# Recruitment into the seedling bank of an undisturbed Mediterranean pinewood: Increasing forest resistance to changing climates

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**A B S T R A C T**

Although typically considered shade-intolerant, Mediterranean pine species may form seedling banks due to the existence of facilitative interactions between seedlings and canopy trees. Consequently, seedling banks could be considered as part of the seedling pool that should restock managed Mediterranean pinewoods, thus increasing the resistance of these forests to climate change. The study investigated the characteristics of the seedling bank in a silviculturally undisturbed forest of *Pinus nigra* subsp. *salzmanii* exposed to increasingly arid conditions. The study site was located in the southernmost range limit of the species. The dynamics of the seedling bank was studied by comparing current seedling (height < 1.30 m, age < 2 yr) and pole tree (height ≥ 1.30 m and diameter at breast height < 12.5 cm) altitudinal distributions, using altitude as a proxy of aridity. Aridity was proved to have increased in the study area along the last four decades. These climatic trends were identified by means of Mann-Kendall tests for trend. Additionally, the effects of summer drought, light availability, soil compaction, litter layer and micro-slope as explanatory variables of the recruitment outcome were analysed by means of Generalized Linear Mixed Models and survival analysis. Altitude affected positively seedling establishment, but had no effect on the current abundance of pole trees, indicating a recent upwards displacement of the regeneration niche due to increasingly arid conditions. Water and light availability, the latter at intermediate levels of irradiance, affected tree recruitment positively, whereas the effects of soil compaction, litter layer depth and micro-slope were negative. Implementing extended rotation periods and maintaining intermediate values of tree cover are proposed as important management recommendations to achieve successful natural regeneration in Mediterranean pinewoods.

## 1. Introduction

In the northern Hemisphere, the low-altitude and southern limits of tree ranges are expected to move upwards and northwards as conditions become more arid due to ongoing climate change (Dyderski et al., 2018). This shift in species distribution should be the product of two processes: increased adult tree mortality and reduced self-recruitment, insufficient to compensate for adult decline. In this regard, some studies have documented recent episodes of adult mortality due to increased climatic dryness in the Mediterranean region (Candel-Pérez et al., 2012; Vilà-Cabrera et al., 2013). However, the long-term impact of climate change on tree recruitment may be difficult to assess for at least two reasons: (i) trees are long-lived, iteroparous plants that may fail many times before achieving successful regeneration, and (ii) desiccation is already the main cause of seedling mortality among Mediterranean tree species (Castro et al., 2005; Ruano et al., 2009; Matías et al., 2012; Tíscar et al., 2017). These limitations can be overcome by combining observational and experimental data as in the present study.

Despite the major importance of water availability for the successful regeneration of Mediterranean tree species, irradiance plays a general key role as well (Puerta-Piñero et al. 2007). The response of tree seedlings to the amount of light reaching the forest floor is specific. Therefore, foresters commonly rank tree species on a continuum of shade tolerance and apply regeneration methods accordingly, removing most trees from the stand in order to regenerate shade intolerant species, or maintaining a canopy of mature trees to allow the establishment of shade tolerant ones (O'Hara, 2014). This general rule can however vary under the stressful conditions of Mediterranean forests. Shade buffers against high temperatures and excessive evapotranspiration, and consequently improves water balance (Gómez-Aparicio et al., 2004). Thus, several studies have reported increased seedling survival of both shade tolerant and intolerant pine species under the canopy of taller plants in Mediterranean forests (Castro et al., 2005; Ruano et al., 2009; Tíscar and Linares, 2014; Andivia et al., 2018). The beneficial effects of shade are still present even when water is artificially added to simulate the stormy summers that sporadically occur in Mediterranean

mountains (Gómez-Aparicio et al., 2008). As a result, shade by itself, or combined with increased water availability during atypically wet summers, may facilitate pine recruitment under the canopy of undisturbed stands. This generates an opportunity to consider tree regeneration in managed Mediterranean pinewoods not only in relation to silvicultural disturbances, but also in relation to the probable presence of seedling banks. Seedling banks are formed by those seedlings that develop beneath an intact canopy and the establishment of which is not consequently related to the entries of planned cutting cycles in managed forests (O'Hara, 2014). Mediterranean pinewoods currently tend to remain silviculturally undisturbed for decades, due to poor conditions of the timber market and/or the implementation of extended rotations for biodiversity conservation and carbon sequestration (Bravo et al., 2008). Consequently, whilst expanded drought due to climate change might prevent seedling establishment at the time planned by management cutting cycles, the seedling bank could be crucial for increasing forest resistance. Resistance was considered to be the ability to recruit new seedlings even though increasingly arid conditions will make this more difficult.

An increasing trend in temperatures and a decreasing trend in precipitation are already being observed in southern parts of the Iberian Peninsula (Linares and Tíscar, 2010; Ruiz-Sinoga et al., 2011). Considering this, I used both observational and experimental data to evaluate the impacts of the resulting more arid conditions on the recent recruitment dynamics of *Pinus nigra* subsp. *salzmannii* (*P. nigra* hereafter) in an undisturbed forest. By working with silviculturally undisturbed stands, I could quantify recruitment into the seedling bank. Forests of *P. nigra* occupy 405,983 ha in the eastern calcareous mountains of the Iberian Peninsula. Summer drought is considered to be the major limiting factor for the recruitment of *P. nigra* (Tíscar and Linares, 2011). However irradiance is equally important, as seedling establishment occurs more frequently under intermediate levels of canopy cover (Tíscar and Linares, 2014).

Models fitted to simulate forest occupancy under a climate change scenario project an important future decline of *P. nigra* forests (Benito-Garzón et al., 2008). Thus, some signs of range contraction could be already evident at the southernmost distribution limit of this species (Matías and Jump, 2014). In this regard, I used observational data obtained from 198 forest inventory plots to test whether the regeneration niche of *P. nigra* has moved upwards during recent decades by comparing current seedling and pole tree distributions along an altitudinal gradient that would reproduce projected climate changes in temperature (Rabasa et al., 2013). Specifically, I understood that a higher positive effect of altitude should be expected on the establishment of seedlings rather than on pole trees, because seedlings would have established under warmer, drier climatic conditions. Since water availability is decreasing for seedling establishment due to contemporary climate change, I also used experimental data from an irrigation experiment to analyse the influence of water availability on the establishment of *P. nigra* seedling banks (Matías et al., 2012). I additionally accounted for the effects of several variables acting at the microhabitat scale that could affect water infiltration and soil desiccation under closed canopies, namely micro-slope, soil compaction, depth and cover of the litter layer, and light availability. Hereafter, I will refer to all these variables including water availability as abiotic factors. Finally, I also used temperature and precipitation data to confirm climate trends towards more arid conditions in the study forest.

The following questions are specifically addressed: (1) is summer aridity progressively increasing in the study area? (2) is the range of *P. nigra* moving upwards in the southernmost forest of the species distribution? (3) what are the effects of abiotic factors on the recruitment of undisturbed *P. nigra* forests? (4) what is the potential role of seedling banks in the natural regeneration of managed *P. nigra* forests?

## 2. Materials and methods

### 2.1. Study site

The study was carried out in the Cazorla, Segura and Las Villas Natural Park (southeast Spain) (37°54′N–2°53′W) in a managed forest named 'Navahondona'. The site is part of the most extensive *P. nigra* forest at the southernmost limit of the species distribution area (Fig. A.1.). Climate is Mediterranean. Snowfalls and frost are common during the winter, but summers are dry and hot. The Navahondona forest covers 16456 ha along an altitudinal gradient from 780 to 2108 m above sea level (a.s.l.). Previous research has found that mean annual temperature decreases linearly in the study area by 0.64 °C for every 100 m of elevation, whereas annual precipitation increases by ∼84 mm for every 100 m of elevation (Linares and Tíscar, 2010). Therefore, altitude is a good proxy of climatic aridity in the study site. *P. nigra* dominates forest stands located between 1000 and 2000 m a.s.l., co-occurring with *Rosa* sp., *Thymus* sp., *Helleborus foetidus* and other shrubs, although the understory is generally weakly developed (Tíscar, 2015a). Other pine (*Pinus halepensis* and *Pinus pinaster*) and oak species (*Quercus ilex* and *Quercus faginea*) are also present. Management prescriptions for Navahondona have varied during the 20th century. As a result, the forest was initially regenerated by applying the shelterwood silvicultural method with a rotation period of 120 years, followed by the selection method with a period of 150 years. While applying the selection method, a BDq system was used, where B is for basal area ($20.5 \, m^2 \, ha^{-1}$ in this case), D for maximum diameter (50 cm in this case) and q is for the q-factor (1.7 in this case) (O'Hara, 2014).

### 2.2. Climatic data

Climatic data were obtained from two meteorological stations: Vadillo-Castril (37°55′20″N–2°55′37″W, 970 m a.s.l.) and Cazorla (37°54′35″N–3°00′07″W, 885 m a.s.l.). Vadillo-Castril occupies a centered position within the Navahondona forest. It has a precipitation record that goes from 1951 to present, but it does not record temperature. For this reason, I obtained temperature records (for the period 1972 to present) from the nearby meteorological station of Cazorla, which were then corrected according to an adiabatic lapse rate of −0.64 °C for every 100 m of elevation to translate them into the altitudinal level of Vadillo-Castril (Linares and Tíscar, 2010). From these data of precipitation and temperature, a monthly water balance was calculated as the monthly difference between precipitation and potential evapotranspiration estimated by the Thornthwaite's method (see Vicente-Serrano et al., 2010). Values of water balance were assumed to reflect aridity.

In order to address question (1), I then estimated temporal trends of monthly mean temperature, monthly total precipitation and monthly water balance using the Mann–Kendall test (Mann, 1945; Kendall, 1975). Mann–Kendall tests (hereafter MK) are non-parametric tests for the detection of trends in a time series. These tests are widely used in environmental science because they are simple and robust and can cope with missing values and values below the detection limit. When significant trends were obtained from MK tests, computed from the year 1972 onwards, the rates of change of the climatic variables were estimated by obtaining their slope from linear least squares regression (Linares and Tíscar, 2010). MK tests were performed with the 'MannKendall' function in the 'Kendall' package of R (R Development Core Team 2014).

### 2.3. Forest inventory data

The observational part of the study was carried out with data that came from the last Navahondona Forest Inventory carried out in 2010 (2010NFI hereafter). The 2010NFI consisted of 15 m radius circular plots systematically distributed on a square grid of 200 m throughout

the forest, which is divided in 249 forest stands for management porpoises. Historical management archives containing forestry information exist for each one of these forest stands. Therefore, I could readily identify a total of 18 stands both with presence of *P. nigra* and with no silvicultural treatments applied over the past 26 years (1984–2010). 307 inventory plots from the 2010NFI were located within these 18 stands, although I only compiled data from the 198 plots in which *P. nigra* stand basal area was at least 50% of the total stand basal area. I noted for each one of these 198 plots the variables: altitude (m a.s.l.), total tree cover (the proportion of the forest floor covered by the vertical projection of the tree crowns, %), stand basal area (m$^2$ ha$^{-1}$) for each one of the tree species present, and percent of dead *P. nigra* trees. Additionally, I noted the number of seedlings (height < 1.30 m, age < 2 yr) and pole trees (height ≥ 1.30 m and diameter at breast height, dbh < 12.5 cm) present in a 5 m radius subplot concentric within the 15 m radius inventory plot, differentiating between species.

In order to address question (2) and compare the effect of altitude on the density of seedlings and pole trees, I fitted two separate Generalized Linear Models (GLM) with a log link function and a negative binomial error distribution with library *MASS* in R (R Development Core Team, 2014). A negative binomial distribution was preferred over a Poisson distribution due to the presence of overdispersion (Crawley, 2013). The predictor variables included in the models were altitude (as a proxy of aridity), stand basal area (as a proxy of irradiance) and their interaction. Given that tree cover and stand basal area were strongly correlated (Pearson's r = 0.97, n = 198, p < 0.0001) and that foresters typically prefer stand basal area to describe forest structure, the effect of tree cover was not tested to avoid multicollinearity. Stand basal area was included as a linear and second-order polynomial term to select the best transformation of this variable to account for nonlinearity (Ruiz-Benito et al., 2012). The minimal models were obtained longhand discarding the less significant predictor at a time (Crawley, 2013).

## 2.4. Irrigation experiment

The experimental part of the study was carried out in a forest stand from Navahondona called 'Nava del Espino'. This was one of the 18 undisturbed stands previously selected. It was chosen to perform the experimental study, because it is located at a mid-altitudinal level within the study site (mean altitude = 1450 m a.s.l.). The experimental layout consisted of 180 demographic plots arranged in five transects. Specifically, four 190-m long and one 90-m long linear transects that were roughly evenly distributed within the forest stand (ca. 56 ha) by the end of 2015. Sampling points spaced at 10-m intervals were marked on the ground along each transect, resulting in 90 sampling points in total. At each sampling point, I firstly measured with a tape the horizontal distance to the nearest adult tree (diameter at breast height, DBH ≥ 12.5 cm), then, I located the nearest viable seedling and measured its height. I discarded two seedlings during the process because ungulate herbivores had cut their apical leader shoot, and substituted them by the next nearest ones. Seedling height in cm was latter used to estimate seedling age in years with the equation:

$$Age = 0.679 \times Height^{0.705} \tag{1}$$

taken from Tíscar (2015b). Since the 2010NFI did not measure seedling height, I used this information to infer seedling age distribution in all the study stands.

Then, I permanently marked two paired 25 × 25 cm$^2$ demographic plots (plots hereafter), approximately 60 cm apart, around each sampling point (180 plots in total) to monitor the survival of seedlings that would naturally emerge in the coming spring. Cones of *P. nigra* mature by the end of the second autumn after pollination, but seeds are not dispersed until next January-March (Lucas-Borja and Vacchiano, 2018). The dispersed seeds remain on the ground until moisture and temperature are adequate for germination, usually in April. As a result,

seedlings of *P. nigra* have little time to grow roots before the recurrent summer drought of the Mediterranean climates begins (Tíscar and Linares, 2011). Within each pair of plots, one plot was randomly assigned to an irrigation treatment and the other to control. Plots assigned to irrigation were watered 7 times at 14 to 21-day intervals from the second week of June to mid-September, i.e. from the beginning until the end of the summer drought period in an average year. Irrigation consisted of adding ca. 1 l of water at each application time, equivalent to 11 mm of rainfall. This pattern of watering was delineated considering the mean length of the dry season (3 months), and the average values of rainfall (65.4 mm) and number of rainy days (7 d) during the drought period in the study area, according to the Vadillo-Castril meteorological station. Water was carefully added to avoid run-off. The surface area irrigated (30 × 30 cm) was greater than the area of the plot in order to avoid border effects. The first watering was applied on the 10th of June. In total, 2387 alive seedlings were censused on that date. Henceforward, their survival was monitored coinciding with the irrigation dates. The probable cause of seedling mortality was annotated in each census, distinguishing between (1) desiccation, seedlings dried out without any visible damage, (2) fungi damage, seedlings exhibit a necrotic region at the root-neck level and (3) others.

I quantified irradiance on the forest ground as the leaf area index (LAI) measured above each sampling point and its nearest seedling with a SunScan plant canopy analyzer system, equipped with a 1-m long probe type SS1 and a BF5 sunshine sensor (Delta-T Devices Ltd., Cambridge, UK). When measuring, the sensor was placed in a large forest gap, while the probe was held horizontally at a height of 1.30 m either above each sampling point, to characterize the light environment above the plots, or above the associated nearest seedling, to characterize the light environment above the seedling bank. The average of two perpendicular readings was recorded at each time for every measurement of LAI. Since the length of the SunScan probe was longer than the distance between paired plots, LAI was measured above the sampling point and the same LAI value noted for the two paired plots.

Additionally, average soil compaction, micro-slope, depth of the litter layer and percentage of litter cover were measured at each plot. A penetrometer, that provided a value of resistance to penetration (kg/cm$^2$), was used to measure average soil compaction (four measurements per plot). Micro-slope was measured with a clinometer placed on the ground inside the plot, while a metal ruler was used for measuring the depth of the litter layer. Litter cover was estimated visually. Soil in the 'Nava del Espino" forest stand originates from a calcite limestone bedrock, a cambisol with a silt loam texture and a pH of 7–8.

Finally, I also measured the percent of volumetric soil-water content (VWC) on different dates, using a handheld soil moisture sensor provided with a 12-cm long probe (Hydrosense, Campbell Scientific, Logan, UT, USA). Thus, I firstly measured VWC at the beginning of August, 24-hours after the last application of water, to study differences in water content between irrigated and control plots. Then, later in August, I measured VWC twice in the control plots only. Specifically, I measured VWC 1-day and 21-days after the occurrence of a stormy rainfall of 30 mm (as read in a rain gauge operating at that time in the study site) in order to analyse the effect of abiotic factors on soil desiccation. At every occasion, I took three VWC measurements within the plot and used the average value for the statistical analysis.

In order to address question (3), I used a multiple forward stepwise regression analysis (p-to-enter = 0.05) to determine the effects of abiotic variables on both measurements of VWC, which were arcsine transformed to satisfy normality assumptions. I also computed Generalized Lineal Mixed Models (GLMM) to evaluate the effects of abiotic factors, as fixed factors, and transect, as a random factor, on seedling survival. LAI was included as a linear and a second-order polynomial term to select the best transformation of these explicative variable to account for non-linearity (Ruiz-Benito et al., 2012). I also included the distance to the nearest adult tree (fixed factor), as a proxy of potential competition between seedlings and canopy trees. Seedling

survival was adjusted to a binomial distribution ("survived/total emerged seedlings per plot") using logit as link function. The full model was progressively simplified in order to uncover the significance of the fixed effects (Crawley, 2013). This statistical analysis was solely conducted with data obtained in irrigated plots, because all seedlings that had emerged in control plots died before the end of the experiment.

The experiment concluded 140 days after initiating the monitoring of seedling survival, because the experimental layout was seriously disrupted by timber harvest operations. Although this latter circumstance did not allow me to follow seedling survival in subsequent years and it is possible to argue that the experiment was too short, I could still analyse both abiotic factors that limit recruitment during the first summer, and differences in seedling survival patterns between irrigated and control plots. Kaplan-Meir estimates of the survival functions were tested for differences between control and irrigated plots with log-rank tests. The exact conditional distribution was approximated via 10,000 Monte-Carlo replications. Survival time was number of days calculated from the beginning of watering onwards. Seedlings that survived until the end of the experiment were regarded as censored data. The GLMM and survival analysis were carried out with R software (R Development Core Team 2014; packages lme4 (function 'glmer') and coin (function 'surv_test')). Throughout the paper, values are means ± standard deviations.

## 3. Results

### 3.1. Climatic trends and recruitment of P. nigra into the forest seedling bank

The monthly mean temperature, precipitation and water balance (precipitation minus potential evapotranspiration) of the study site are shown in Table 1. The Mann-Kendall tests showed significant increases in the tendency of mean temperature since 1972. Thus, all months with the exception of September yielded significant temperature increases. A negative significant precipitation trend was found for the month of June, whereas water balance showed a significant negative trend in the summer months of June, July and August.

The 198 inventory plots used to perform the observational part of the study covered an altitudinal gradient from 1047 to 2029 m a.s.l. (1561 ± 222 m a.s.l.), while the range of stand basal area was 0–54 m$^2$·ha$^{-1}$ (19.99 ± 12.65 m$^2$·ha$^{-1}$). The study stands harboured more pole trees than seedlings of *P. nigra* (499 ± 1159 > 145 ± 200 ind.ha$^{-1}$; Wilcoxon matched pairs test, n = 198, Z = 4.73, p < 0.0001). Furthermore, pole tree and seedling density responded differently to altitude. Thus, seedling density increased with altitude, whereas altitude did not affect the density of pole trees (Table 2). This result combined with the observed climatic trends suggests that the current range of *P. nigra* is moving upwards in the study area

responding to progressively more arid conditions. GLMs detected no interaction between altitude and stand basal area. This latter variable affected positively seedling establishment, but had no significant effect on the current abundance of pole trees, indicating the potential existence of ontogenetic niche shifts during *P. nigra* development (Lucas-Borja et al., 2012). However, a nonlinear response was observed along the gradient of stand basal area for both pole tree and seedling density, suggesting that the establishment of juvenile individuals might be enhanced in the long-term at intermediate values of stand basal area, i.e. of irradiance levels onto the forest ground.

Additional results suggested that *Quercus ilex* could become the dominant tree species to the detriment of *P. nigra* in the lower altitude stands. Thus, seedlings of *Quercus ilex* were found up to 1643 m a.s.l. and they were more abundant than *P. nigra* seedlings within that elevation upper limit (1.54 ± 8.90 > 0.81 ± 8.86 seedling per plot for *Quercus ilex* and *P. nigra* respectively; Wilcoxon Matched Pairs Test, n = 130, Z = 5.53, p < 0.0001). Yet, adult trees of *Quercus ilex* were present in just 31 out of the 198 study plots, whereas *P. nigra* seedlings were present in a total of 95 plots. In contrast, adult trees of *Pinus pinaster* were present in 37 out of the 198 study inventory plots up to 1597 m of elevation, but its recruitment was negligible (only two plots contained *Pinus pinaster* seedlings). The percent of *P. nigra* dead trees was 1.48% in the study plots.

The height of the seedlings sampled next to each sampling point of the experimental lay out was 57.0 ± 24.4 cm (range: 11 – 117 cm). According to Eq. (1), these latter results imply that seedling age ranged between 4 and 19 years in the study site, and that the average time needed by *P. nigra* to reach a height of 130 cm is 21 years. This number of years is pretty similar to the time needed by *P. nigra* individuals to surpass the pole tree stage (Fig. A.2.). Therefore, I concluded that the comparison between seedling and pole tree densities was an
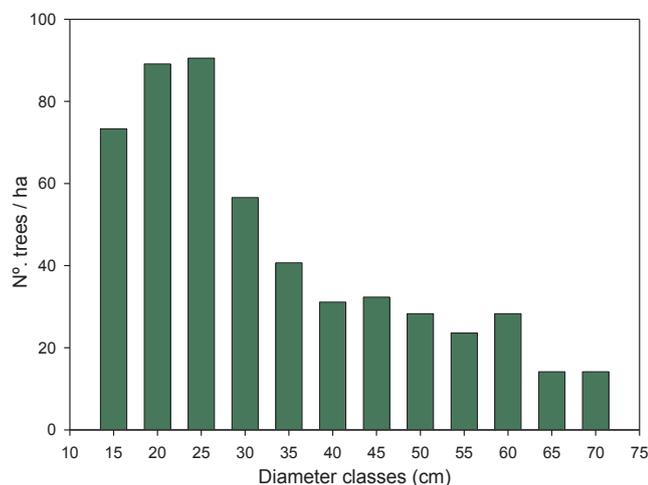
**Table 2**

Summary of the best Generalized Linear Models fitted with a log link and a negative-binomial distribution to test for the effects of altitude and stand basal area on the seedling (height < 1.30 m, age < 2 yr) and pole tree densities (height ≥ 1.30 m and diameter at breast height < 12.5 cm) in silviculturally undisturbed stands from the Navahondona forest.

| Effect | Seedling density | | | Pole tree density | | |
|---|---|---|---|---|---|---|
| | Estimate | SE | P(> \|Z\|) | Estimate | SE | P(> \|Z\|) |
| Intercept | −3.531 | 0.911 | 0.0001 | 1.314 | 0.141 | 0.0000 |
| Altitude | 0.002 | 0.001 | 0.0001 | | | |
| Stand Basal Area | 3.496 | 1.611 | 0.0210 | −2.529 | 2.042 | 0.2155 |
| (Stand Basal Area)^2 | −2.968 | 1.534 | 0.0531 | −4.358 | 2.075 | 0.0357 |

**Table 1**

Temporal trend of monthly mean temperature, monthly total precipitation and monthly water balance estimated by the Mann–Kendal test. Significance is noted as ***P < 0.001; **P < 0.01; and *P < 0.05. The trends (slopes) of the significant months were estimated by linear least squares regression.

| Time span | Temperature (°C) 1972–1999, 2006–2016 | | | Precipitation (mm) 1972–1992, 1996–2016 | | | Water balance (mm) 1972–1992, 2006–2016 | | |
|---|---|---|---|---|---|---|---|---|---|
| Month | Mean | MK-Stat | Slope (°C/decade) | Mean | MK-Stat | Slope (mm/decade) | Mean | MK-Stat | Slope (mm/decade) |
| January | 6.2 | 0.494*** | **0.84** | 150.9 | −0.027 | | 1467 | −0.020 | |
| February | 7.2 | 0.361** | **0.54** | 129.1 | −0.059 | | 1252 | −0.052 | |
| March | 9.7 | 0.402*** | **0.96** | 113.3 | −0.134 | | 881 | −0.173 | |
| April | 11.9 | 0.420*** | **1.17** | 124.3 | −0.064 | | 862 | −0.076 | |
| May | 15.9 | 0.390*** | **1.17** | 98.4 | −0.137 | | 273 | −0.155 | |
| June | 21.2 | 0.361** | **1.18** | 33.4 | −0.303* | −10.02 | −849 | −0.337** | −15.14 |
| July | 25.3 | 0.412*** | **1.28** | 6.7 | −0.215 | | −1521 | −0.443*** | −14.11 |
| August | 24.7 | 0.604*** | **1.54** | 13.4 | −0.061 | | −1283 | −0.322** | −8.53 |
| September | 20.5 | 0.160 | | 44.0 | 0.199 | | −56 | 0.072 | |
| Octuber | 15.0 | 0.495*** | **1.50** | 101.3 | −0.047 | | 392 | −0.155 | |
| November | 10.0 | 0.312** | **0.79** | 125.9 | 0.135 | | 1092 | 0.193 | |
| December | 7.2 | 0.513*** | **0.95** | 137.6 | −0.206 | | 1199 | −0.182 | |

**Fig. 1.** Diameter size distribution of trees present in the 'Nava del Espino' forest stand. The density of pole trees (height ≥ 1.30 m and diameter at breast height < 12.5 cm) was 393 ind. ha$^{-1}$.

appropriate proxy of the impact of climatic trends on *P. nigra* regeneration. Moreover, the time span for which I analised climatic trends matched adequately the number of years needed by a *P. nigra* individual to emerge and grow beyond the pole tree stage (~ 42 years).

### 3.2. Effects of abiotic factors on P. nigra recruitment into seedling banks

Forest structure in the 'Nava del Espino' stand, within which the experimental study was arranged, proved to be multi-aged, as can be deduced from the diameter class distribution drawn with data from the twelve 2010NFI plots located within it (Fig. 1).

Moreover, total tree cover was 78 ± 16% and, consequently, most of the seedlings were expected to be growing under the influence of taller trees. LAI was 2.8 ± 2.1 above the sampling points and 2.6 ± 1.5 above the sampled seedlings, this difference being non-significant (*t*-test for matched samples, N = 90, t = 0.63, p > 0.10). Control and irrigated plots did not differ in the measured abiotic variables either (*t*-test for matched samples, N = 90, p > 0.10 in all the comparisons).

With regard the irrigation treatment itself, water addition increased VWC in irrigated plots by 4.1 ± 2.8% (*t*-test for dependent samples, t = −12.2, d.f. = 66, p < 0.00001). The increment of VWC (after the storm mentioned earlier) was affected by the abiotic variables considered in the study ($F_{3,6} = 8.11$, p < 0.0001, $R^2 = 0.22$). Thus, the distance to the nearest tree positively affected VWC, whereas LAI and the percentage of litter cover had a negative effect. The contribution of soil compaction, micro-slope and depth of the litter layer was non-significant (Table 3). On the other hand, VWC diminished by 9.6 ± 5.5% during a 21-day period without rain. The abiotic variables: LAI and distance to the nearest tree, significantly explained this reduction ($F_{2,87} = 6.35$, p < 0.01, $R^2 = 0.12$). Thus, the VWC reduction

**Table 3**
Results of forward stepwise regression analysis with volumetric soil–water content after a stormy rainfall as the dependent variable and Leaf Area Index, average soil compaction, micro-slope, depth of the litter layer, percentage of litter cover and distance to the nearest adult tree as the candidate predictor variables.

| Effect | *b* | *SE* | *t* | *P* |
|---|---|---|---|---|
| Intercept | 0.522 | 0.018 | 28.354 | < 0.00001 |
| Leaf Area Index | −0.009 | 0.003 | −2.781 | 0.0067 |
| Percent litter cover | −0.062 | 0.022 | −2.853 | 0.0054 |
| Distance to adult | 0.002 | 0.001 | 2.344 | 0.0214 |

**Table 4**
Results of forward stepwise regression analysis with difference in volumetric soil-water content after 21-days of dry weather as the dependent variable and Leaf Area Index, average soil compaction, micro-slope, depth of the litter layer, percentage of litter cover and distance to the nearest adult tree as the candidate predictor variables.

| Effect | *b* | *SE* | *t* | *P* |
|---|---|---|---|---|
| Intercept | 0.337 | 0.017 | 20.212 | < 0.00001 |
| Leaf Area Index | 0.015 | 0.005 | −3.103 | 0.0025 |
| Distance to adult | 0.002 | 0.001 | 2.182 | 0.0214 |
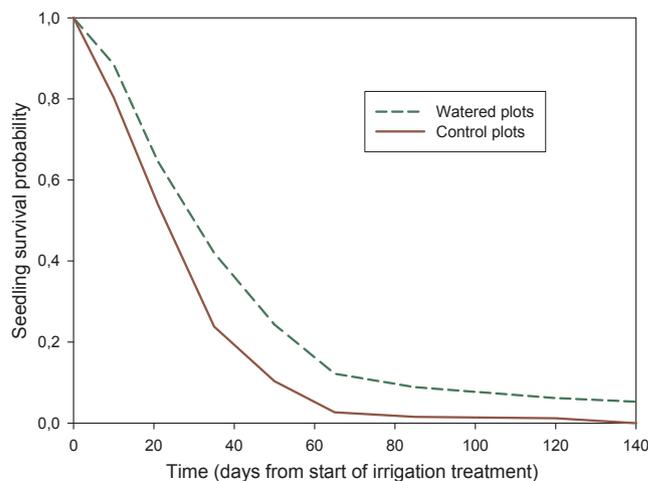


**Fig. 2.** Kaplan-Meier survival functions of control and irrigated plots from the starting (on the 10th of June) to the end of the irrigation experiment 140 days later.

was lower in plots exhibiting a higher value of LAI, whereas the distance to the nearest tree was positively associated with the loss of water in the soil (Table 4).

Seedling density did not differ between control and irrigated plots at the beginning of the experiment (Mann-Whitney U Test, U = 3743, p > 0.10), with 205 ± 101 and 219 ± 105 individuals per square meter, respectively. The rates of seedling survival from this date onwards are shown by the survivor function estimates represented in Fig. 2.

Survival functions of irrigated and control plots differed significantly (Z = -11; p < 0.00001), indicating a positive effect of water addition on seedling survival. In fact, seedling mortality due to desiccation was higher in control plots (Kolmogorov-Smirnov test, D = 0.36, p < 0.001), although it was also high in the irrigated ones (84.7 ± 16.6% *vs.* 67.1 ± 22.8 for control and irrigated plots, respectively). On the contrary, more mortality due to fungi damage occurred in the irrigated plots (8.3 ± 12.3% *vs.* 1.8 ± 5.4%; Kolmogorov-Smirnov test, D = −0.34, p < 0.001). This elevated seedling mortality resulted in only 4.46% of all the monitored seedlings surviving until the end of the experiment in the irrigated plots. There was at least one surviving seedling in 21% of these plots, although the mean number of surviving seedlings per plot was just 0.61 ± 1.47. However, no seedlings survived beyond the drought period in control plots. The Kaplan-Meir survival functions showed that most mortality took place during the first few weeks after initiating the censuses in all plots (Fig. 2). Hereafter, the survivor function estimates levelled off, although some seedling mortality continued to occur. Beyond the transcendent influence of water availability, LAI had a positive significant effect on seedling survival, whereas average soil compaction, micro-slope, horizontal distance to the nearest tree and litter depth had a significant negative effect. Interestingly, the parameter of the second-order term was negative for LAI, suggesting that establishment of

**Table 5**
Summary of the Generalized Linear Mixed Model fitted with a log link and a negative-binomial distribution to test for the effects of several biotic and abiotic variables on the recruitment of *Pinus nigra* in silviculturally undisturbed forests.

| Effect | Estimate | SE | Z | P |
|---|---|---|---|---|
| Intercept | − 0.372 | 0.867 | − 0.429 | 0.6679 |
| Leaf Area Index | 0.839 | 0.31 | 2.703 | 0.0068 |
| (Leaf Area Index)^2 | − 0.092 | 0.047 | − 1.937 | 0.0527 |
| Litter depth | − 0.565 | 0.152 | − 3.719 | 0.0002 |
| Soil compaction | − 0.762 | 0.306 | − 2.49 | 0.0128 |
| Micro-slope | − 0.118 | 0.031 | − 3.793 | 0.0001 |
| Distance to adult | − 0.298 | 0.133 | − 2.243 | 0.0248 |

seedlings might be enhanced at intermediate values of canopy cover (Table 5). Finally, the effect of litter cover expressed as a percentage was non-significant.

## 4. Discussion

### 4.1. Climatic trends and recruitment into the seedling bank

Results indicated, at the local scale provided by the study site, a trend towards hotter and drier summers in congruence with climate change models that predict increased aridity for the Mediterranean Region due to both progressive warming and decrease in precipitation (Giorgi and Lionello, 2008). Considering that elevated seedling mortality due to desiccation during the summer is generally acknowledged as the main limiting factor for *P. nigra* recruitment (Tíscar and Linares, 2011; 2014), as it has been further confirmed by the present study, the future prospect of *P. nigra* forests at the southern range of its distribution appears to be rather gloomy. In fact, envelope distribution models project a major decline of *P. nigra* populations in the Iberian Peninsula and a contraction of the species' range as a result of climate change (Benito-Garzón et al., 2008). Although I did not detect increased rates of adult tree mortality (the percent of *P. nigra* dead trees was as little as 1.48% in the study site), I detected both an impoverishment of regeneration conditions related to progressively increased arid conditions, as shown by climatic trends and the comparison between the current densities of seedlings and pole trees, and an uphill movement of the *P. nigra* optimum elevation in the study area, as shown by the newly positive effect of altitude on seedling establishment (Table 2). These findings are congruent with the observation that dominant tree species may shift the central position of their distribution towards upper elevations in response to warming climates, while maintaining the limits of their existing ranges (Breshears et al., 2008). This type of distributional change would reinforce the previously stated idea that managing seedling banks may became an important operational approach to maintain the present range limits of *P. nigra* under changing climates. Moreover, it seems unlikely that *Pinus pinaster* could readily replace *P. nigra* under the current environmental conditions, since results suggest that the establishment of new *Pinus pinaster* individuals might be controlled by competition with adult trees of *P. nigra* rather than by aridity thresholds. Similarly, it is not possible to conclude that *Quercus ilex* is going to replace *P. nigra* either, since results from the present study could be explained either by climate change or by the occurrence of a plant succession process (Zavala and Zea, 2004).

The undisturbed study stands exhibited a very low seedling density in comparison with the seedling banks of shade-tolerant conifers from other natural regions (Antos et al. 2005). Nevertheless, the current seedling density (145 ± 200 individuals per hectare) represents 47% of the stocking density planned for the 5-cm diameter class in the study forests (recently managed according to the BDq system explained before) and, consequently, the existing seedling bank is not negligible, but of significant importance to achieve natural regeneration.

Seedlings of *P. nigra* surpass a height of 1.30 m in an average of

21 years, whereas other shade-tolerant conifers take much longer (Antos et al., 2000). This would suggest that light conditions generally found in Mediterranean forests do not affect *P. nigra* height growth during the early seedling stage. Seedlings thus increase their height progressively, although vertical growth must be done at the expense of underground biomass. As a result, seedlings growing in the shadiest conditions attain the lowest root-to-shoot ratios and are exposed to a higher risk of desiccation (Gómez-Aparicio et al., 2006). This fact could explain why most *P. nigra* seedlings establish at intermediate levels of irradiance across the species distribution area (Tíscar and Linares, 2014), since shade would be beneficial as long as it simultaneously helps to maintain soil water availability and does not compromise carbon balance (Climent et al., 2006). Congruently, results from this study showed a significant negative second-order parameter for stand basal area as an explanatory variable of both seedling and pole tree densities in the Navahondona forest (Table 2).

Although the rate of pine seedling mortality is usually high during the first summer (it reached 100% in the experiment reported here), it decreases as seedling survival increases the following years and, thus, surviving seedlings become well established in the Mediterranean understory within few years (Thanos et al., 1996; Castro et al., 2005; Ruano et al., 2009). In this regard, only 2.2% of the sampled seedlings exhibited severe damage by ungulates, suggesting that herbivory is low on the grown seedlings of the study species. Additionally, recruitment was benefited by the proximity of adult trees (Table 5), indicating the absence of competition between adult and juveniles and the existence of intraspecific facilitation between young and adult trees as recently shown by Abellanas and Pérez-Moreno (2018). It is latter on, when seedlings reach the pole size, that they frequently die out, being suppressed by the canopy trees above them (Palahí and Grau, 2003). Finally, recruitment into the seedling bank could alternatively have been limited by seed availability, if seed production was reduced in dense stands, but the high seedling density found in demographic plots suggests the opposite. At this point, it is worth to mention that *P. nigra* is a mast-seeding species and it is consequently seed limited most years, although the irrigation experiment coincided with a mast-seeding year and there was not seed limitation then. In fact, the observed average density of seedlings was clearly above the threshold used to define masting years in *P. nigra* (Lucas-Borja and Vacchiano, 2018). Therefore, abiotic rather than biotic factors seem to have been of greater importance in explaining the observed density of the seedling bank studied in the Navahondona forest.

### 4.2. Abiotic factors affecting recruitment into the seedling bank

Even though the irrigation experiment lasted for just one year, it provided insights about some potential mechanisms that ultimately affect the long-term recruitment into the seedling bank of the study site. Thus, water availability during the summer season was the most limiting factor for *P. nigra* recruitment. No seedlings survived in control plots and surviving seedlings were always found in irrigated plots, even though water addition induced some mortality due to fungal infection. This finding offers a distressing perspective for the future of the southern *P. nigra* forests, since summers are becoming more arid in the area (Table 1). Additionally, this fact can explain results from the observational study that indicate a progressive impoverishment of the regeneration conditions. The Kaplan-Meir estimates of the survival functions interestingly revealed that mortality patterns were similar in both control and irrigated plots with mortality rates peaking during the first month of observation at the beginning of summer (Fig. 2). Tíscar et al. (2017) have suggested that consecutive days of elevated temperatures during the summer season could be more deleterious than water shortage for the survival of recently emerged seedlings, but this possibility should be confirmed by further research.

Along with water availability, light availability also affected *P. nigra* recruitment (Table 5). Congruently with previous research and with

results from the observational study, the effect of light availability was nonlinear (humped-back shaped), indicating that the benefits of tree cover are stronger at intermediate levels of LAI and less important at higher or lower levels (Holmgren et al., 2012; Tíscar and Linares, 2014). The fact that the light environment did not differ between the sampling points and their associated seedlings indicated that light availability interacted concomitantly with other factors during the *P. nigra* regeneration process. For instance, LAI had a negative effect on VWC after the summer storm that occurred during the study period, probably because LAI intercepted precipitation, as did the litter layer (Table 3). In contrast, higher LAI values reduced the rate of soil desiccation (Table 4). Together, these two findings suggest that few storms with much rainfall would be more effective than many storms with little rain in order to warrant seedling survival during summer.

Soil compaction had a negative effect on seedling survival, probably because root growth is mechanically impeded in the more compacted soils, thus limiting access to water and nutrients (Gomez et al., 2002). However, it was less clear how micro-slope negatively affected seedling survival, since both micro-slope and soil compaction were expected to impede water infiltration, but neither affected VWC (Tables 3 and 4).

### 4.3. Implications for management

A first management implication is that forests of *P. nigra* should be managed using longer rotation periods, allowing more time for the establishment of regeneration. This recommendation is justified by results indicating that the best circumstance to achieve *P. nigra* successful regeneration would be for the overlap of a masting year with a summer wetter and/or cooler than usual, confirming previous research (Calama et al., 2017). However, favorable summers for *P. nigra* recruitment are expected to become more sporadic as climate is changing towards more arid conditions and, thus, the time lapse between successful regeneration events should extend in the study area, recommending the subsequent extension of the rotation period.

Secondly, management should take advantage of all the successful regeneration events. This would imply taking care of the seedling bank that is likely to establish in significant numbers beneath the intact canopy before any planned regeneration felling is carried out. In this regard, silvicultural treatments could be used to release well establish seedlings and saplings. The latter implies that regeneration fellings should be gradually applied over time and, according to results, should additionally aim to maintain mid-shade conditions in the understory. Tíscar and Linares (2014) observed in this respect that most *P. nigra* seedlings establish in naturally regenerated forests under tree cover values between 55% and 85%, which correspond to 19–27 m$^2$/ha of stand basal area in the study site. In order to accommodate the aforementioned recommendations, management plans should be likely characterized by the absence of a planned cyclic harvest-and-regeneration pattern, selective harvesting, and undefined stand age (Tíscar et al., 2015). The contribution of seedling banks to stand restocking will depend in any case on how seedlings respond to the felling of overtopping trees. To my knowledge, this question remains unanswered, but it has been proved that pole-sized *P. nigra* trees exhibit abrupt spurts in growth after neighboring trees are felled, i.e. they respond positively to release cutting (Tíscar, 2015b). Management should also explore the variability of abiotic conditions due to topography (Tíscar, 2015a) and the potential existence of local adaptations to specific environmental conditions (Tíscar et al., 2018).

Previous research has shown that removing the soil litter layer has a positive effect on *P. nigra* seedling emergence, but does not affect posterior seedling survival (Lucas-Borja et al., 2012). Since I did not record seed density, I cannot discuss how the litter layer could have affected seed germination. However, seedling emergence was high (> 200 individuals per plot), hence the litter layer favoured seedling survival during the summer, probably because it formed a barrier between the soil and the surface air that prevented water evaporation.

Although the likelihood of emergence, and the subsequent density of surviving seedlings, should be higher in the disturbed patches of soil, taking care of the existing seedling bank might thus be more critical than disturbing the soil.

In conclusion, climate is changing in the study area towards more arid conditions, particularly during the summer season. As a result, regeneration conditions for *P. nigra* are deteriorating progressively, although a significant number of seedlings may establish at any time beneath the intact canopy. This seedling bank may be crucial for the persistence of future *P. nigra* forests. Thus, in order to favour the seedling bank, flexible silvicultural schedules should be applied. Although the study was performed in just one forest from the southern limit of the *P. nigra* range, these recommendations are readily applicable to the whole distribution area of the species as shown by Tíscar and Linares (2014). Moreover, recommendations would probably work with most Mediterranean pinewoods progressively exposed to more arid conditions (Calama et al., 2017).

### Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.09.058.

### References

Abellanas, B., Pérez-Moreno, P., 2018. Assessing spatial dynamics of a Pinus nigra subsp. salzmannii natural stand combining point and polygon patterns analysis. For. Ecol. Manage. 424, 136–153.

Andivia, E., Madrigal-González, J., Villar-Salvador, P., Zavala, M.A., 2018. Do adult trees increase conspecific juvenile resilience to recurrent droughts? Implications for forest regeneration. Ecosphere 9, e02282.

Antos, J.A., Guest, H.J., Parish, R., 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. J. Ecol. 93, 536–543.

Antos, J.A., Parish, R., Conley, K., 2000. Age structure and growth of the tree-seedling bank in subalpine spruce-fir forests of south-central British Columbia. Am. Midl. Nat. 143, 342–354.

Benito-Garzón, M., de Dios, R.S., Ollero, H.S., 2008. Effects of climate change on the distribution of Iberian tree species. Appl. Veg. Sci. 11, 169–178.

Bravo, F., Bravo-Oviedo, A., Diaz-Balteiro, L., 2008. Carbon sequestration in Spanish Mediterranean forests under two management alternatives: a modeling approach. Eur. J. For. Res. 127, 225–234.

Breshears, D.D., Huxman, T.E., Adams, H.D., Zou, C.B., Davison, J.E., 2008. Vegetation synchronously leans upslope as climate warms. Proc. Nat. Acad. Sci. 105, 11591–11592.

Calama, R., Manso, R., Lucas-Borja, M.E., Espelta, J.M., Piqué, M., Bravo, F., et al., 2017. Natural regeneration in Iberian pines: A review of dynamic processes and proposals for management. For. Syst. https://doi.org/10.5424/fs/2017262-11255.

Candel-Pérez, D., Linares, J.C., Viñegla, B., Lucas-Borja, M.E., 2012. Assessing climate-growth relationships under contrasting stands of co-occurring Iberian pines along an altitudinal gradient. For. Ecol. Manage. 274, 48–57.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2005. Alleviation of summer drought boosts establishment success of Pinus sylvestris in a Mediterranean mountain: an experimental approach. Plant Ecol. 181, 191–202.

Climent, J.M., Aranda, I., Alonso, J., Pardos, J.A., Gil, L., 2006. Developmental constraints limit the response of Canary Island pine seedlings to combined shade and drought. Forest Ecol. Manage. 231, 164–168.

Crawley, M.J., 2013. The R Book, second ed. Wiley 1051pp.

Dyderski, M.K., Paź, S., Frelich, L.E., Jagodziński, A.M., 2018. How much does climate change threaten European forest tree species distributions? Glob. Change Biol. 24, 1150–1163.

Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. Global Planet. Change 63, 90–104.

Gomez, A., Powers, R.F., Singer, M.J., Horwath, W.R., 2002. Soil compaction effects on growth of young ponderosa pine following litter removal in California's Sierra Nevada. Soil Sci. Soc. Am. J. 66, 1334–1343.

Gómez-Aparicio, L., Pérez-Ramos, I.M., Mendoza, I., Matias, L., Quero, J.L., Castro, J., Marañón, T., 2008. Oak seedling survival and growth along resource gradients in

Mediterranean forests: implications for regeneration in current and future environmental scenarios. Oikos 117, 1683–1699.

Gómez-Aparicio, L., Valladares, F., Zamora, R., 2006. Differential light responses of Mediterranean tree saplings: linking ecophysiology with regeneration niche in four co-occurring species. Tree Physiol. 26, 947–958.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E., 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecol. Appl. 14, 1128–1138.

Holmgren, M., Gómez-Aparicio, L., Quero, J.L., Valladares, F., 2012. Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. Oecologia 169, 293–305.

Kendall, M.G., 1975. Rank correlation methods. Charles Griffin, London.

Linares, J.C., Tíscar, P.A., 2010. Climate change impacts and vulnerability of the southern populations of Pinus nigra subsp. salzmannii. Tree Physiol. 30, 795–806.

Lucas-Borja, M.E., Vacchiano, G., 2018. Interactions between climate, growth and seed production in Spanish black pine (Pinus nigra Arn. ssp. salzmannii) forests in Cuenca Mountains (Spain). New Forests 49, 399–414.

Lucas-Borja, M.E., Fonseca, T., Linares, J.C., Morote, F.G., Serrano, F.L., 2012. Does the recruitment pattern of Spanish black pine (Pinus nigra Arn ssp. salzmannii) change the regeneration niche over the early life cycle of individuals? Forest Ecol. Manage. 284, 93–99.

Mann, H.B., 1945. Nonparametric tests against trend. Econometrica 13, 245–259.

Matías, L., Jump, A.S., 2014. Impacts of predicted climate change on recruitment at the geographical limits of Scots pine. J. Exp. Bot. 65, 299–310.

Matías, L., Zamora, R., Castro, J., 2012. Sporadic rainy events are more critical than increasing of drought intensity for woody species recruitment in a Mediterranean community. Oecologia 169, 833–844.

O'Hara, K.L., 2014. Multiaged silviculture: managing for complex forest stand structures. Oxford University Press, USA.

Palahí, M., Grau, J.M., 2003. Preliminary site index model and individual-tree growth and mortality models for black pine (Pinus nigra Arn.) in Catalonia (Spain). For. Syst. 12 (1), 137–148.

Puerta-Piñero, C., Gómez, J.M., Valladares, F., 2007. Irradiance and oak seedling survival and growth in a heterogeneous environment. For. Ecol. Manage. 242, 462–469.

R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabasa, S.G., Granda, E., Benavides, R., Kunstler, G., Espelta, J.M., Ogaya, R., et al., 2013. Disparity in elevational shifts of E uropean trees in response to recent climate warming. Glob. Change Biol. 19 (8), 2490–2499.

Ruano, I., Pando, V., Bravo, F., 2009. How do light and water influence Pinus pinaster Ait.

germination and early seedling development? Forest Ecol. Manage. 258, 2647–2653.

Ruiz-Benito, P., Gómez-Aparicio, L., Zavala, M.A., 2012. Large-scale assessment of regeneration and diversity in Mediterranean planted pine forests along ecological gradients. Divers. Distribut. 18, 1092–1106.

Ruiz-Sinoga, J.D., Marin, R.G., Murillo, J.F.M., Galeote, M.A.G., 2011. Precipitation dynamics in southern Spain: trends and cycles. Int. J. Climatol. 31, 2281–2289.

Thanos, C.A., Daskalakou, E.N., Nikolaidou, S., 1996. Early post-fire regeneration of a Pinus halepensis forest on Mount Párnis, Greece. J. Veg. Sci. 7, 273–280.

Tíscar, P.A., García-Abril, A.D., Aguilar, M., Solís, A., 2015. Gestión Forestal Próxima a la Naturaleza: potencialidades y principios para su aplicación en los pinares de montaña mediterráneos como medida de adaptación al cambio climático. In: Herrero, A., Zavala, M.A. (Eds.), Los bosques y la biodiversidad frente al cambio climático: impactos, vulnerabilidad y adaptación en España. MAPAMA, Madrid, pp. 555–564.

Tíscar, P.A., 2015a. Patterns of shrub diversity and tree regeneration across topographic and stand-structural gradients in a Mediterranean forest. For. Syst. 24. https://doi.org/10.5424/fs/2015241-05887e-011, 11 pages.

Tíscar, P.A., 2015b. Modelo de ciclo forestal para la gestión sostenible de los bosques de Pinus nigra subsp. salzmannii deducido a partir de datos dendrocronológicos. Ecosistemas 24, 30–36.

Tíscar, P.A., Candel-Pérez, D., Estrany, J., Balandier, P., Gómez, R., Lucas-Borja, M.E., 2017. Regeneration of three pine species in a Mediterranean forest: A study to test predictions from species distribution models under changing climates. Sci. Total Environ. 584, 78–87.

Tíscar, P.A., Linares, J.C., 2011. Structure and regeneration patterns of Pinus nigra subsp. salzmannii natural forests: A basic knowledge for adaptive management in a changing climate. Forests 2, 1013–1030.

Tíscar, P.A., Linares, J.C., 2014. Large-scale regeneration patterns of pinus nigra subsp. salzmannii: poor evidence of increasing facilitation across a drought gradient. Forests 5, 1–20.

Tíscar, P.A., Lucas-Borja, M.E., Candel-Pérez, D., 2018. Lack of local adaptation to the establishment conditions limits assisted migration to adapt drought-prone Pinus nigra populations to climate change. For. Ecol. Manage. 409, 719–728.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim. 23, 1696–1718.

Vilà-Cabrera, A., Martínez-Vilalta, J., Galiano, L., Retana, J., 2013. Patterns of forest decline and regeneration across Scots pine populations. Ecosystems 16, 323–335.

Zavala, M.A., Zea, E., 2004. Mechanisms maintaining biodiversity in Mediterranean pine-oak forests: insights from a spatial simulation model. Plant Ecol. 171, 197–207.