	3.31±0.12 *b*	3.86±0.14 *c*
Herb cover (%)	0.3±0.2 *A*	5.2±2.2 *B*	21.4±9.9 *C*	0.0±0.0 *a*	0.1±0.0 *a*	0.2±0.1 *a*
Shrub cover (%)	5.5±2.0 *A*	33.9±18.0 *B*	14.2±7.6 *A*	5.7±0.9 *a*	22.1±1.4 *b*	33.5±1.3 *c*
Shrub height (cm)	11.4±4.0 *A*	25.3±13.4 *A*	16.4±5.6 *A*	52.6±4.6 *a*	59.9±2.6 *a*	73.1±2.1 *b*

Values are means±standard error of several probes for microclimatic data and several sampling points for understory data. For each site, different letters (uppercase for Ayora, lowercase for St Mitre) indicate differences between treatments detected by Tukey post hoc tests following linear mixed models. Maximum PPFD in the open was 2300 μmol m^{2} s^{-1} in both sites. [1] Summer values are calculated using July–August data

17 %). At St Mitre, between-treatment differences were not significant (p=0.5), but there was a strong date×treatment interaction (p<0.001, Fig. 1): in the rainy seasons, soil water content tended to be higher in the thinned treatments while in summer, soil water content decreased sharply and tended to be lower in the heavy thinning treatments.

Canopy opening induced the development of spontaneous vegetation in the understory at both sites, but with different compositions (Table 3). Herb cover increased in response to thinning at Ayora, from 0.3 % in the unthinned plots to 21.4 % in heavily thinned plots, whereas at St Mitre, herbs were only found on a few thinned plots and remained very scarce, accounting for less than 1 % of soil cover. At St Mitre, shrub cover and height increased progressively with thinning intensity, whereas at Ayora shrub, cover was only higher under the moderate thinning treatment.

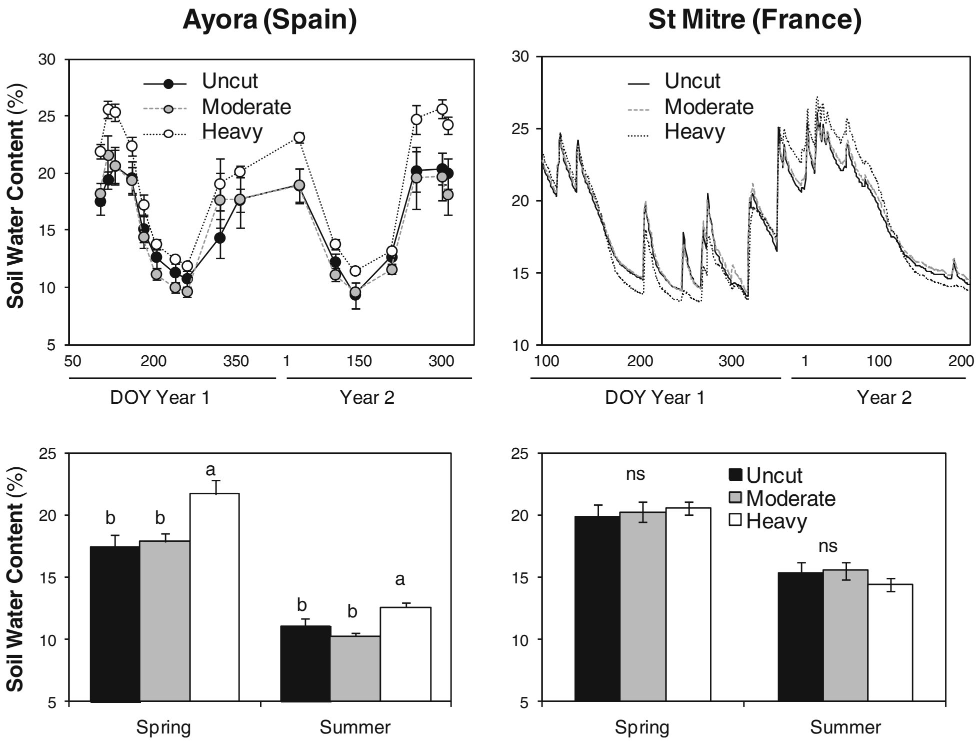

Fig. 1 Effects of thinning treatments on soil water content. *Upper panel* dynamics of soil water content (30-cm depth) according to treatments. The *x*-axis plots day of the year (DOY) for two consecutive years. *Lower panel* mean seasonal soil water content. *Bars* give the standard errors of 9 (Ayora) to 12 (St Mitre) probes per treatment. *Different letters* indicate differences between treatments (p<0.05). At both sites, soil water content in autumn and winter followed a similar trend to soil water content in summer and spring

3.2 Seedling survival and growth

Seedling survival rate was influenced by thinning treatment (log-rank=13.2, $p<0.01$ at Ayora and log-rank=59.7, $p<0.001$ at St Mitre), with few differences between the moderate and heavy thinning treatments. Seedling survival ranged from 22 to 99 % at St Mitre and from 52 to 100 % at Ayora (Fig. 2). At Ayora, survival of half of the species was decreased under thinning treatments. However, the decrease in survival rate never exceeded 23 % even for the most severely affected species which still showed high survival rates in the most open treatments (minimum 77±6 % for *R.alaternus*). In contrast, at St Mitre, thinning had a positive effect on the survival of all species (except *F. ornus*, with survival rates remaining very high 97.2–98.6 %). Thinning had particularly strong positive effects on *A. unedo* and *Q. pubescens*, leading to 3-fold and 2-fold increases in survival rates, respectively.

Survival was also affected by species identity in both sites (log-rank=74.8, $p<0.001$ at Ayora, log-rank=189.0, $p<0.001$ at St Mitre). The species with the lowest survival rates were the two deciduous trees *Q. faginea* and *A. granatense* at Ayora and the evergreen *A. unedo* and *C. siliqua* at St Mitre.

Thinning had a positive effect on stem diameter growth for all species at both sites (Table 4, Fig. 2). Thinning also strongly improved all-species height growth at St Mitre, whereas at Ayora, thinning decreased the height growth of two species: *Q. faginea* and *R. alaternus*. The best growing species in terms of diameter were *R. alaternus* and *A. unedo* at Ayora and *Q. ilex* at St Mitre. At Ayora, thinning changed the pattern of species responses in terms of height growth. The best performing species was *R. alaternus* in the unthinned treatment and *F. ornus* and *A. granatense* in the thinning treatments. At St Mitre, *F. ornus* and *S. domestica* showed particularly dynamic height growth, whereas *C. siliqua* showed negative growth rates in all treatments as well as *A. unedo* in unthinned treatments. This pattern reflected a destruction of aboveground biomass of the two latter species followed by resprouting during the experiment. *C. siliqua* is known to be frost-sensitive, and the bulk of its biomass destruction occurred after an extreme frostwave. However, even in this case, thinning improved seedling growth after resprouting.

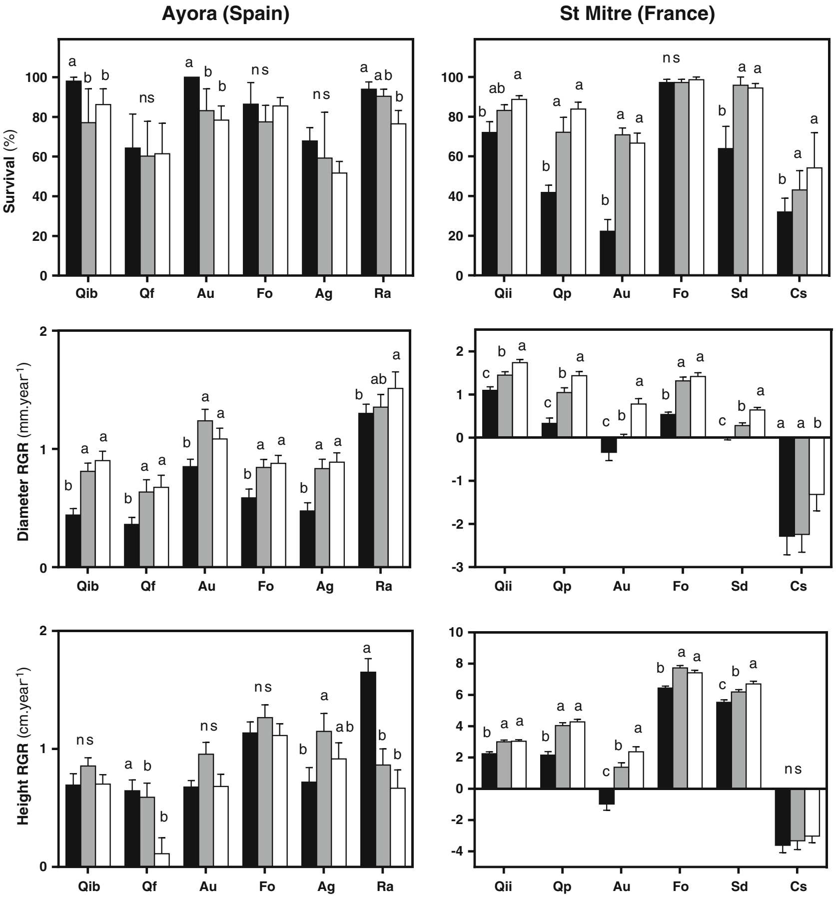

Fig. 2 Species performances under the different thinning treatments: uncut (*black bars*, 32 m^2/ha), moderate thinning (*gray bars*, 19 m^2/ha at St Mitre and 12 m^2/ha at Ayora) and heavy thinning (*white bars*, 10 m^2/ha at St Mitre and 7.5 m^2/ha at Ayora). Survival rates are shown at 3 years after seedling introduction, values are means of 4 or 3 plots per treatment, and different letters indicate differences in time-course of survival over the 3 years, as evaluated by Kaplan-Meier functions followed by a log-rank test. Relative growth rates (RGR) were calculated for 10–90 3-year-old seedlings per treatment. Negative RGR is explained by above-ground biomass destruction followed by resprouting. *Error bars* represent the standard error of the mean. *Different letters* indicate differences between treatments for a given species according to Tukey post hoc tests. Differences were considered significant at $p<0.05$. See Table 2 for species codes

Table 4 Results of ANOVAs testing for effects of species identity, thinning treatment and their interaction on diameter and height growth

	Ayora (Spain)						St Mitre (France)					
	Basal diameter RGR (mm $year^{-1}$)			Height RGR (cm $year^{-1}$)			Basal diameter RGR (mm $year^{-1}$)			Height RGR (cm $year^{-1}$)		
	DF	*F*	*p value*	*DF*	*F*	*p value*	*DF*	*F*	*p value*	*DF*	*F*	*value*
Species (S)	5	**26.76**	**<0.001**	5	**6.22**	**<0.001**	5	**138.32**	**<0.001**	5	**510.31**	**<0.001**
Treatment (T)	2	**17.22**	**<0.001**	2	**7.86**	**<0.001**	2	**69.39**	**<0.001**	2	**73.8**	**<0.001**
S × T	10	1.03	0.42	10	**3.31**	**<0.001**	10	1.77	0.06	10	**4.46**	**<0.001**
Residuals	681			677			1639			1644		

4 Discussion

Mixed pine–hardwood forests are expected to be more resilient to disturbances than monospecific pine stands (Jactel et al. 2009; Vallejo et al. 2006), particularly to allow quicker vegetation recovery after frequent large fires (Puerta-Piñero et al. 2012). Favoring the establishment of resprouting hardwood seedlings under Aleppo pine stands is thus recommended, but no clear management methods have yet been established. The aim here was to study how active management by overstory thinning could modify environmental factors and influence the seedling establishment of various resprouting hardwood species.

4.1 Thinning effect on understory microclimate

Our results showed a buffering effect on air temperature and VPD that increased with tree basal area. This effect was more pronounced during the drier season, as also found by Rambo and North (2009), which may prove important for seedling survival in this critical period. Heavy thinning increased soil moisture only in wet seasons at St Mitre but even during summer at Ayora. Although time elapsed between thinning and soil measurement was longer at Ayora than at St Mitre, this lag probably had little effect on the observed trends. In fact, contrary to what was observed at Ayora, long-term studies (e.g., Gray et al. 2002) have found an absence of differences in soil moisture between thinned and unthinned treatments after several years due to vegetation development in thinned stands. Other studies diverge on the effects of tree thinning on soil water content, with some reporting positive outcomes (Bellot et al. 2004; Bréda et al. 1995; Rodriguez-Calcerrada et al. 2008) but others reporting negative outcomes (Primicia et al. 2012; Simonin et al. 2007). This divergence illustrates the fact that tree cover has diverse impacts on water balance: trees intercept rainfall and consume soil water, but also reduce understory evapotranspiration (Aussenac 2000). Understory vegetation is known to account for a substantial share of total pine stand evapotranspiration, in particular in dry seasons due to pine stomatal closure (Simonin et al. 2007). Thus, differences between sites may be linked to differences in understory vegetation: tall shrubs at St Mitre probably consumed more water at 30-cm depth in summer than the herbs and dwarf shrubs at Ayora.

4.2 Thinning effect on seedling survival and growth

Thinning improved stem diameter growth of seedlings at both sites, but had site-specific effects on seedling survival and height growth.

The higher mortality in heavily thinned stands at Ayora revealed that these stands were more stressful for seedlings despite their higher summer soil moisture. Soil water content is not always related to water availability for seedlings, which is strongly dependent on root development (Padilla and Pugnaire 2007). Moreover, higher evaporative demand, temperatures, and light levels in thinned plots can increase drought stress and directly damage seedling tissues and the photosynthetic machinery (Chaves et al. 2002; Valladares 2004), which probably overrode the benefits of higher soil moisture. Seedlings were more likely to die in heavily thinned stands at Ayora due to more stressful conditions in summer, but the surviving seedlings grew better in diameter due to the higher light availability during the growing season. Such life-stage conflicts of canopy shelter effects on seedling survival and growth are frequently reported in the Mediterranean (e.g., Caldeira et al. 2014; Gómez-Aparicio et al. 2008; Marañón et al. 2004; Soliveres et al. 2010). Furthermore, height growth is the result of a balance between growth ability and elongation in response to changes in light quantity and quality (red/far-red ratio; Franklin 2008), which probably explains the species-dependent effect of thinning on height growth at Ayora.

The conflict between survival and growth did not occur at St Mitre, where thinning strongly stimulated survival, diameter, and height growth. Light transmission in dense stands was lower at St Mitre than at Ayora. Although this difference was small (5 %), at low light levels, a small change in light availability can trigger a large drop in survival rates (e.g., Sánchez-Gómez et al. 2006), which may explain the low survival of several species under dense stands at St Mitre. Thinning thus increased survival and growth despite slightly lower summer-season soil moisture, as also found by Rodriguez-Calcerrada et al. (2010) in central Spain. The higher light availability in thinned stands thus fostered better overall above-ground seedling development (in both diameter and height) and probably also below-ground development, enabling seedlings to better cope with summer drought. In this case, the positive effect of light availability was not cancelled out by the parallel increase in heat stress and evaporative demand like at Ayora, almost certainly because the summer conditions in the heavy thinning treatments were less stressful at St Mitre than at Ayora, as shown by the lower light transmission (38 vs 63 %), maximum temperature (34.8 vs 36.0 °C) and VPD (3.9 vs 4.9 kPa) values. In Rodriguez-Calcerrada et al. (2010), the highest light transmission was a similar 35 %, and conditions may not have been stressful enough to trigger decreased survival. Indeed, the interplay between light and water stress is a complex issue, and it has been suggested that drought is more severe for plants at both low and high light levels yet ameliorated at intermediate light levels (Holmgren et al. 2012). Our results thus suggest that intermediate pine densities are the most favorable for hardwood seedling establishment. This adds support to results by Gómez-Aparicio et al. (2009) in an observational study of *Q. ilex* recruitment under Aleppo pine woodlands, and by Paquette et al. (2006) in a meta-analysis including contrasted climatic areas. In water-limited Mediterranean areas, this result seems to be driven by a trade-off between light availability and abiotic summer conditions determining mortality rates.

4.3 Understory vegetation development and potential impact on seedling establishment

Thinning fostered the development of different types of understory vegetation, mostly herbs and dwarf shrubs at Ayora and tall shrubs at St Mitre, which may have partly shaped the thinning effects (Paquette et al. 2006). Understory vegetation can have a distinct impact on seedling establishment depending on morphology, growth rates, and/or ability to deplete resources (Balandier et al. 2006). Herbaceous species present in thinned plots at Ayora are known to be highly competitive with young seedlings (e.g., Caldeira et al. 2014; Cuesta et al. 2010), while at St Mitre, the understory of thinned plots was mainly colonized by shrubs that are often involved in positive interactions in Mediterranean settings (Castro et al. 2004). There has been little research into shrub effects in Mediterranean understory, but the evidence suggests that shrubs may have positive effects by mitigating the increase in extreme temperatures and creating lateral shading which favors height growth (Prévosto et al. 2011). Spontaneous vegetation development is difficult to foresee and depends on landscape context and seed sources, but this aspect warrants further study and should be taken into account when designing a thinning strategy.

4.4 Species selection to increase forest diversity and resilience

The outcome of plant–plant interactions can vary widely with target species identity and strategy (e.g., Liancourt et al. 2005). In this study, all target species at each site responded to thinning in the same direction but with different magnitudes, probably reflecting different stress tolerances and competitive abilities. For instance, light-demanding drought-tolerant species probably benefited more from post-thinning canopy opening, but the fact is that the precise ecological requirements of many hardwood species used in this study are still largely unknown. The thermophilous species (*C. siliqua*) used at St Mitre performed badly in all treatments, probably due to its frost sensitivity, which highlights how selecting species adapted to expected future climate conditions remains a very risky strategy (Lindner et al. 2008). Between sites, no common pattern of species performance according to life-form or leaf habit (as described in Table 2) emerged. For instance, at Ayora, the best-performing species were evergreen drought-tolerant shrubs, *R. alaternus* and *A. unedo*, while at St Mitre, *A. unedo* posted some of the poorest survival and growth rates. Deciduous species have been reported as intolerant to high irradiance (Gómez-Aparicio et al. 2006). Here, *Q. faginea* growth was indeed strongly reduced under heavy thinning treatments at Ayora, but other deciduous species showed intermediate-to-good performances. Although these species may be affected by higher irradiances, under moderate pine cover, they seem to represent a suitable opportunity for pine forest diversification. Their different leaf habit promotes a higher functional diversity, which has been shown to be of interest for forest resilience (Pedro et al. 2015). Species performances were higher and differences between species less important under moderate pine cover than under very dense or very light cover, which allows a wider range for species choice. In addition to resprouting ability, other properties may be key factors for species selection, such as valuable wood (*F. ornus*, *S. domestica*), fleshy fruits favoring bird diversity (*A. unedo*, *S. domestica*), or conservation of an endangered species (*A. granatense*).

5 Conclusion

Mixing Aleppo pine stands with hardwood species require appropriate management of the overstory layer to enhance hardwood seedling establishment. Thinning is necessary to release light limitation in dense pine stands, but excessive thinning may aggravate the already tough summer conditions and reduce the likelihood of seedling survival, particularly if drought events come frequently. Our results suggest that intermediate pine densities of about 15–20 m^2/ha offer the most suitable conditions to boost introduced seedling growth and foster high later survival, although longer-term studies are needed to confirm the potential of this management strategy to create mixed stands. Several native resprouter species can be introduced under intermediate pine densities which should allow for diversification and increased resilience of Aleppo pine stands. However, site-specific climate conditions and interactions with understory herb and shrub layers can influence the effects of thinning on microclimate and seedling establishment, and thus warrant further investigation.

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