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Assessing the effects of nurse shrubs, sink patches and plant water-use strategies for the establishment of late-successional tree seedlings in Mediterranean reclaimed mining hillslopes

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ABSTRACT

The use of ecohydrologically suitable microsites, such as sink patches (i.e. zones intercepting and infiltrating runoff) and nurse shrubs, have largely been proposed as tools to improve the establishment of late-successional trees in Mediterranean reclaimed landscapes. Nonetheless, this technique needs to be accurately tested along with the influence of seedling water-use strategy. To that purpose, we monitored the short- and mid-term (i.e. 4 and 8 years, respectively) influence of sink patches and nurse shrubs (*Genista scorpius*) on seedlings of two species with contrasted water-use strategies, *Pinus nigra*, a more drought avoider and isohydric species, and *Quercus ilex*, a more drought tolerant and anisohydric species. In the short term, *G. scorpius* shrubs enhanced the establishment of seedlings planted in shaded spots under its canopy. This positive interaction was more relevant for *Q. ilex* in drier years, while *P. nigra* was more facilitated in wetter years. Sink patches ameliorated the survival of both species, but only promoted greater growth during wetter years. *P. nigra* seedlings showed a high sensitivity to precipitation reduction. Their survival and growth were strongly constrained in dry years, resulting in a very high cumulative mortality at the end of the 8-year study period regardless of the microsite the seedlings were planted in. *Q. ilex* showed better seedling performance than *P. nigra* in the mid-term, keeping also the positive effects of suitable microsites on plant survival in the mid-term, after 8 years of plantation. Our results support the use of suitable microsites that ameliorate ecohydrological conditions as key spots for enhancing ecological succession in reclaimed mining sites, particularly the use of *G. scorpius* as nurse shrub for improving *Q. ilex* seedling establishment and growth. Our results also suggest that seedling functional strategy to cope with drought is a critical factor conditioning the overall plantation performance in the mid-term. Thus, seedling water-use strategy should constitute a key species selection criteria in future restoration programs focused on Mediterranean ecosystems, especially under climate change.

1. Introduction

Tree planting and forest restoration have been recently examined among the most effective strategies for climate change mitigation (Bastin et al., 2019; Veldman et al., 2019). In addition to their importance for carbon sequestration, restoration of late-successional tree species in degraded ecosystems is essential to recover their services, biodiversity, and landscapes (Ellison et al., 2005, 2017; Löf et al., 2019; Yu et al., 2021). Nonetheless, the introduction of tree vegetation and the establishment of functional communities is a hard task that

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requires a deep ecological knowledge of the assemblage drivers of native species, particularly in areas affected by opencast mining activities, where ecosystems are severely impacted (Alday et al., 2016; Milder et al., 2013).

In Mediterranean climates, reclaimed mine ecosystems are characterized by water scarcity and usually poor-nutrient soils prone to runoff and erosion (Nicolau and Asensio, 2002). Moreno-de las Heras et al. (2008) analysed succession trajectories in reclaimed mine slopes under dry Mediterranean environments, pointing out that initial treatments (i.e. soil management and revegetation), soil erosion and both the proximity and quality of seed sources were the main drivers of vegetation succession in these systems. These results were confirmed by Vidal-Macua et al. (2020), who also found that the design of reclaimed landforms that minimize soil erosion (Nicolau, 2003; Zapico et al., 2018) and seed sources vicinity were critical for vegetation recovery after opencast mining. Indeed, passive regeneration from nearby areas with pristine vegetation has been usually regarded as an effective, low-cost tool to restore native species in mining settings (Alday et al., 2016; Martínez-Ruiz et al., 2007; Prach et al., 2013; Prach and Hobbs, 2008; Prach and Pyšek, 2001). However, this option is not feasible for reclaimed areas located far from natural seed sources, which require active reforestation practices for introducing late-successional woody species.

The success of seedling establishment and growth in Mediterranean environments is strongly conditioned by water scarcity. Indeed, important amounts of seedling mortality are triggered by summer drought, especially during the first year after plantation (Alday et al., 2010; Castro et al., 2006; Matías et al., 2011; Mendoza et al., 2009). Poor conditions of reclaimed mining soils, typically characterized by low infiltration capacity and nutrient availability, can intensify these important limitations imposed by Mediterranean climate (Löf et al., 2019). Runoff and soil erosion can also exacerbate water stress in these landscapes if overland flow exceeds a threshold and both rill and gully networks are formed (Espigares et al., 2011; Moreno-de las Heras et al., 2010), as they efficiently drain surface water out from the reclaimed systems (Merino-Martín et al., 2015; Moreno-de las Heras et al., 2010).

In this context, there has been an important research effort during the last decades focused on the interactions between vegetation and hydrology (Puigdefábregas, 2005; Tongway and Ludwig, 1996), aiming to optimize the reforestation techniques that ameliorate the prospects of vegetation development in reclaimed sites (Löf et al., 2019). In Mediterranean hillslopes, in cases where sheet flow dominates runoff, vegetation is often organized in a heterogenous mosaic of source (i.e. zones generating runoff) and sink (i.e. zones intercepting and infiltrating runoff) patches that redistribute water and sediment resources (Calvo-Cases et al., 2003; Merino-Martín et al., 2012a; Nicolau, 2002). The ecohydrological behaviour of sink patches can be regarded as a feedback mechanism, described by the TTRP (i.e. Trigger-Transfer-Reserve-Pulse) conceptual model proposed by Ludwig et al. (1997, 2005). According to this model, sink runoff obstruction and infiltration promotes vegetation growth pulses following rainfall episodes, which, in turn, increase sink infiltration capacity. Recent works suggest that such sink patches can be used as key spots for vegetation recovery, given their positive ecohydrological properties that offer high water contents and nutrient availability (Espigares et al., 2013; Merino-Martín et al., 2015; Moreno-de las Heras et al., 2020).

Positive plant-plant interactions (i.e. facilitation) have also received special attention as a possible tool to introduce late-successional tree species, specifically the use of shrubs as nurse plants (Alday et al., 2016; Castro et al., 2004b; Castro et al., 2002; Gómez-Aparicio et al., 2004; Torroba-Balmori et al., 2015). Shrubs with canopies that grow horizontally act as sinks retaining overland flow and increasing infiltration capacity (Maestre et al., 2009; Merino-Martín et al., 2015). In addition, nurse shrub shade can significantly enhance microclimatic conditions under their canopy (Padilla and Pugnaire, 2006), reducing soil temperature and vapour pressure deficit (VPD) (Gómez-Aparicio et al., 2008). Physical soil properties (i.e. bulk density and surface crusting) and nutrient availability (i.e. N, P, K, organic matter) can also be ameliorated under the canopy of nurse shrubs, overall facilitating the establishment of both herbaceous and woody species (Gómez-Aparicio et al., 2005; Merino-Martín et al., 2015). This positive behaviour has been commonly observed for a variety of leguminous Mediterranean shrub species, including *Retama sphaerocarpa*, *Genista scorpius*, *G. florida* and *Ulex parvifolius*, among others (Gómez-Aparicio et al., 2005; Maestre and Cortina, 2005; Merino-Martín et al., 2015).

Tree species selection can also have a critical importance for seedling establishment in reclaimed Mediterranean environments. In fact, del Campo et al. (2020) found that selecting species based in their functional strategies to cope with water scarcity, particularly stomatal regulation, is a key tool for designing resilient communities. In that context, plants are often classified along an isohydric-anisohydric continuum (Klein, 2014; Martínez-Vilalta and Garcia-Forner, 2017; Tardieu and Simonneau, 1998). Plants with isohydric strategies strictly regulate water loses closing stomata facing drops in soil moisture to avoid dehydration and damages in the xylem (drought avoidance strategy). However, prolonged periods of strong stomatal closure can constrain plant growth and ultimately lead to decay and mortality due to carbon starvation (McDowell et al., 2008; Roman et al., 2015). On the contrary, anisohydric plants allow greater stomatal conductance under low soil water content conditions, presenting functional adaptations to tolerate tissue dehydration and resist fluctuations in water potentials (drought tolerant or drought resistant strategy) (Grossiord et al., 2020; Roman et al., 2015). Nevertheless, anisohydric strategies are more vulnerable to intense droughts, as excessive drops in water potentials can increase the risk of hydraulic failure and eventually lead to plant decay and mortality (Cochard, 2020; Will et al., 2013).

Nonetheless, there are still many uncertainties concerning late-successional tree species restoration in mine ecosystems and its sustainability. Reforestation techniques based on the use of potentially favourable microsites, such as sink patches and nurse shrubs, need to be further tested under the harsh conditions of mine environments (Alday et al., 2016; Merino-Martín et al., 2015). In addition, the effect of seedlings' water use strategy and its interaction with favourable microsites is unexplored in such systems. This information can be especially relevant for improving future restoration and revegetation programs in mining ecosystems under harsh, Mediterranean and dry environments, especially regarding their mid- and long-term performance.

This study assesses the short- (4 years) and mid- (8 years) term influence of ecohydrologically suitable microsites (sink patches) and nurse shrubs (*Genista scorpius*) on seedlings of two tree species with contrasted water use strategies: *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco and *Quercus ilex* L. subsp. *ballota* Desf. in two reclaimed open-cast mining hillslopes. *P. nigra* has been reported to perform a more conservative water use, following a more isohydric and drought-avoidance behaviour than *Q. ilex* trees in Mediterranean-dry environments (Forner et al., 2018b; Forner et al., 2014). Contrarily, *Q. ilex* is usually classified as a drought tolerant and more anisohydric species, promoting a delayed stomatal closure and allowing greater gas exchange rates under drought conditions (Aguadé et al., 2015; Forner et al., 2018b). Our main objectives are to assess the effectiveness of these microsites to enhance seedling establishment (i.e. survival and growth) in the short- and mid-term, as well the role of species water use strategy on the overall plantation performance. Our hypotheses are that (i) sink and nurse shrub microsites will improve seedling establishment based on enhanced ecohydrological conditions (i.e. higher water availability, infiltration capacity, runoff retaining effects, shading effect…); (ii) *Q. ilex* will be more successful than *P. nigra* in the mid-term due to its more anisohydric and drought tolerant water use strategy; (iii) there will be an interaction between microsite and water use strategy, with a more relevant positive effect of sink and nurse shrub microsites for the more drought avoider *P. nigra* seedlings.

2. Materials and methods

2.1. Study area

This study was carried out in two reclaimed hillslopes in El Moral mine site (40°47′24″ N, 0°47′24″ W, 1100 m above sea level), located in the Teruel coalfield (Fig. 1), northeast Spain. The climate on this area is classified as dry Mediterranean, according to Papadakis (1966). Mean annual precipitation vary around 400–500 mm, and it is usually exceeded by evapotranspiration, which ranges between 600 and 760 mm. Most precipitation falls in autumn and spring, whilst rain events in summer are scarce and consist mainly in intense, erosive storms. Nonetheless, the interannual precipitation pattern is irregular, with wet years occasionally alternating the usual trend of dry years (Peña-Monné et al., 2002). Mean annual temperature is 14 °C. July and December are respectively the warmest and coldest months. Overall, long summer droughts and a long frost period between October and April are the main climatic limitations for vegetation development in this area (de León-Llamazares, 1991). The natural vegetation consists mainly in *Pinus* sp. and *Quercus* sp. forest patches, with an important presence of *P.nigra* and *Q. ilex*, and shrub species occupying old abandoned terraces (Rivas-Martínez, 1987).

The hillslopes were built following the same protocol between 1987 and 1990 by the Minas and Ferrocarril de Utrillas mining company. Their slope gradient is 20° and they are north-faced oriented (i.e. shade side). They were covered by an 80–100 cm layer of clay-loam overburden substratum without any organic or chemical amendment. Revegetation was carried out by sowing a mixture of perennial grasses and perennial leguminous herbs. However, vegetation development and succession in the slopes differs greatly due to a contrasted hydrological behaviour. This is caused by the existence of a bare soil, 40° steep berm at the top of one of the experimental slopes (Slope 2), that acts as a water-contributing area promoting runoff generation and erosion. Such berm is absent in the other experimental slope (Slope 1), where runoff production and soil erosion is negligible (Merino-Martín et al., 2012a, 2012b; Moreno-de las Heras et al., 2020). This has facilitated the development of dense vegetation cover in Slope 1 (Nurse-Shrub slope), dominated mainly by *G. scorpius* shrubs (Merino-Martín et al., 2015). On the contrary, the presence of the berm in Slope 2 has favoured the formation of active fluxes of runoff and sediments, and the development of a spatially discontinuous rill network along the hillslope (Merino-Martín et al., 2012a, 2012b; Moreno-de las Heras et al., 2020). Vegetation cover in this hillslope is organized in source and sink patches that behave according to the TTRP model (Source-Sink Slope) (Merino-Martín et al., 2012a, 2012b; Merino-Martín et al., 2015). Source patches consist mainly in a bare soil matrix scattered by small shrubs (*Santolina* sp. and *Thymus vulgaris L.*) located in interrill areas. Sink patches, commonly developed in rill discontinuities and micro-topographical splays where runoff is discharged, are covered by perennial grasses (mainly *Lolium perenne* L.). Apart from their different vegetation patches, Merino-Martín et al. (2012a, 2012b) demonstrated that sources and sinks in Slope 2 are clearly differentiated by their hydrologic behaviour. Sources have higher runoff rate (i.e. runoff coefficient = 20%) and sediment yield, while sinks produce scarce amounts of runoff (i.e. runoff coefficient = 7%), presenting also fine sediments collected from the sources. Details of both slopes and soil properties of microsites are collected in Tables S1 and S2. For more details on the study site see (Merino-Martín et al., 2015; Moreno-de las Heras et al., 2009).

2.2. Experimental design and field acquisition methods

Two years old *P. nigra* and *Q. ilex* seedlings produced in 375 cm^3 plant nursery containers were planted in the hillslopes in November 2012. A set of suitable microsites was selected in each slope for planting the seedlings. Three different microsite types were applied in Slope 1 (Nurse-Shrub Slope): next to *G. scorpius* nurse shrubs in (1) upwards and

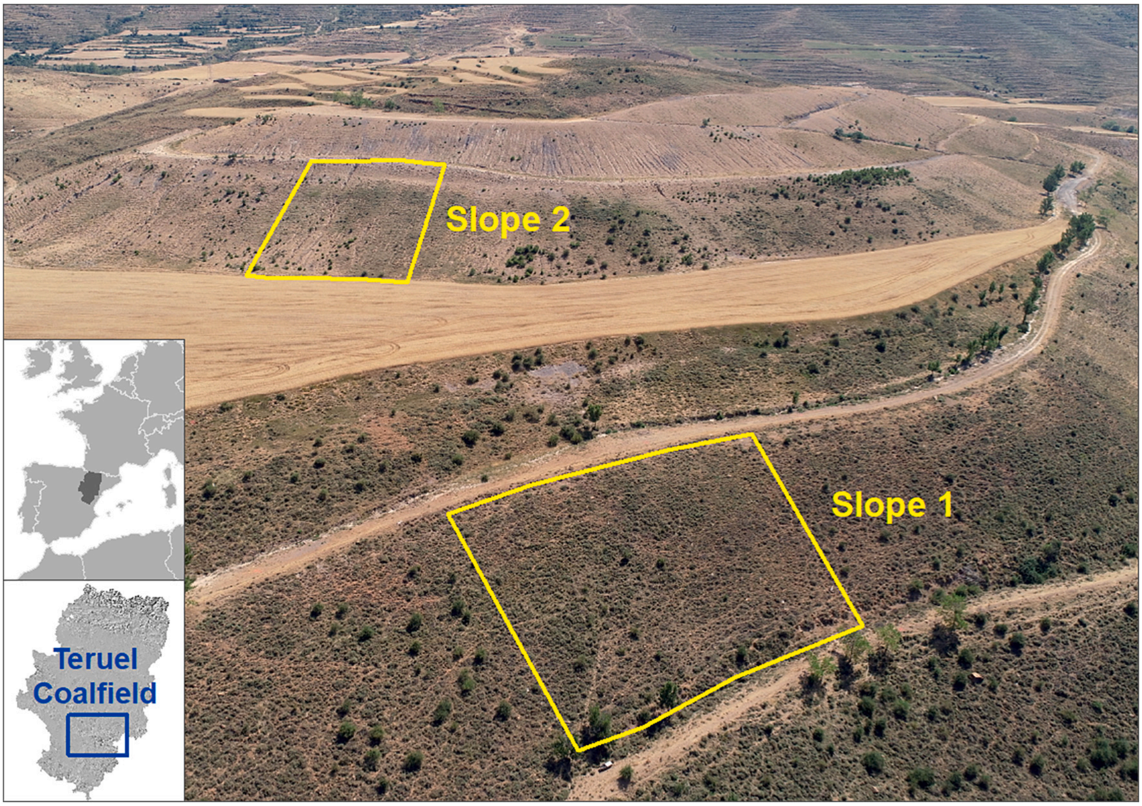

Fig. 1. Study area. Maps on the bottom-left show the location of the Teruel coalfield in west-Europe. The background image shows the experimental site of El Moral mine with the two hillslopes under study.

(2) downwards position relative to the shrub, and in (3) open areas out of the influence of *G. scorpius* (Fig. 2A). For Slope 2 (Source-Sink Slope), the seedlings were planted in two microsite types according to its ecohydrological dynamics: (1) source patches and (2) sink patches (Fig. 2B). Overall, 40 individuals of each tree species were planted per type of microsite, totalling 240 seedlings in Slope 1, and 160 in Slope 2. Both hillslopes were fenced to minimize the impact of herbivores and livestock on seedling performance. However, we found wool locks and ungulates trails in Slope 2 during our field campaigns, where many pines were bitten particularly during the first year. No herbivory signals were found in Slope 1 and in the *Q. ilex* seedlings of both slopes.

2.2.1. *Abiotic variables and microsite characterization*

Monthly precipitation data for the study site was interpolated from two nearby meteorological stations (Palomar de Arroyos and Montalbán, located at 7.8 and 5.3 km, respectively from the study site). Precipitation data for analysis was aggregated annually in hydrological years (from September of the present year to August of the next year) from 2012 to 2020.

In order to assess microsite soil moisture dynamics, 50 cm-long TDR probes were vertically installed in 6 representative points of each microsite type (i.e. 6 replicates per microsite type). Soil moisture assessments were carried out periodically between March 2013 and October 2016 (monthly frequency from 2013 to 2014, and every 2 months from 2014 to 2016). A TDR (Tektronix® 1502C) cable tester was used to collect the data, following the methodology proposed by Cassel et al. (1994).

Incident photosynthetic active radiation (PAR) was recorded for each microsite in Slope 1 with a luxmeter in a summer day with no clouds cover (28th June 2013). PAR in Slope 2 was considered similar between all microsites as no physical obstacles for light existed and vegetation is not tall enough to create differences in the radiation received between them. Last, the distance from each plantation microsite to the corresponding top-edge position of the hillslopes was calculated via GIS. A point layer with every seedling location was obtained using a GPS. Potential inaccuracies derived from the GPS data were corrected checking every point with an aerial picture and a photogrammetric DEM (both, 10 × 10 cm spatial resolution) derived from a UAV flight that was developed over the study area in June 2013. Distances were then calculated using the UAV-based DEM.

2.2.2. *Seedling survival and plant growth assessment*

Seedling survival and growth (i.e., increments of basal diameter, stem length and top-leaf height) were monitored annually during a four-year period, from summer 2013 to summer 2016 to characterize the short-term performance of the plantation. Basal diameter (mm) measurements were taken using a micrometer, while stem length and top-leaf height (cm) data were taken using a measuring tape. A last seedling survival/growth sampling campaign was carried out in October 2020 to assess the mid-term performance of the plantation.

2.3. *Data analysis*

2.3.1. *Microsite characterization: soil moisture dynamics and PAR*

To characterize TDR soil moisture dynamics and its potential differences between microsites, we applied linear mixed models (LMM). Microsite (shrub-up, shrub-down, and out in Slope 1; Source and Sink patches in Slope 2), Distance from the top the of the hillslope, and Date were included as fixed effects, while TDR-probe ID was included as a random effect to control for the effects of repeated measurements. Differences between microsite types on soil moisture were assessed using Tukey HSD tests. Differences between microsites on incident PAR for

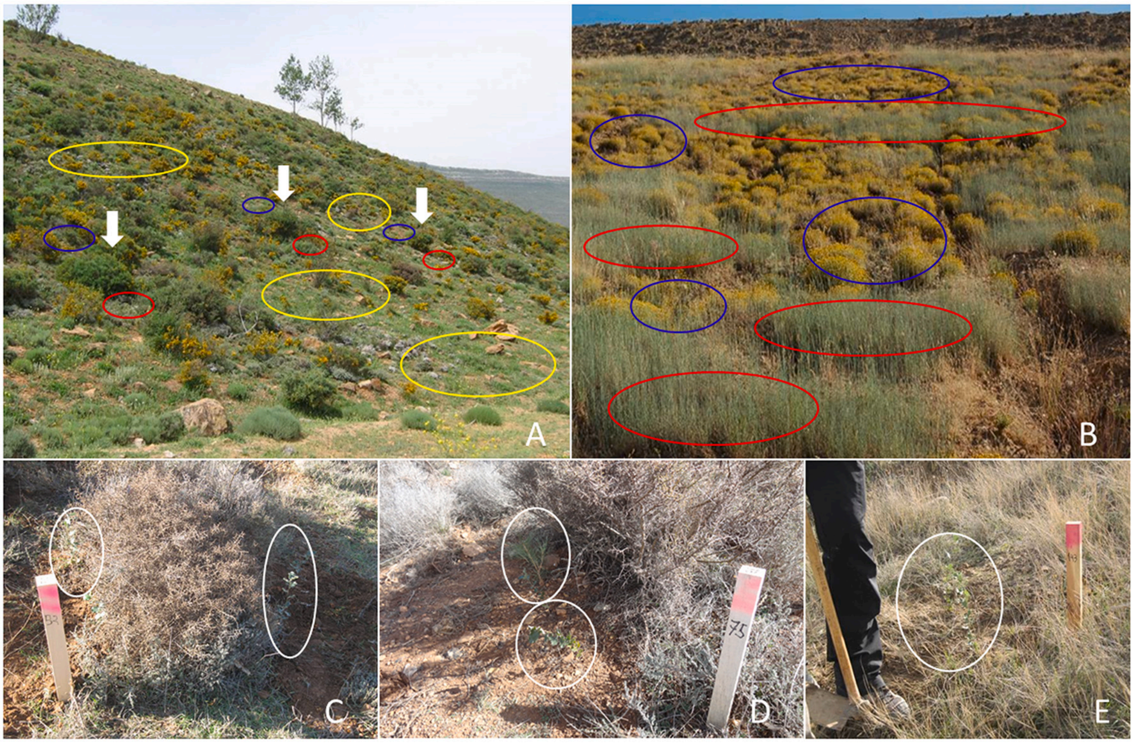

Fig. 2. Example of microsites. A and B show a general view of Slope 1 (Nurse-Shrub Slope) and Slope 2 (Source-Sink Slope), respectively. Examples of *G. scorpius* nurse shrubs in A are marked with arrows; blue ellipses depict shrub up microsites; red ellipses depict shrub down microsites, yellow ellipses depict zones out of the influence of nurse shrubs. Blue ellipses in B depict source patches; red ellipses depict sink patches. Pictures at the bottom show examples of seedlings planted in specific microsites. C: *Q.ilex* seedlings growing in shrub up (left) and shrub down (right) microsties. D: *Q.ilex* and *P.nigra* seedlings planted in shrub down microsite. E: *Q.ilex* seedling planted in a sink patch from slope 2 (Source-Sink slope). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Slope 1 were further evaluated using ANOVA and post-hoc Tukey HSD tests.

2.3.2. Short-term (2013–2016) seedling survival and growth

We applied a set of generalized linear mixed models (GLMM) and linear mixed models (LMM) to analyse seedling survival and growth rates (i.e. basal diameter and stem length annual increments) corresponding to the first 4 years of the experiment for each slope. To fit survival models, we applied GLMMs of the binomial family with the logit-link function (i.e., logistic regression), while we applied LMMs to fit seedling growth models. We used Species, Microsite, Annual (September to August) precipitation, Distance from the top of the hillslope, and Initial seedling size (i.e. shoot length and diameter, as proxies of seedling quality (Alía et al., 2005)) as fixed factors and covariables to explain seedling survival and growth dynamics. First order interactions were also included, while seedling ID was used as a random effect in each model to account for the effects of repeated measurements. In order to find the most parsimonious model configurations, alternative GLMMs and LMMs were compared for different combinations of the fixed factors and covariables according to the Akaike information Criterion (AIC; (Akaike, 1973)). AIC is a model optimality measure that trades off complexity and the fit of the model. The selected, optimal GLMM and LMM configurations for seedling survival and growth were tested for statistical significance of the included fixed factors, covariates and interactions. Significant differences between microsite types were further evaluated using Tukey HSD tests. To better assess the individual performance of the two species, we adjusted additional, separate models for each species, one for *Q. ilex* and the other for *P. nigra*, removing Species as fixed variable.

2.3.3. Mid-term (2013–2020) seedling survival and growth

We evaluated the mid-term performance of the seedlings (i.e. total survival and growth after 8 years of the experiment) for each slope using the same statistical procedure described above for the short-term dynamics. Absolute survival and the accumulated increments of basal diameter, stem length and top-leaf height until 2020, were assessed using GLMMs and LMMs respectively, that were optimized for model configuration using the AIC metrics. We applied Species, Microsite, Distance from the top of the hillslope, and their first order interactions as fixed effects to determine the optimized model configurations, including seedling ID as a random factor. A second set of separate models for each species was further adjusted removing Species as fixed effect to better capture the individual species performance.

All statistical analyses were carried out within R 4.0.2, using packages lme4, nlme and MuMIn (Barton, 2020; Bates et al., 2015; Pinheiro et al., 2020; R Core Team, 2020).

3. Results

3.1. Precipitation, soil moisture and photosynthetic active radiation among microsites

Annual precipitation during the study period shows an important rainfall irregularity (Fig. 3). The first hydrological year (2012–13) was exceptionally wet, with 630 mm (average precipitation in the study area ranges 400–500 mm), and was followed by the driest annual hydrological period in the series (2013–14), with 350 mm. The rest of the years presented a fluctuation between relatively dry and regular behaviours, accounting also for another extraordinarily wet period at the end of the series (690 mm in 2019–20).

We did not register significant differences in soil moisture between microsites for Slope 1 (Table S3), although it tended to be lower in positions out of the influence of *G. scorpius* nurse shrubs (Fig. S1.A). On the contrary, soil moisture dynamics in Slope 2 were significantly affected by both microsite type and the distance from the top of the hillslope (Table S4). Soil moisture was significantly higher in sink patches than in source ones and it also increased significantly towards the bottom of the hillslope (Fig. S1·B). For both experimental slopes, the lowest soil moisture contents were registered at the end of summer 2013.

Photosynthetic active radiation (PAR) was significantly lower in shrub-down microsites than in shrub-up and out microsites (Table S5, Fig. S2), due to the shadow projected by the shrubs. No significant differences in PAR were found between shrub-up and out microsites.

3.2. Seedling survival and growth in Slope 1 (Nurse-Shrub Slope)

Annual survival in the short-term (Table S6) was higher for *Q. ilex* than for *P. nigra*, and was favoured by the shrub-down microsite positions (i.e., under the influence of *G. scorpius* nurse shrubs, in downwards position relative to the shrub) for both species. Seedlings planted next to *G. scorpius* in upwards position as well as out of the influence of nurse shrubs showed lower survival rates and no significant differences between them. Seedling mortality increased significantly during drier years for both *P. nigra* and *Q. ilex*, although pine seedling survival was far more sensitive to precipitation reduction than oak seedlings. For example, *P. nigra* survival in Slope 1 was below 50% during the driest hydrological year (2013–14), while *Q. ilex* survival was around 75% for

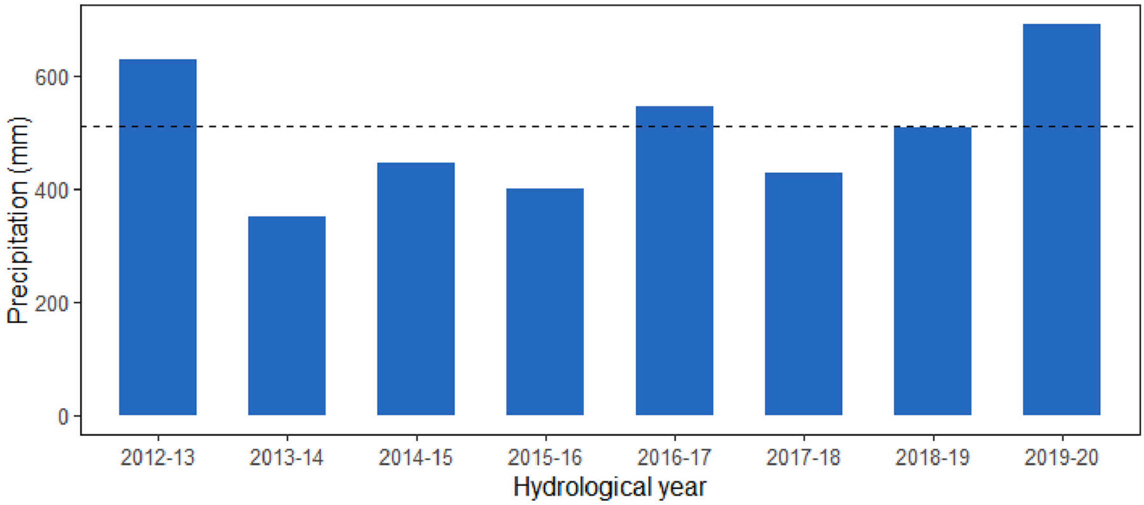

Fig. 3. Precipitation for each hydrological year along the study period. The dotted line indicates mean annual precipitation in the studied area for the period 1950–2020 (~500 mm).

the same period and experimental slope (Fig. 4.A-B and Fig. 5.A-B). Initial seedling diameter was significantly determinant for *Q. ilex* survival. Seedlings with wider diameters at the beginning of the experiment showed greater mortality during the first 4 years.

In the short-term, *P. nigra* showed higher growth rates than *Q. ilex* for all registered variables (i.e., basal diameter and stem length) (Fig. 6 A-D, Tables S7–S8). Stem length increments were enhanced in shrub-down microsites but not basal diameter increments. Shrub-down microsites were particularly more favourable for *Q. ilex* stem length growth during drier years. Differently, *P. nigra* seedlings planted next to *G. scorpius* shrubs, either in shrub-down or shrub-up positions, experienced greater stem growth during wetter years, while the growth rates were similar between all microsites in drier years. Initial stem length was negatively related to shoot growth rates for both *Q. ilex* and *P. nigra* seedlings.

We found very contrasting differences in mid-term survival of *Q. ilex* and *P. nigra* seedlings for Slope 1 (Table S9). Almost all pine seedlings died after 8 years of plantation (i.e., only 7 seedlings out of the original 120 remained alive at the end of the experiment), while an important fraction of oak seedlings survived during the experiment (Fig. 4 A and B). Same as for the short-term records, *Q. ilex* mid-term survival was significantly improved in shrub-down microsites (Fig. 5 C—D). In addition, *Q. ilex* seedlings with wider initial diameter also decreased their survival chances in the mid-term (Fig. S3A). The distance from the top of the hillslope was not determinant for the short- and mid-term survival rates of both, pine and oak seedlings.

Regarding accumulated growth after 8 years (Tables S10–S11), *Q. ilex* seedlings planted in shrub-down microsites showed higher stem-length increments (Fig. 6 E–F). In addition, *Q. ilex* seedlings with narrower diameters at the beginning of the experiment showed greater accumulated growth in the mid-term (Fig. S3 B—D). No analysed variable significantly influenced in the mid-term the accumulated growth of *P. nigra* seedlings, as they were affected at the end of the experiment by a very large mortality. Distance from the top of the hillslope was not determinant for the short- and mid-term seedling growth dynamics of the pine and oak seedlings.

3.3. Seedling survival and growth in Slope 2 (Source-Sink Slope)

Annual survival rates during the first 4 years of the study were quite high for both *Q. ilex* and *P. nigra* seedlings in Slope 2 (Fig. 4 A-B, Fig. 7 A–B). No significant differences were found between them (Table S12), although *P. nigra* seedlings registered a slight overall mortality during the driest year (2013–14). According to the model including both species, sink patches significantly ameliorated seedling survival, and seedling initial diameter and height were inversely related to survival probability. However, these effects were not yielded by the separate models for each species. No analysed variable affected *Q. ilex* seedling survival in the short-term, and only the interaction between initial size and precipitation had a significant effect on *P. nigra* survival.

During the first 4 years of experiment, *P. nigra* showed higher stem length increase (Table S13) than *Q. ilex* in Slope 2, although no differences between species were registered for basal diameter increment (Table S14). *Q. ilex* stem length growth was higher in sinks than in sources, particularly significant during wetter years (Fig. 8A–B), which favoured overall *Q. ilex* growth rates. However, neither microsites nor precipitation significantly influenced *P. nigra* growth in Slope 2 (Fig. 8 C–D). *P. nigra* shoot growth was affected by their initial size (Table S13). The taller the seedlings were at the beginning of the experiment, the

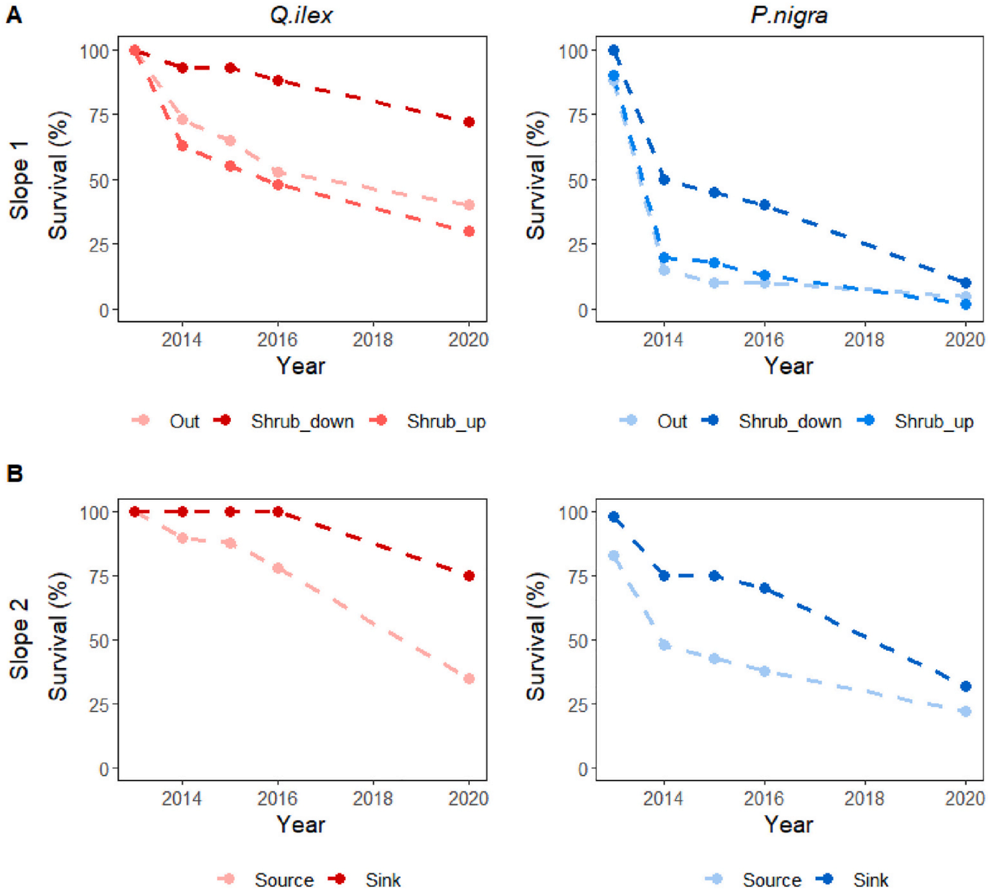

Fig. 4. Observed survival percentage for every species and slope during the study period. A: Slope 1 (Nurse-Shrub Slope); B: Slope 2 (Source-Sink Slope). Red colours represent *Q. ilex* seedlings; blue colours represent *P. nigra* seedlings. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

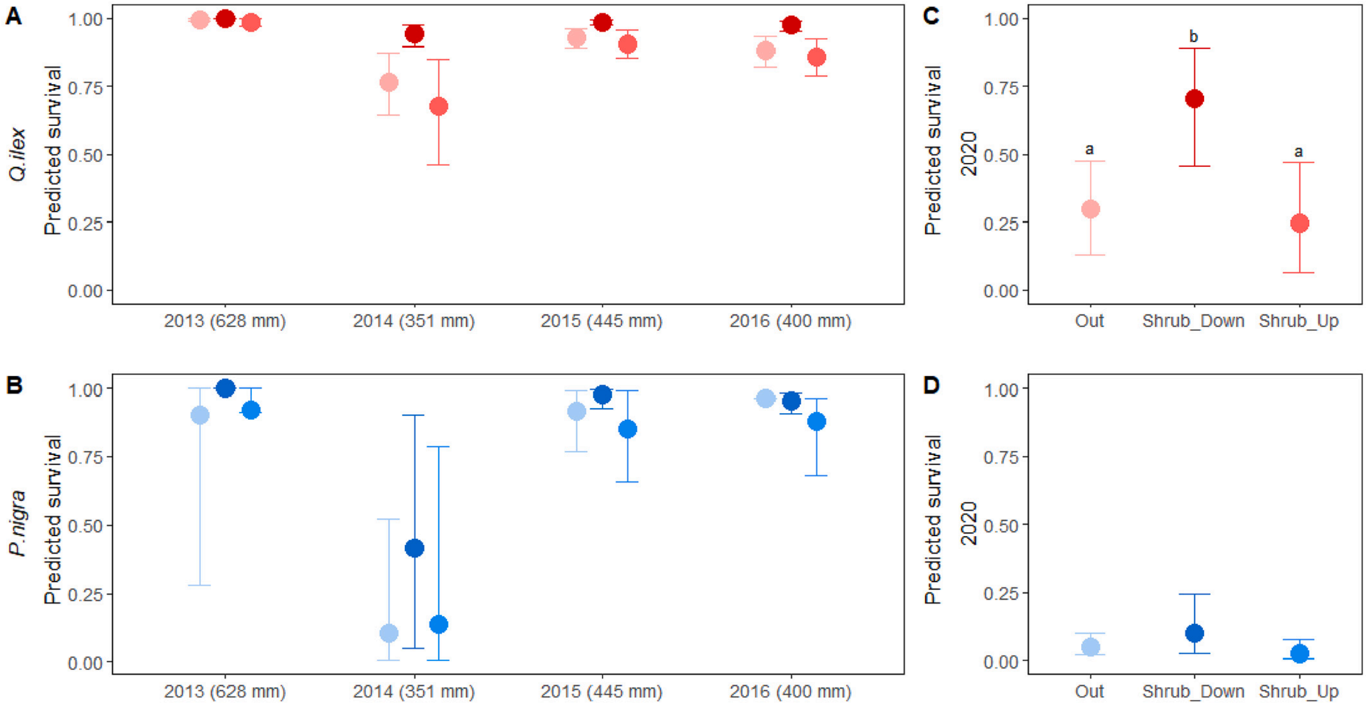

Fig. 5. Predicted survival of each species during the study period in Slope 1 (Nurse-Shrub Slope). A-B: predicted yearly survival in the short-term (2013–2016); C-D: predicted survival in the mid-term (after 8 years from the plantation). Small letters depict significant differences between microsites and water years. Error bars denote standard error of the predicted mean. Red colours represent *Q. ilex* seedlings; blue colours represent *P. nigra* seedlings. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lower was their growth rate during the first 4 years of the experiment.

After 8 years of experiment (Table S15), *Q. ilex* seedlings in Slope 2 showed greater survival than *P. nigra* seedlings. Sink microsites improved seedling survival chances, but only significantly for *Q. ilex* (Fig. 7C–D). *P. nigra* seedlings mid-term survival showed no significant response to any variable included in the model, although we registered marginal tendencies of increased survival probability for pines located at the bottom of the hillslope and for pines that were initially smaller.

Results from the mid-term assessment indicate that accumulated basal diameter and stem length after 8 years were significantly higher for *P. nigra* than for *Q. ilex* (Tables S16–S17). Microsite, seedling initial size, and distance from the top of the hillslope did not influence mid-term accumulated seedling growth in Slope 2.

4. Discussion

We monitored the short- and mid-term (i.e., 4 and 8 years, respectively) performance of planted late successional tree seedlings for two species that have two contrasted water use strategies, *P. nigra*, a more drought avoider and isohydric species, and *Q. ilex*, a more drought tolerant and anisohydric species, in two reclaimed mining slopes with different hydrological behaviour and availability of nurse shrubs. Our aims focused on exploring (i) the emergence of positive microsite effects of nurse shrubs and sink patches on the dynamics of seedling survival and growth, and (ii) the impact of the different water-use strategies of the planted species for seedling performance. Our results indicated that sink patches and nurse shrubs favoured seedling establishment and growth, particularly in the short term. Furthermore, species hydric strategy had a critical importance for the overall plantation performance, as *P. nigra* and *Q. ilex* responded differently to precipitation variations and drought. In addition, our results also reflected an overall negative impact of initial plant size on seedling performance.

4.1. *The role of suitable microsites: nurse plants and sink patches*

Tree seedlings under the canopy of *G. scorpius*, specifically seedlings planted in downward position relative to the nurse shrub, clearly increased their survival and growth rates in the short-term, although in the mid-term, this positive effect was only recorded for *Q. ilex*. Interestingly, *Q. ilex* seedlings planted in shrub-down microsites were more facilitated by *G. scorpius* in drier years, while the positive effects on *P. nigra* took place only during the wet years. This suggests that the way *G. scorpius* facilitates tree seedling performance is species-specific. Indeed, Alday et al. (2014) also found that the positive effects of nurse shrubs on *Quercus* sp. seedlings were stronger under more stressful abiotic conditions. Nonetheless, Gómez-Aparicio et al. (2008) and Soliveres et al. (2014) pointed out that nurse shrubs can only facilitate other plants up to a stress threshold determined by the functionality of the species. In this line, Maestre et al. (2009) and Soliveres et al. (2012, 2014) suggested that functional traits are primary drivers determining pairwise plant-plant interactions and its variation along environmental gradients. This seems to be particularly the case for our more drought avoider *P. nigra* seedlings. The positive effects of the nurse shrubs did not overcome the restrictions imposed by drier years for this species in Slope 1, where almost all pine seedlings had died at the end of the experiment.

According to our results, nurse shrub shading seems to be one of the main mechanisms involved in the improvement of seedling establishment by *G. scorpius*. In fact, the most significant difference in the abiotic conditions between the microsites of Slope 1 (Nurse-Shrub Slope) was the lower PAR registered in the shrub-down positions, as soil moisture was similar between all microsite types along time. Accordingly, previous experiments using nurse plants highlight that abiotic stress alleviation constitutes the main involved facilitating process, especially by means of shading (Gómez-Aparicio et al., 2008). This effect can be especially advantageous for shade-tolerant or shade-adapted species, such as *Quercus* species (Maestre et al., 2009; Pugnaire et al., 2011). Indeed, (Rey Benayas, 1998) found that *Q. ilex* seedlings survival and growth was clearly favoured under shading conditions. Furthermore, *Q.*

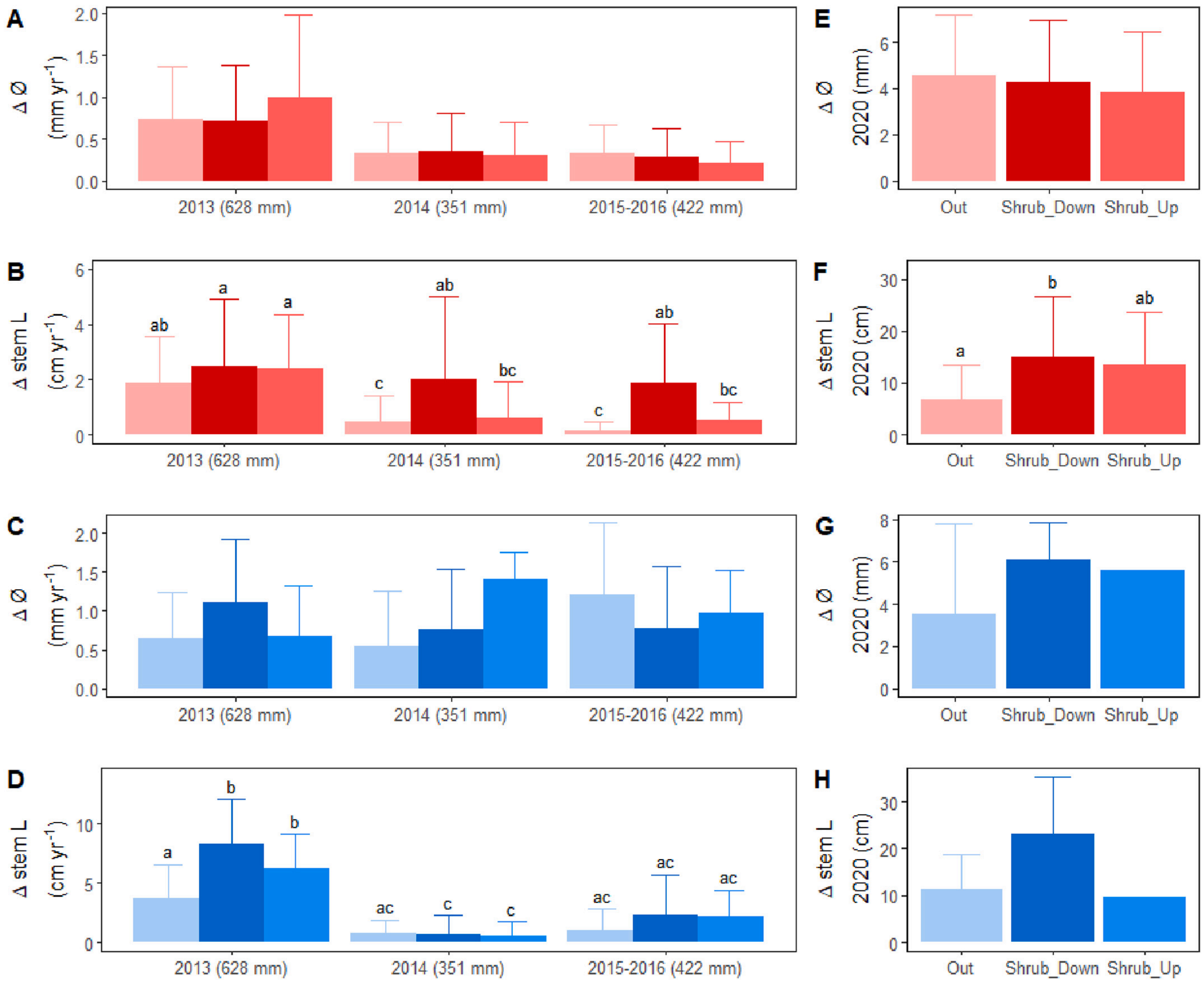

Fig. 6. Growth rates of each species during the study period in Slope 1 (Nurse-Shrub Slope). A-D: yearly growth rates in the short-term (2013–2016); E-H: accumulated growth in the mid-term (after 8 years from the plantation). Δ Ø: basal diameter increment; Δ stem L: stem length increment. Small letters depict significant differences between microsites and water years. Error bars denote standard deviation of the mean. Red colours represent *Q. ilex* seedlings; blue colours represent *P. nigra* seedlings. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ilex is prone to show photoinhibition under high radiation conditions (Valladares et al., 2005) while *P.nigra* exhibits low photoinhibitory stress (Lapa et al., 2017). This may have also enhanced *Q.ilex* growth under the shaded canopy of G.scorpius. Shade projected by nurse plants promote lower VPD and reduce soil evaporation, therefore buffering water stress for plants under their canopy (Castro et al., 2004a; Gómez-Aparicio et al., 2008). It must be noted that, although we found no difference in soil water content between shrub-down and shrub-up microsites, those results should be understood as a balance between water (rainfall and overland flow retention) inputs and (direct evaporation and plant transpiration) outputs. Therefore, lower soil evaporation and VPD in shrub-down positions may have allowed higher water availability for seedling transpiration, which would also reduce hydraulic failure risk in *Q.ilex*.

The positive effects of sink patches in Slope 2 (Source-Sink Slope), which increased overall seedling survival, is in general agreement with the greater water availability observed along time at those microsites. Their effect over seedling establishment also varied between species, as *Q. ilex* seedlings were more favoured by sinks than *P. nigra*. Differently to *G. scorpius* nurse shrubs in Slope 1, sink patches in Slope 2 only enhanced *Q. ilex* growth during the wettest year, and no growth differences between seedlings in sinks and sources was found during the rest of the series. This could be explained by a stronger sink behaviour during wetter years, as more precipitation events would allow sources to produce more runoff and sinks to retain a greater amount of overland flow, hence promoting more growth pulses according to the TTRP framework (Ludwig et al., 2005; Ludwig et al., 1997). However, the low frequency of wetter years in the study area may have limited this ecohydrological advantage, which could explain the lack of mid-term seedling growth enhancement in the sinks. Besides, the growth of *P. nigra* seedlings was neither ameliorated significantly by sink patches nor by higher precipitation, which contradicts existing evidence of the key importance of soil moisture for *Pinus* sp. growth (Manrique-Alba et al., 2017; Móricz et al., 2018). This unusual response of our pine seedling growth records could have been caused by the herbivory pressure we observed in Slope 2.

Overall, these results suggest that *G. scorpius* nurse shrubs and sink patches that behave according to TTRP model could be used to enhance late-successional tree species establishment in reclaimed mine sites. The observed positive interaction between *G. scorpius* and *Q. ilex* can result particularly useful for that purpose, as the nurse shrub clearly

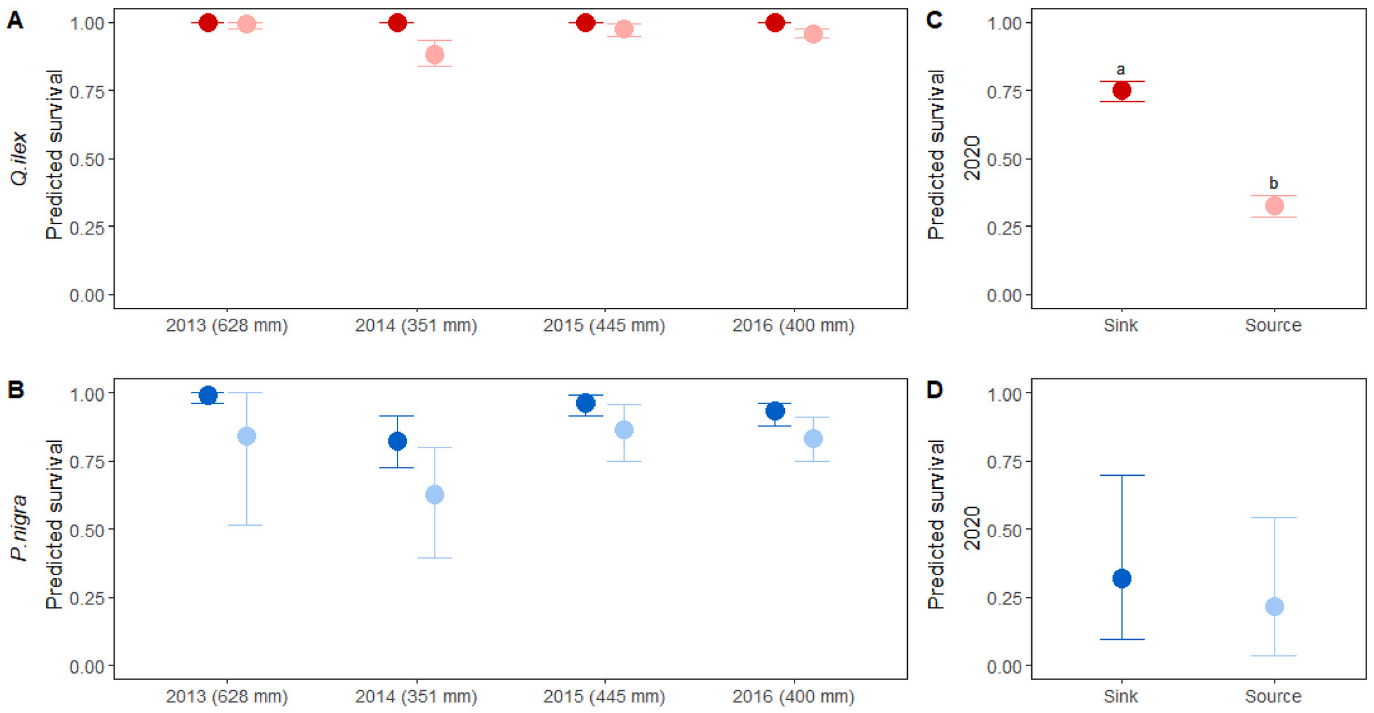

Fig. 7. Predicted survival of each species during the study period in Slope 2 (Source-Sink Slope). A-B: predicted yearly survival in the short-term (2013–2016); C-D: predicted survival in the mid-term (after 8 years from the plantation). Small letters depict significant differences between microsites and water years. Error bars denote standard error of the predicted mean. Red colours represent *Q. ilex* seedlings; blue colours represent *P. nigra* seedlings. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ameliorated *Q. ilex* survival and growth during the drier years. However, it should be considered that *G. scorpius* shrubs did not facilitate *P. nigra* seedlings, whose performance was strongly constrained by drought even under the canopy of nurse shrubs. In this sense, we suggest that future research should focus on clarifying which functional strategies and traits are more favoured by nurse shrubs along a broader range of climates and taxa.

4.2. Different drought sensitivity led to contrasted species establishment

Overall, *Q. ilex* seedlings showed a better short- and mid- term performance than *P. nigra*. The contrasted success of the species is reflected by the *Q. ilex* high survival rates during drought conditions. Contrarily, *P. nigra* was quite sensitive to precipitation reduction. This suggests that the species different hydric strategy to cope with drought had a determinant role for the overall plantation results, and that the more drought tolerant and anisohydric behaviour of *Q. ilex* was advantageous over *P. nigra* in our study site. Similarly, Aguadé et al. (2015) found that *Q. ilex* outcompeted more isohydric and drought avoider *Pinus sylvestris* in mountain Mediterranean landscapes, as the former was able to keep transpiration and functioning longer during drought conditions. Forner et al. (2018a, 2018b) documented earlier stomatal closure and longer periods of transpiration reduction during drought in *P. nigra* coexisting with *Q. ilex* in Mediterranean continental ecosystems. Furthermore, these authors found that *P. nigra* experienced greater water stress than *Q. ilex* under particularly intense drought conditions, suffering damages in the hydraulic system despite the more drought avoider strategy of the pine species. They also suggested that this contrasted behaviour may trigger *P. nigra* replacement by *Q. ilex* in the next decades.

Worth of notice is the particularly poor performance registered for *P. nigra* in Slope 1 (Nurse-Shrub Slope), where seedling mortality during dry years of the series was more drastic. This suggest that water stress conditions for this species were exacerbated in this experimental hillslope. This greater water stress could be explained by the denser vegetation cover and extensive presence of shrubs that may increase competition for water and reduce net precipitation during low-intensity rain events (Raz-Yaseef et al., 2012; Vicente et al., 2018). Besides, it should be noted that *Q.ilex* seedlings showed low growth rates in both slopes despite their greater success than *P.nigra*. However, these small growth rates are in line with other studies analysing recruitment and growth of *Quercus* species in Mediterranean montane environments (Castro et al., 2006; Gómez-Aparicio et al., 2008). It must be noted that, in our case, seedling growth is likely hindered by the harsh climatic conditions of our study site, which are further exacerbated due to the presence of poorly developed, reclaimed mining soils.

These results highlight the importance of functional strategies in species selection for reclamation and reforestation projects, especially hydric strategies to cope with drought in water-limited ecosystems. For instance, our results suggest that the use of *P. nigra* and other drought avoider species with low tolerance to frequent and/or severe droughts should be reconsidered for future reclamation projects in Mediterranean-dry ecosystems, particularly regarding climate change predictions for the next decades.

4.3. Effects of the initial size of the seedlings

Initial seedling shoot size has often been regarded as a quality proxy for seedlings of the same age. In many cases it has been found to be positively correlated with their performance in Mediterranean environments (Luis et al., 2009; Oliet et al., 2009). The main argued mechanism behind these positive effects is the greater capacity to mobilize water and nutrients of large seedlings (Villar-Salvador et al., 2012). However, our results contradict these general tendencies, as we found that, when the effects of initial seedling size were significant, they had a negative impact on seedling survival and growth. It must be noted, however, that the negative relationship between *P. nigra* initial seedling size and their performance in Slope 2 could have been also caused by the herbivory pressure. Nonetheless, similar results have been found in dry environments with poor, oligotrophic soils, where smaller size was correlated with the expression of functional traits that promote stronger

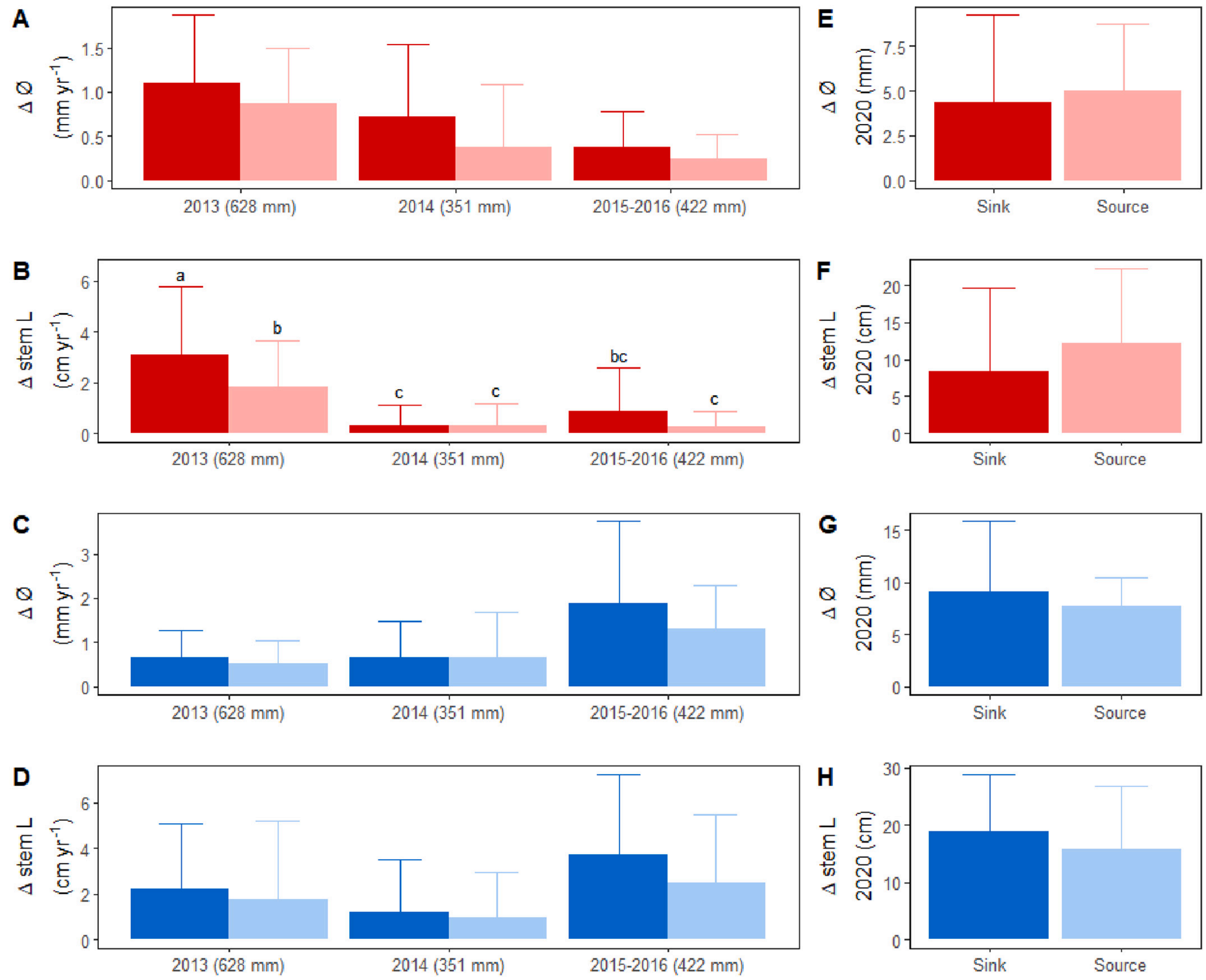

Fig. 8. Growth rates of each species during the study period in Slope 2 (Source-Sink Slope). A-D: yearly growth rates in the short-term (2013–2016); *E*-H: accumulated growth in the mid-term (after 8 years from the plantation). Δ Ø: basal diameter increment; Δ stem L: stem length increment. Small letters depict significant differences between microsites and water years. Error bars denote standard deviation of the mean. Red colours represent *Q. ilex* seedlings; blue colours represent *P. nigra* seedlings. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

drought resistance. Specifically, smaller seedlings in such conditions have been reported to show higher root/shoot ratio, lower leaf area transpiration, and greater water use efficiency compared to larger seedlings, overall reducing their risk of dehydration and hydraulic failure by declining water potentials (Leiva and Fernández-Alés, 1998; Tan and Hogan, 1997; Trubat et al., 2011). Indeed, soils in reclaimed mining landscapes, such as those developed in our study site, are characterized by low contents of nutrients and organic matter, a massive soil structure and a shallow profile (Moreno-de las Heras, 2009; Nicolau, 2002), which could have favoured the emergence of the observed results.

5. Conclusions

Our study showed that, in reclaimed mining Mediterranean dry environments, suitable microsites like sink patches and nurse shrubs enhanced late-successional tree seedling establishment. Besides, seedling water-use strategy to cope with drought turned out to be a critical factor conditioning their mid-term success, which also modulated the effect of suitable microsites facing variations in annual precipitation. In our work, survival and growth of the more drought-sensitive and isohydric *P. nigra* species was strongly constrained by precipitation. Ameliorated conditions in suitable microsites did not overcome such limitations, especially in a densely vegetated slope system, where high cover exacerbated water stress by competition. In turn, *Q. ilex* establishment was more favoured by suitable microsites than *P. nigra*. *G. scorpius* nurse shrubs facilitated seedlings planted in shaded spots under their canopy, and this effect was particularly effective for *Q. ilex* during dry years. Sink patches enhanced overall seedling survival and promoted greater growth for wet years, but this positive effect was not observed for dry years. These outcomes support the use of suitable microsites that ameliorate ecohydrological conditions (i.e., higher soil moisture, infiltration capacity, reduced VPD due to shade effect) as critical locations for enhancing ecological succession in reclaimed mining sites, especially nurse shrubs as key spots for planting late-successional tree seedlings. However, their success is highly dependent on seedlings functional strategies to cope with drought. This suggests that water-use strategies should constitute a key species selection criteria for designing resilient communities in future restoration programs in water limited ecosystems, especially regarding future climate change predictions. According to our results, the use of *G. scorpius* as nurse shrubs is an interesting and useful mechanism for introducing *Q. ilex* seedlings in reclaimed mining sites under dry Mediterranean conditions, while the use of *P. nigra* should be reconsidered due to its poor performance facing water stress. Future studies should focus on determining which functional strategies and traits of seedlings and trees are more advantageous for their long-term resilience against drought in a broader scale of climatic conditions, as well as on identifying specific traits that promote positive relationships between nurse shrubs and tree seedlings.

Declaration of Competing Interest

Authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2021.106538.

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