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Reforesting drylands under novel climates with extreme drought filters: the importance of trait-based species selection

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Abstract

Having regard to the substantial world-scale forest restoration needs, the efforts must be done efficiently, which necessarily forces to consider the adaptation of new forests to the extremes arising from climate change. In this context, species selection strategies should enhance long-term functional resilience in the face of novel environmental scenarios. The use of plant functional traits for selecting species under climate change might be advantageous over more traditional taxon-based criteria as an adaptive forestry management strategy. In this work, we studied which functional traits (across species) have played a relevant role on field performance and fitness in a multi-species reforestation trial in a Mediterranean dryland affected by an extreme drought event. Different traits both from the individual plant and from the species were studied in seven species both at the short and the mid-term (10 years). The relative importance (RI) or contribution of the different traits to plantation performance was assessed through boosted regression tree models. The results showed that, under favorable climatic conditions, mean survival was above 70 % and individual plant functional traits held up to 60 % of importance on such value. The impact of species functional traits was low in this case (less than 18%) pointing out that all the species were performing within their niche at this point. However, after the driest year on record, the role of the latter on survival rose up to 53 % of RI and survival sharply decreased to 33%, with some species showing negligible survival rate (< 10%). The dynamic response of stomata and xylem resistance to cavitation, together with rooting depth, were the main traits (species traits) identified in successful performance facing the extreme environmental factors. Thus, trait-oriented approach to select species represent a key tool in the implementation of new and successful forest restoration strategies to design resistant and resilient ecosystems adapted to the climate change challenges.

Keywords: adaptive forest management, ecosystem restoration, Quercus, Pinus, Juniperus, Fraxinus, Arbutus, boosted regression tree (BRT).

1. Introduction

Forest restoration is gaining appealing and momentum in the last years given its usefulness to recover goods and services from degraded forest ecosystems and its role on addressing global environmental threats (Löf et al., 2019). Protective reforestations have been deployed for decades in drylands with the aim to protect soil from erosion, regulate water fluxes, and protect reservoirs and other infrastructure from siltation whilst enhancing biomass production and biodiversity. Millions of hectares of planted forests cover the Mediterranean basin, providing multiple services to local economies and societies such as in Spain, which has been one of the most active countries in the world implementing forest restoration works since mid-19th century, with about 5 Mha artificially regenerated (FAO, 2010; Vadell et al., 2016). This long experience has set a strong technical and scientific expertise in the many subjects that together integrate the body of forest restoration, such as nursery production and stock quality assessment (del Campo et al., 2010; Villar-Salvador et al., 2012), biophysical characterization of the land (Elena-Roselló, 2004), site preparation and pre-existing vegetation removal (Navarro-Garnica, 1977; Martínez de Azagra, 1996; Löf et al., 2012), site-species matching (Rivas-Martínez, 1987; Pemán-García et al., 2006), application of cultural treatments (Ceacero et al., 2012, 2014), etc. On the one hand, this effort has provided a fairly valued and recognized know-how that can be used elsewhere in the reforestation of harsh and degraded drylands (Coello et al., 2015). On the other hand, however, this long experience has created its own discipline, procedures, and rules by force of habit that present some rigidity and might need revision, as targets and historical references may be no longer valid (Willians and Dumroese, 2013).

In the context of climatic and global changes, some questions have arisen about certain aspects of forest reforestation, particularly those related to future habitat suitability either for species or populations (provenances), as seedlings planted following conventional guidelines would increase their dependence on conditions that are becoming rarer (Willians and Dumroese, 2013; Hällfors et al., 2017). Within the framework of novel climates, reforestation strategies need to focus on restoring and reinforcing ecosystem processes towards the provision of goods and services (e.g. water, soil protection, C sequestration, etc.) by putting the emphasis on key species managed and used for many years that necessarily will lead restoration goals (Sansilvestri et at., 2015; Jacobs et al., 2015; Hof et al., 2017; Jandl et al., 2019). In this context, species/populations selection must be based on a robust genetic makeup and ability to adapt, rather than focusing on particular species composition within a phytosociological framework. This may imply in-depth revision of the current site-species matching procedures, strongly biased towards auto-ecological and floristic-phytosociological information that has been gathered under historical conditions (Rivas-Martínez, 1987; Gandullo and Sánchez-Palomares, 1994; Farris et al., 2010). Moreover, the floristic-phytosociological approach has been criticized due to its lack of agreement with palynological records in some cases (Carrion and Fernandez, 2009). Novel climates bring along with them ecological filters and extremes that some native species may not overcome while others will do (Lindner et al., 2014). Severe drought events out of historical series have been pointed out as triggers that cause severe dieback and mortality on mature plantations in drylands (Allen et al., 2010; García de la Serrana et al., 2015; Navarro-Cerrillo et al., 2019). Changes in the core habitat of species can be preferentially driven by limiting soil moisture rather than by increasing air temperature (Fei et al., 2017). Modeling results, either from mechanistic or species distribution models, agree that suitable species' performance based in historical climate and/or range is uncertain (Lindner et al., 2014; Al-Qaddi et al., 2017).

Plant functional traits (PFT) are defined as morphological, physiological and phenological traits that impact individual fitness via their effects on growth, reproduction and survival of the plant (Violle et al., 2007). Several initiatives for the construction of databases of PFT (e.g. BROT 2.0, TRY plant trait database) are emerging as key tools in ecological processes and ecosystem functioning studies (Tavşanoğlu and Pausas, 2018; Kattge et al., 2019). The role of PFT for selecting species under climate change grounds on the identification of key traits that best suit novel environmental conditions (Padilla et al., 2009), and hence could be more associated to reforestation success beyond taxonomical limits. Given the wide variation of traits that co-occurring species deploy to face drought and water stress (Brodribb et al., 2014; Pratt et al., 2015; Garcia-Forner et al., 2017), different performance in plantation establishment can be expected. Xylem hydraulics, leaf, root and growth traits are usually behind a successful strategy facing water scarcity (Ryser, 1996; Choat et al., 2012; Johnson et al., 2012; Stahl et al., 2014). However, in spite of the considerable amount of literature published on PFT, climate change, adaptive forest management and plantation success, there is very little information from plantation trials addressing specifically which traits might suppose an advantage. According to a recent review (Löf et al., 2019), we are still in the infancy of issues related to species adaptiveness in the future. Species selection at present will have long-lasting consequences related to the resilience of future forests and the need to undertake urgent and costly actions related to dieback and climate dislocation problems (Navarro-Cerrillo et al., 2019). Not just the species or seed zones, but other technical issues might need re-assessment in a context of climate change in order to match future climatic conditions, such as site preparation, planting densities, cultural treatments and so on. In this sense, mid to long-term experimental trials in forest restoration programs might provide reliable results that encompass enough inter-year climatic variability to study the integrated effect of climate, species and traits. Plants respond more to climate extremes than to changing averages, which partially explains differences between models' output and experimental data (Lindner et al., 2014). Reforestation projects mostly occur at small to mid-scale, which better reflects environmental heterogeneity related to soil and physiographic features (e.g. microsites) (González-Rodríguez et al., 2011; Ceacero et al., 2012), and hence field studies can provide better insights in reforestation success (in spite of a warming climate) than other approaches based on regional climate projections. Thus, field experimentation remains undoubtfully necessary to address the change of paradigm in forest restoration programs. This work aims to assess the short and mid-term (10 years) performance of a multi-species reforestation in a Mediterranean dryland affected by an extreme drought event and harsh conditions. Specific objectives are to i) identify which species have presented a superior performance and fitness to the planting site, and which PFT (across species) have played a relevant role in this response; ii) assess the relative importance of different PFT (as well as their threshold/range) in successful survival and growth performance under extreme drought conditions; iii) assess whether the traits involved in early successful response match those involved in the mid-term response after the drought. By addressing these objectives, we bring to the fore the appropriateness of current methods for species selection under novel climatic extremes, i.e., are ecological or phytosociological criteria still valid to select species in reforestation programs? or should we move towards a more trait-oriented approach?

2. Materials and methods

2.1 Site characterization

The experiment was conceived with an experimental plot within a reforestation program carried out in 2008 at "La Muela de Cortes" site, municipality of Cortes de Pallás, province of Valencia, eastern Spain (39º13' N; 0°53' W; 794 m a.s.l.; Figure SM1-SM2). The results have remained unpublished until now. The geomorphology corresponds to a flat-topped mountain (butte) where parent material is a consolidated cretaceous limestone with a haplic calcisol developed over it. The soil is shallow (<30 cm), very rocky and has a pale brown surface horizon, more reddish with depth, with substantial accumulation of lime; pH in 1:2.5 water suspension was 8.04. Texture analyses carried out close to the experimental site revealed a clay-loam to silty-clay-loam soil (39±5 clay, 38±5 silt, 22±7 sand, figures in %) with organic carbon content of 3.07±0.12 % (organic matter 6.1 %). Climate is dry sub-humid Mediterranean with annual precipitation of 510 mm (10 % in summer, 1999-2019, Cortes de Pallás-Casa del Barón station, from the CHJ-SAIH weather network) and average temperature of 13.8 ºC (2005-2019, adjusted for the site from Requena-Cerrito station, SIAR network). The natural vegetation in this area is composed by Mediterranean ephemeral grasses, shrubs and trees that form a sparse to closed canopy depending on site conditions and previous disturbance regimes. In the reforestation area, current vegetation is mostly composed by xerophytic shrubs (*Rosmarinus officinalis, Quercus coccifera, Q. ilex, Ulex parviflorus, Thymus spp., Juniperus oxycedrus, J. phoenicea* and the grass *Brachypodium retusum)* and sparse pine trees (*Pinus halepensis* Mill. and *Pinus pinaster* Ait.) that survived the last wildfire in the early 90's.

2.2 Selected species and experimental design

A total of seven species were tested in this study (Table 1). All the species are native to the area and grow spontaneously; they were chosen for the reforestation project (709 ha) following auto-ecological and floristic-phytosociological approaches, including pines (90% of the plantation), oaks (8%), juniper (1.5%), strawberry tree and ash (<1%). These species include the most typical main and secondary species used in reforestation programs in Mediterranean areas (Vadell et al., 2016). In the experimental plot (see below), two contrasting stocklots from different forest nurseries were used in each species, in order to experimentally control this important factor on plantation establishment (Burdett, 1990). In all cases the stock was grown for use in large-scale reforestation programs and fitted in the regional quality standards (Hermoso, 2017).

To study field performance in the seven species, an experimental plot was established within the boundaries of the reforestation site. The experimental design of the plot consisted in a complete randomized block array with three blocks of 150 x 50 m each, containing a reiteration 50 plants per stocklot (150 seedlings per stocklot, 2100 seedlings in total). In a block, each stocklot was planted on a same 150 m-long row with distance between plants set at 3 meters, with the stocklots of a same species planted right next to each other. Site preparation in the experimental plot was done in the same way than in the reforestation area, consisting in the removal of pre-existing natural vegetation and opening of 40x50x50 cm (depth, width, length) planting pits by means of a backhoe excavator. Planting was done manually between late Jan-2008 and early Feb-2008 by the same planting gang, so that all planters planted same proportion of a same stocklot. Pines and juniper species were planted without treeshelter, whereas in the remaining species, a ventilated, 60 cm-tall shelter was used. Each plant was individually labeled with the species, stocklot, block and plant number.

Environmental conditions were monitored along the study period. The precipitation (P), temperature (T), relative humidity (RH) and soil moisture (SM) were recorded in the vicinity of the experimental plot for years 2008-2009 (SM only in 2008) by appropriate sensors (Davis 7852, Hobo S-THA-M002 and Decagon EC-10 for P, T/RH and SM respectively) connected to a data logger (HOBO® Micro Station H21-002) and averaged or totalized on a daily basis. P and T/RH series were gap-filled and lengthened (only T/RH) to longer periods by regressing the measured values on the corresponding series recorded in nearby observatories from SIAR and SAIH Spanish networks (r^2=0.85 and r^2=0.72 for T and RH respectively).

2.3 Traits selected and post-planting monitoring

In this study, different traits have been selected and categorized as plant functional traits (Table 2) and species functional traits (Table 3).

Individual plant functional traits. These traits were measured or estimated on each planted seedling and include morphological and early growth rates. Height (Hp, cm; vertical distance from ground to terminal leader tip) and diameter (Dp, mm; on main stem at approximately 1 cm above ground) were directly measured on each individual seedling right after out-planting (Feb-2008). From these, sturdiness index (Hp/Dp) and stem volume (Vol, cm^3) were computed; Vol was calculated as an integrated metric of seedling's size by using the formula for an elliptical cone: $V=(\pi D^2/4)H/3$ (Van den Driessche, 1992). By using Hp and Dp together with additional information gathered for each stocklot prior to planting (dry weights and image-based metrics), additional plant functional traits were estimated for each planted seedling by means of artificial neural networks (this method yielded better fit than linear allometric equations). The database used to run and validate these models included the surveyed stocklots (measured between Dec-07 and Jan-08, n = 50 per species for dry weight of foliar, shoot and root parts, and n=10 per species for foliar and root areas) plus additional cases from seedlings of the same seven species and similar stocktypes surveyed in the last 20 years by the authors (n = 2757 and 312 in total for dry weight and image-based determinations respectively), completed with additional independent variables (container volume, culturing nursery and species). The performance of the neural networks for the estimated traits was tested on random sub-samples that included the plants of this study ($r^2 > 82$ % in the testing set) and is presented in Tables SM1 and SM2. By this means, besides dry weights, foliar area (FAp, cm^2), and root area (RAp, cm^2), we calculated for each planted seedling the Dickson index (QI= total dry weight divided by the sum of shoot/root + sturdiness), the specific leaf area (SLAp, cm^2/g) and an estimator of wood density (Vol divided by the estimated stem dry weight) (Table 2). Details on the methods used for these attributes are described elsewhere (del Campo et al., 2007a,b, 2010).

Early growth-related traits derive from field assessment campaigns. These were carried out during the first two years after out-planting (Feb-2008, Jun-2008, Nov-2008, Nov-2009) and in the tenth year (Jul-2018), by repeated measurements of height, diameter and survival on all planted seedlings. Seedling growth in height, diameter and volume during the first growing season (Feb-2008 to Jun-2008), and in the first summer or drought period (Jun-2008 to Nov-2008) were computed from the difference between consecutive assessments and considered as early growth plant functional traits.

The growth was expressed as monthly absolute increments in height (cm/month), diameter (mm/month) or volume (cm^3/month) and noted as: IncH1, IncH2, IncD1, IncD2, IncVol1 and IncVol2, where 1 and 2 refer to the first growing season and first summer period respectively. Relative growth rates (RGR) were discarded for the analyses (Turnbull et al., 2008) but computed in any case in order to better frame and discuss our results in the context of previously published work.

Species functional traits. Shoot and root-related traits were also considered at the species level, given their role under drought conditions (Choat et al., 2012; Comas et al., 2013). Some of these traits were drawn from the above-mentioned database, while some others were retrieved from a literature review (Table 3), a common approach when comparing species traits (Choat et al., 2012; Bouche et al., 2014; Tavşanoğlu and Pausas, 2018; Kattge et al., 2019). In the first set, the traits considered were root fibrosity (Fib_r, % of total root length with diameter < 0.5 mm), specific root length (SRL, cm/g, calculated as the ratio of root length -RL- to root dry weight -DW_r); root average diameter (AD_r, cm); and root tissue density (RTD, g/cm^3, estimated as the ratio of DW_r to root volume, the latter calculated from AD_r and RL assuming cylindrical form of the roots). The averaged specific leaf area of the species in the database (SLAsp, cm^2/g) was also included. In the second set, the traits retrieved from the literature were: type of xylem (ring-porous, diffuse-porous and tracheid), rooting depth habit (deep, shallow), zonality to the region (zonal, intrazonal), mean diameter of early wood conduits (cond_diam, µm), water potential causing 50% loss of conductivity (Ψ_{50} or WP_PL50, -MPa), midday water potential in summer and/or on water stressed plants (Ψ_{md}, -MPa) and stomatal conductance under water stress (gs, $mmol/m^2$ s).

2.4 Data analysis

Data were quality-controlled in all cases by using spreadsheet software. Traits were grouped into root, shoot and early growth traits. The assignment of some traits combining both shoot and root attributes (i.e., QI, sturdiness index and shoot/root ratio), to the shoot or root set was done by a factor analysis using the principal component analysis extraction method. Accordingly, S/R and

H/D were assigned to the shoot set, whereas QI was to the root set. Variance explained was 86 %. Values presented are means ± SD. Artificial Neural Networks (ANN) were performed by means of the MLP (Multilayer Perceptron Network) in SPSS 22.0 (IBM Corp., 2013).

The study of importance of the different traits and other experimental factors (experimental block and stocklot) on plantation establishment was done for both survival (Nov-2008, 2009 and 2018) and early growth rates (IncH1,2; IncD1,2 and IncVol1,2). In the survival analysis, early growth rates from both the spring and the summer assessments (i.e. suffixes 1 and 2) were also included as predictor traits for survival 2009 and 2018, whereas only the spring early growth rate (suffix 1) was considered in the case of survival Nov-2008 (as summer growth was only computed on alive plants in Nov-2008). The relative importance or contribution of predictors was assessed through boosted regression tree (BRT) models performed in R software (R Core Team, 2015) using the "gbm" package (Ridgeway, 2017; Elith and Leathwick, 2017). This machine learning technique has provided clear evidence of strong predictive performance and reliable identification of relevant variables and interactions in ecological studies (Elith et al., 2008). In the BRT analysis, a Bernoulli (for survival) or Gaussian (for growth variables) distribution family, learning rates of 0.001-0.0001, tree complexity of 4-15, and bag fractions of 0.5-0.75 were considered. The minimum number of trees was in most cases above 1500. In the survival models, the area under the ROC curve was used as goodness of fit, while in the growth models the correlation coefficient was used. The results of this analysis provide the relative influence (RI) of the predictors set on the response variable (survival and growth). RI measures the number of times a predictor variable is selected for splitting, weighted by the squared improvement in the model as a result of each split, averaged over all trees, and scaled so that the sum adds to 100 (Elith et al., 2008). The higher the RI, the stronger the influence of the predictor in the response variable. For those predictors with higher RI, partial dependency plots (PDP) were produced by using the same package in R.

3. Results

3.1 Meteorological conditions during the 10-year period after out-planting

The mean precipitation in the 10-year studied period in the nearest weather station was 525 mm, higher than the 20-year (1999-2019) average (510 mm, Figure 1). These values fairly agreed with our rain gauge data at the experimental site in the common spells. Rainfall irregularity was noticeable: the first year after planting was the wettest on record (2008, 730 mm), the second one was slightly above the average (2009, 558 mm), whilst both years 2012 and 2014 accumulated less than 75% of the average. Particularly, the period from Sep- 2013 to Aug- 2014 recorded less than 200 mm, which means below 40% the average, producing a severe drought all across the region with many observatories (with much longer series) registering the driest year on record. In 2009, however, there was a shorter and acute dry spell (Apr-09 to Aug-09), with a cumulated rainfall of only 64 mm, about 35% of the 2000-2019 expected value for the same months. With regard to the temperature, mean annual temperature ranged between 12.9 ºC (2008) and 15.2 ºC (2015), with the first half of the period being colder than from year 2014 onwards (Figure 1). Soil moisture during the critical first year after planting was above wilting point in the undisturbed soil except for the expected summer months. In the planted spots, however, volumetric water content was lower due to the lower bulk density of the stirred soil (data not shown).

3.2 Species performance in the short and mid-terms: out-planting survival and growth

Survival rates across species were 88.8±11.2 %, 70.8±25.5 % and 33.0±30.0 % for years 2008, 2009 and 2018 respectively. Inter-species rates were very dissimilar: during the first two years of establishment, both oaks (QUFA, QUIL) and Maritime pine (PIPR) presented higher mortality than the remaining species, with rates close to 70 % in the case of the Lusitanian oak (QUFA, Figure 2). Flowering ash (FROR) and Strawberry tree (ARUN) showed low mortality values at the establishment stage (2008-2009, < 16 %), although it sharply increased in the mid-term assessment in 2018 (>75 %). On the other hand, Phoenician juniper and Aleppo pine showed the best performance in survival both in the short and the mid-term assessments (Figure 2).

Growth performance also varied across species and time (Figure 2). Three patterns could be observed: in the pines, both species presented the largest increments in height, diameter and stem volume that were well above the values in the remaining species. This departure took place mostly from the second year onwards (Figure 2). Second, all hardwoods showed very low growth rates and even decreasing height (FROR and QUFA also in diameter and volume), resulting in a 10-year height value lower than at planting time. In Figure 2, negative growth means that either the seedlings are top dying to resize their aerial part or that only smaller seedlings are surviving and hence the sample average decreases. Finally, the juniper showed always positive increments for the three growth variables but showing markedly lower rates than the pines.

3.3 The influence of traits on out-planting performance along time.

Several sets of variables were researched in order to explain out-planting performance: individual plant functional traits at planting time, early growth rates and species functional traits. The stocklot and the experimental blocks (considered as indicative of site variation) were also included as predictors in the BTR as control factors.

Relative importance on survival performance

The analyses performed through BRT models yielded cross-validation ROC scores that ranged between 0.77 and 0.91 for survival at years 1 and 10 respectively, while training data ROC score was always above 0.9 (Table 4), highlighting the high explicative ability of the fitted models. The set encompassing individual plant traits (root and shoot morphology and early growth rates) presented an overwhelming importance on the early survival response (1-2 years), with RI > 60 % (Figure 3, values weighted by the cv-ROC score; RI > 70 % if weighting by the training data ROC score, data not shown). Shoot and especially early growth attributes, caught most of the RI, being remarkable the impact of the first growing season growth (IncVol1, IncD1 and IncH1) on first year's survival (2008), and the impact of first summer's growth (IncH2 and, to a lesser degree, IncD2) on 2nd year's survival (2009) (Figure 4). Root attributes of the plant showed lower RI than shoot or growth traits and decreased with time (12 to 5 % for 2008 and 2018 respectively, Figure 3). Plants with higher root dry weight (DW_r) and higher average root diameter (AD_r) scored negatively in the fitted functions for survival for the first two years, i.e., presented less survival (Figure 4). The RI of plant traits in the mid-term survival, after 2013-2014's drought, decreased sharply though.

Species traits presented a very different pattern (Figure 3), with low impact on survival at the beginning of the plantation (RI ≈ 8-10 % in 2008, depending on the weighting factor), a slightly increasing value in 2009 (RI ≈ 18-20 %) and the highest RI at the mid-term survival after the drought filter had taken place, with a RI value of 53 %. It is also remarkable, the dramatic shift in RI from root to shoot species traits between the early and the mid-term assessments, which was due to the overwhelming influence of Ψ_{50} over rooting habit in 2018 (Figure 4). Rooting depth habit on second year's survival showed that deep-rooted species scored negatively in the fitted function whilst the opposite was true for shallow-rooted species (Figure 4). The control factors included in the analysis, site and stocklot, presented poor RI on out-planting performance regardless the assessment date. In the case of stock quality, this influence was higher in the first year as expected, losing importance afterwards but in any case, below 4 %. Site variation also showed little RI that decreased with time.

Relative importance on early growth performance

Early growth performance is a key indicator of plantation success and in our case these traits proved to be very influential on survival as above-mentioned. The BRT models fitted for the early growth rates yielded cross-validation (cv) correlations that ranged between 0.27 for summer's growth increments and 0.71 for the spring's increment of height (IncH1) (Table 5). These figures are lower than those observed for the survival modeling, although they increase, obviously, for the training data correlation, yielding values between 0.55 (IncD2) and 0.77 (IncVol1) (Table 5). The former correlations are indicative of the predictive ability of the models, while the latter indicate the explicative performance of the predictors set. In any case, spring's growth rates were always better explained/predicted than summer's ones (Table 5, Figure 5). The impact of plant functional traits was noticeable, with higher RI than the species functional traits, the stocklot and the site (Figure 5); in particular, the set of plant shoot traits: sturdiness, stem volume, FAp and SLAp showed marked influence on the springs' growth rates, while wood density, QI and planting height, were more associated with summer's growth (Figure 6). It can be observed also a change in the sign of the relationships (pattern in the PDP, Figure 6) between spring and summer's growth for some traits; for instance, higher stem volume enhanced IncVol1, but the opposite was true for the summer's growth (IncVol2), where a threshold of Vol $\approx$ 3 cm^3 for stem volume was identified. Sturdiness values above 7-8 scored positively in IncD1 but negatively in IncH1, as expected (slender plants preferably develop their root system). In general, spring's growth was enhanced in plants exhibiting higher value in shoot traits such as SLAp, FAp and Vol.

Species traits presented little importance on the early growth performance (between 0-25 %, weighted by the cv, Figure 5) with conduit diameter, xylem type and SRL standing out in height or diameter increment in the first growing season (Figure 6). Thus, tracheid-bearing species with smaller conduit diameter scored negatively on IncH1, whereas SRL > 1000 cm/g scored positively on the function fitted for IncD1 (Figure 6). It must be reminded that 2008 was the wettest year in the series. Stock quality and site factors had low RI on all growth rates (0-6 %, Figure 5), although one model identified block 3 with higher growth rates.

4. Discussion

The results presented in this work, yet a single study case, allow for an objective assessment about forest landscape restoration (FLR) in drylands in the face of novel and future climatic extremes. In this discussion we firstly make a general assessment of the species' performance and then we move from a species-centered narrative towards a trait-centered view, where the different water stress strategies are used as a framework to better address site-species matching under novel climates.

4.1 Species' performance assessment

Our results show important differences in performance among the different species planted in this dryland ten years after out-planted and exposed to extreme drought. The poor performance observed for some species has an impact that goes beyond our experimental plot to the whole planted area (709 ha) and to the practice of reforestation itself in the Eastern part of Spain, with about 5,700 ha reforested in 2008 in the Valencian region with a mix of conifers and hardwoods at an average cost of ca. 2,000 €/ha (MAPA, 2019). Species selection in forest restoration is a crucial step or decision taken in regeneration plans and technical projects (Dougherty and Duryea, 1991) and the results presented here underline the need of including novel climatic extremes as limiting factors that eventually condition successfulness in drylands reforestation programs. The arising question is whether traditional criteria for selecting species are still valid under current and future climates (Williams and Dumroese, 2013).

The seven species selected in this work were those included in the technical reforestation project, all of them native to the zone and already present in the vicinity of the experimental plots, thus, there is evidence that the seven species grow naturally under the same environmental conditions than planted trees. In fact, early performance results can be considered as very good in most species when compared to those reported for the same species under similar site and climatic conditions. For instance, in Aleppo pine, two-year survival in six contrasting sites of Valencia ranged between 12 % and 99 % (89 % in this study) (del Campo et al., 2007a). Regarding growth, first year growth rates for diameter and height across those six sites averaged respectively (this study's values between parenthesis): 0.16 (0.32) and 0.82 (0.93), all values as month^{-1}, indicating higher growth in this work. Longer periods' works (Pausas et al., 2004; del Campo et al., 2008c) have reported averaged (across several sites) survival between 40 and 65 % after 7.5-11 years (70 % in this work); and plants of 210 cm tall (139 cm here) and 8.7 cm of basal diameter (5.5 cm here), these figures of growth out of several afforestation programs carried out in central Spain during 1994.

PIPR presents a scattered distribution mostly limited by water availability, alkaline soils and forest fires, presenting very low natural recruitment rates (Vizcaíno-Palomar et al., 2014). Previous records for the province of Valencia (del Campo et al., 2005a, 2005b, 2008a, 2008b; del Campo and Segura, 2009) reveal poor early plantation performance with mean survival of 50 % (±37 %), similar to the one recorded in this study in 2009. However, filtering in those records for clay, shallow and limestone-derived soils (similar site conditions to La Muela), that average drops to survival rates less than 20 %, pointing out a higher early survival in this work and the same can be said for early growth. However, 10-year's survival rate in this work is unacceptable and prevents about the use of this species. Higher survival both in this species (60 %) and Holm oak (92 %) has been reported in a nearby location after 40 months (Valiente et al., 2011). The most remarkable issue about this species is its contrasted response between growth and survival, with very low survival (11 %) but the highest growth increments (volume and diameter) in the surviving plants after 10 years out-planted (Figure 2). The reasons of this behavior cannot be explicitly addressed within our experimental setup, but we reasonably argue in Supplementary Material (SM1) that they could be explained by pH-related factors operating at the microsite (planting spot) scale.

In this work, Holm oak early survival (2009: 58 %) and growth are comparable to or slightly better than those reported elsewhere (Pausas et al., 2004; Palacios et al., 2009), demonstrating the fitness of the species to the site in absence of extreme drought. Very low survival values are common for this species during the first years of establishment (Navarro-Cerrillo et al., 2009; del Campo et al., 2010; Ceacero et al., 2012, 2014) and it has been recognized its poor performance when planted on limestones and exposed to severe drought, with survival rates close to 15 % (Pausas et al., 2004), similar to the value reported here. Ten-year's survival in central Spain was around 40-45 %, height of 90 cm and basal diameter of 3.5 cm (del Campo et al., 2008c), clearly above the values reported here (Figure 2) and evidencing a failure on the selection of this species.

The information published for the remaining species is scarcer even for short-term assays, so we will make use of our database (del Campo et al., 2008a, 2008b; del Campo and Segura, 2009) and cite existing literature whenever it is relevant to our conditions. QUFA performance was the worst among the seven species tested, either for growth or survival, and either in the short or the long run (Figure 2). The species belongs to a marcescent, sub-sclerophyllous forest-type, typical from continental climates, although it can grow in intrazonal domains associated either to soil or topography (Ruiz de la Torre, 2006). This would be the case in the area studied here, where it is native and grows nearby the experimental plots, although it is mostly found on north-facing slopes. Plantation trials with this species in zonal sites reveal high survival (>80 %) and growth (stem volume >5 cm^3) after 5-year in the field (Villar-Salvador et al., 2013); or 2-year's survival > 70 % in a terrace plantation (Domínguez-Núñez et al., 2006). Our database for Valencia (del Campo and Segura, 2009) gives an average survival of 73 % and 43 % for first and second year respectively, thus confirming the inadequacy of the species to this site.

Establishment of ARUN on similar sites can be very variable, with survival averaging 72 % and 31 % for first and second year respectively (del Campo et al., 2008a; del Campo and Segura, 2009) (95% and 85% in our plot, respectively), and average relative growth rate for the first two years of 0.020 and 0.012 month^{-1} for H and D respectively (0.038 and 0.045 month^{-1} in our plot respectively), thus indicating a superior early performance at La Muela experimental site but also the high impact of droughts on the mid-term performance. Very similar assertion can be done for the ash (FROR): good early establishment but severely affected by mid-term drought. The values reported for this species are scarce given its little use in forest restoration (<1% in mixed plantations, given its intrazonal character), but some works report very good early performance in plantation with almost full survival rates, which may remain above 80% after ten years and cumulated height of 130 cm by that time (del Campo et al., 2012; Muzzi and Fabbri, 2007).

Finally, the JUPH has been commonly assayed in semiarid drylands under more xeric conditions than in this study (Alrababah et al., 2008; Padilla et al., 2009, 2011), with absolute survival values usually below 45 % in early establishment stages, but relatively high survival when compared with other co-assayed species. Under dry sub-humid conditions (this site) survival rate increases as observed in our database (67 and 51 % for first and second year respectively) and in North Eastern Spain (Badía et al., 2007), with 70 and 62 % survival for second and tenth year respectively. These authors also reported 10-year height growth in this juniper which is equivalent in relative terms to ours. Hence, it can be argued that this species has presented a good performance in our study site either at the short or the mid-term.

4.2 Looking beyond the taxon: traits-based performance assessment

Previous rationale provides a qualitative, taxon-based assessment of the plantation that can have limited utility beyond our ecoregional context or under new drought regimes. Given the co-occurrence of all studied taxa in the area, differences observed in performance must have relied necessarily on the wide variation of morphological, physiological and hydraulic traits facing drought and water stress among species (Brodribb et al., 2014; Pratt et al., 2015; Garcia-Forner et al., 2017). Relating field performance in our species to these strategies (Table 6) can have a more meaningful application of our results elsewhere. Angiosperms are usually more exposed to xylem failure during drought (Choat et al., 2012; Johnson et al., 2012), being embolism the final cause of mortality. This rationale fits to our experimental data, as angiosperms presented lower fitness than conifers and less potential for adaptation to extreme drought. The four angiosperms assayed here presented evidence of runaway xylem cavitation and partial recovery capability as observed on the re-sprouting either from shoot (presenting dead tops) or root (Figure SM3) which resulted in lower 10-year final height than at planting time (Figure 2). Re-sprouting for ARUN, FROR, QUFA and QUIL in 2009 reached 23, 2, 41 and 17 % of surviving seedlings respectively, whilst in 2018 these figures rose up to 83, 47, 100 and 26% (data not shown). Given the high mortality after 10-year in the four angiosperms, the assessment of field performance is more meaningful in the early establishment stage, when most differences among species came up. Here, both oaks showed high mortality as opposed to FROR and ARUN. According to the species functional traits compiled for this study (Table 6), both oaks possess deep root systems (as indicative of predictable water supply), wider xylem vessels and higher stomatal conductance under water stress than the other angiosperms tested. Also, in QUFA previous work has observed that the diameter of earlywood vessels has little climate sensitivity (Corcuera et al., 2004), affecting its capability to adjust the diameter of vessels to soil moisture availability, which would be disadvantageous in shallow-rooted seedlings planted on shallow soils, and would explain why this species suffered high mortality from the very beginning. Similarly, holm oak is a species with high vulnerability to xylem embolism and low recovery capacity of embolized vessels (Trifilò et al., 2015; Martínez-Vilalta et al., 2003). Garcia-Forner et al. (2017) have studied the response of this species to experimentally induced severe and recurrent drought in deeper soils and reported mortality rates lower than 20 % and re-sprouting recovery capacity. In our case, the high mortality and the low re-sprouting values, underlie the intensifying effect of the drought on shallow soils, this aggravated by the use of shallow-rooted stock, that ends up preventing access to deep soil moisture and mismatching the species' strategy to water shortage. Our BRT model for survival in 2009 confirmed that deep-rooting species survived less in this site because of the shallow soil and the stock (necessarily short-rooted). Summarizing for oaks, deep-rooting habit, vulnerable xylem (wider vessels), relatively high gs under water stress, and the extreme level of water deficit (2013-2014) are the combination of factors that led to poor performance from the very beginning. It has been reported that limestone, clay, rocky and shallow soils as those found in our study site can hold as little as 19 mm of available water (Serrasolses and Alloza, 2004). ARUN, although vulnerable to cavitation (Table 6), presents lower conduit diameter either in roots or stems and lower hydraulic and stomatal conductance than Holm (Martínez-Vilalta et al., 2003), thus explaining its better early performance. These traits match its shallow rooting habit and allow for an improved water-stress response; also, root re-sprouting was high in this species, which in turn improves water relations and growth more than in mature tissues (Castell et al., 1994). FROR has also been reported to have reduced leaf hydraulic and stomatal conductance (Gortan et al., 2009) under low water availability, with lower values than Holm oak (Fusaro et al., 2017). Also, it possesses safety xylem traits such a large safety margin (≈ 1.5–2.0 MPa) and high wood density (Petruzzelli et al., 2019) conferring a good drought response in overall. In both species (ARUN and FROR), lower gs under water stress, together with small conduit diameter and shallow-rooting habit might have played a role in their better early survival rates. However, none of these traits was enough to overcome the 2014's drought.

Conifer species clearly differed from angiosperms, with no height decrease in the 10-year study period, implying that xylem hydraulic functionality was preserved, and no runaway cavitation took place in the alive seedlings, although growth was very different between both genera. Juniper species usually present very high resistance to xylem cavitation (Martínez-Vilalta et al., 2003, Brodribb et al., 2014), which is related to narrow mean tracheid lumen, high wood density (Oliveras et al., 2003; Pratt et al., 2015) and especially to the degree of torus-aperture overlap (i.e. the ratio of the torus diameter to pit aperture diameter) (Delzon et al., 2010; Pittermann et al., 2010). In PIHA and JUPH similar tracheid diameters have been reported (Table 6, Mohareb et al., 2016). The pit membrane resistivity has been stressed as the key trait that ultimately determines the air-seeding resistance of torus-margo pit membranes and allows juniper species to grow competitively in very xeric areas (Pittermann et al., 2010). These authors reported torus-aperture overlapping values close to 2 for other *Juniperus sp.* and demonstrated its increasing value with more negative cavitation pressure. However, high torus-aperture overlap values have been also observed in PIHA, between 1.6 (Delzon et al., 2010) to more than 3 (David-Schwartz et al., 2016). Pine species possess higher tracheid lumen (Oliveras et al., 2003) and mostly rely on a strong stomatal control of transpiration to overcome water stress (Martínez-Ferri, et al., 2000; Baquedano and Castillo, 2006; Table 6), mediated by abscisic acid (ABA) metabolism (R-Type Gymnosperm, according to Brodribb et al., 2014). Accordingly, both juniper and Aleppo pine rely on different strategies to cope with water shortage and both resulted in successful fitness under the ecological constraints observed in this work. The Junipers' strategy is advantageous under extremely water-limited environments and has costs associated with building highly cavitation-resistant xylem and desiccation-tolerant leaves (Brodribb et al., 2014). However, this extreme does not seem the only alternative here, as the threshold identified in our BRT model for Ψ_{50} is slightly below that of the Aleppo pine (-4.8 MPa), so that, under the extreme climate observed here, there is ecological space for the pine's strategy too, with less conservative growth traits and a more efficient use of resources (e.g. higher SLA) (Wright et al., 2004). It must be said, however, that the importance of the selected traits grounds not on the magnitude considered here, but on the selection of a particular trait in discriminating species' performance under severe drought events and the RI value assigned to it in the BRT analysis; Table 6 is a clear example on the variability of magnitudes found in the literature (see for instance Ψ_{50} in PIHA and QUIL, that averages -4.8 and -4.0 MPa respectively across studies).

Conclusions

Emerging circumstances derived from global change imparts high uncertainty regarding future condition (ecological and societal) of forest ecosystems to be restored (Jacobs et al., 2015). Thus, forest managers must make decisions efficiently based on incomplete information and in a context of great uncertainty. One important question to address is whether ecological or phytosociological criteria based on historical conditions are still valid to select species. Here we have demonstrated that the suite of species incorporated in restoration programs should be enhanced in terms of functional resilience to emerging environmental conditions. Whist plant functional traits were important in plantation performance under normal conditions, their importance sharply dropped in favor of the species functional traits after a historical drought took place. Thus, a trait-oriented approach to select species might represent a key tool in achieving the adaptive forest restoration targets in a climate change context. According to reviewed data and the evidence of our results, the dynamic response of stomata and xylem traits are the set of PFT that allowed the assayed species with the capacity to adjust their morphology and physiology in response to varying environmental factors and especially to water availability. Conifer species clearly differed from angiosperms. The suite of factors that led to poor performance in oaks were deep-rooting habit, vulnerable xylem, relatively high gs under water stress, and the extreme level of water deficit. In contrast, conifer seedlings preserved xylem hydraulic functionality and no runaway cavitation took place, although growth was very different between genera. Our experimental data revealed that angiosperms presented lower fitness to the planting site conditions than conifers and less potential for adaptation to extreme drought.

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TABLE CAPTIONS

Table 1. Species and provenances used in this work

Table 2. Individual plant functional traits used in this work, with the across-species range and mean, and the species average and standard deviation. Height (Hp, cm); Sturdiness (HDp, cm/mm); Foliage dry wt., (DW_f, g); Shoot dry wt., (DW_s, g); Total dry wt., (DW_t, g); Shoot/root (S/R); Foliar area, (FAp, cm^2); Specific leaf area, (SLAp, cm^2/g); Stem volume, (Vol, cm^3); Wood Density (WD, g/cm^3); Basal diameter, (Dp, mm); Root dry wt., (DW_r, g); Dickson index (QI); and Root area (RAp, cm^2). Dry weights (DW), SLAp, FAp and RAp estimated with the use of artificial neural networks, ann (SLAp was also estimated as the ratio FAp/DW_f).

Table 3. Species functional traits used in this work. Specific leaf area (SLA_sp, cm2/g), specific root length (SRL, cm/g), root tissue density (RTD, g/cm3), root average diameter (AD_r, cm), root fibrosity (Fib_r, %), mean diameter of early wood conduits (cond_diam, µm), water potential causing 50% loss of conductivity (Ψ50 or WP_PL50, -MPa), midday water potential under water stress (Ψmd, -MPa) and stomatal conductance under water stress (gs, mmol/m2 s). Values for the categorical traits (type of xylem, rooting depth and zonality), are presented in Table 6 together with the references. The species average and standard deviation is presented for the figures retrieved

from the author's database. The dataset was obtained after several years of implementing reforestation improvement programs in the region of Valencia. Image analysis for foliar area and root morphology performed as described in del Campo et al., (2007a, 2007b).

Table 4. Summary of the Boosted Regression Trees (BTR) models fitted for survival in the first (2008), second (2009) and tenth (2018) year after out-planting. In BRT, the measure of model fit is the total % deviance explained and model predictive performance (the mean CV correlation coefficient of observed vs predicted values derived from 10 folds). Cross-validation correlation coefficients were used to weight the relative importance of the predictors. se: standard error of the coefficients. ROC: area under the ROC curve (0-1).

Table 5. Summary of the Boosted Regression Trees (BTR) models fitted for traits of early growth performance: monthly increment in diameter (D), height (H) and stem volume (Vol) either in the spring after planting (1) or in the first summer (2). Cross-validation correlation coefficients were used to weight the relative importance of the predictors. se: standard error of the coefficients.

Table 6. Morphological, physiological and hydraulic traits retrieved from the literature used to relate drought and water stress strategies of the species to field performance. Type of xylem: RP: ring-porous, DP: diffuse-porous and T: tracheid. Ψ_{50}, water potential causing 50% loss of conductivity. Ψ_{md} midday water potential in summer and/or water stressed plants. gs, stomatal conductance under water stress. (1) in *Juniperus* sp. (2) pre-dawn water potential.

FIGURE CAPTIONS

Figure 1. 12-moths (Sep-Aug) cumulated precipitation gathered at Cortes de Pallás-Casa del Barón weather station (CHJ, MITECO) for the last 20 years, showing the extreme meteorological drought in 2013-2014. The inset represents mean and total precipitation and average temperature values for the years in this study (2008-2018).

Figure 2. Mean species value of mortality (%), height (cm), diameter (mm) and stem volume (cm^3) along the 10-year period studied for field performance. In 2008 (planting year), both the spring and the summer performance values are shown. Figures outside the bars (open dots), indicate final (2018) values. Bars correspond to standard deviations.

Figure 3. Relative importance (RI, %, obtained from BRT models) of the different sets of traits and independent variables on plantation survival (for 2008, 2009 and 2018). The set of predictors for survival are site (or experimental block), stock quality (stocklot), individual plant functional traits (grouped in shoot, root and early growth performance) and species functional traits (grouped in shoot and root). Partial dependence of the 4 highest-ranked predictors (higher relative importance in the BRT models) are presented in Figure 4.

Figure 4. Partial dependence plots (PDP) for the of the 4 highest-ranked predictors (higher relative importance in the BRT models) on plantation survival performance (2008, 2009 and 2018). The Y axis is centered to have zero mean over the data distribution and spans the same range (in units of logit(p) from the mean predicted response value) across all plots to make the magnitude of the effects comparable among predictors. X-axes show rug plots that visualize the distribution of the respective data space in deciles, in order to avoid overinterpreting regions with almost no data. Note (*): WP_PL50* in -MPa; ann* = artificial neural network

Figure 5. Relative importance (RI, %, obtained from BRT models) on the early-growth performance (increments in diameter, height and volume) in the first growing season (1) and in the first summer (2) after planting of the different sets of traits and independent variables. The set of predictors for the early growth response are site (or experimental block), stock quality (SQ, stocklot), individual plant functional traits (grouped in shoot and root, Pt_s and Pt_r respectively) and species functional traits (grouped in shoot and root, Sp_s and Sp_r respectively). Partial dependence for the most influential independent variables presented in Figure 6.

Figure 6. Partial dependence plots (PDP) for the four most influential variables or predictors

(higher relative importance in the BRT models) on early growth performance: diameter growth in the first spring and first summer after planting (ΔD1 and ΔD2 respectively), height growth in the first spring and first summer after planting (ΔH1 and ΔH2 respectively) and volume increment in the first spring and first summer after planting (ΔVol1 and ΔVol2 respectively). The Y axis is centered to have zero mean over the data distribution and spans the same range (in units of standard deviation from the mean predicted response value) across all plots to make the magnitude of the effects comparable among predictors. X-axes show rug plots that visualize the distribution of the respective data space in deciles, in order to avoid overinterpreting regions with almost no data. Note (*): WP_PL50* in -MPa; ann* = artificial neural network

Table 1.

Scientific name	**Common name, number of stocklots planted in this work (Code)**	**Provenance**
Arbutus unedo L.	Strawberry tree, 2 (ARUN)	E-25 Range Iberic Meridional
Fraxinus ornus L.	Flowering ash, 1 (FROR)	Range Iberic of Valencia
Juniperus phoenicea L.	Phoenician juniper, 2 (JUPH)	E-25 Range Iberic Meridional
Pinus halepensis Mill.	Aleppo pine, 3 (PIHA)	ES-10 Eastern inland
Pinus pinaster Ait.	Maritime pine, 2 (PIPR)	ES-16 East
Quercus faginea Lam.	Lusitanian oak, 2 (QUFA)	ES-10 Alcarria Serrania Cuenca
Quercus ilex subsp. *ballota* (Desf.) Samp.	Holm oak, 2 (QUIL)	ES-12 La Mancha-Montiel

Table 2.

Trait type	Abbrev.	All species [range]mean	ARUN	FROR	JUPH	PIHA	PIPR	QUFA	QUIL
Shoot	Hp	[1.1,62]17.7	16.2±8.7	15.2±4.8	12.7±3.3	17.6±4.5	17.8±6.3	26±15	15.1±7.2
	HDp	[0.7,22.5]6.5	6.2±2.2	3.2±1.2	8.7±3.8	7.5±2.8	6.9±2.7	7.3±3.7	4±1.6
	DW_f	[0.01,2.88]0.76	0.83±0.37	0.42±0.23	0.45±0.18	0.77±0.27	1.01±0.45	0.61±0.42	0.95±0.53
	DW_s	[0.01,6]1.28	1.39±0.73	1.07±0.65	0.72±0.35	1.09±0.33	1.4±0.57	1.64±1.24	1.45±0.91
	DW_t	[0.16,12.31]2.69	1.9±0.96	2.81±1.52	1.58±0.62	2.02±0.54	2.2±0.72	4.65±2.63	3.47±1.95
	S/R	[0.18,6.39]1.2	2.75±0.74	0.61±0.13	0.84±0.3	1.16±0.14	1.72±0.42	0.48±0.17	0.69±0.09
	FAp	[0.01,171]51	59±28		10±5	55±18	57±30	60±27	50±24
	SLAp	[1,436]69	67±20		23±8	74±13	54±16	123±63	56±12
	SLAp_ann	[18,114]70	88±5		24±6	83±13	69±16	87±8	51±6
	Vol	[0.01,9.56]0.56	0.4±0.36	1.35±1.12	0.11±0.11	0.3±0.15	0.37±0.2	1.09±1.15	0.66±0.58
	WD	[0.1,12]1.4	2.1±1.4	0.5±0.1	2.8±1.1	1.2±0.6	1.2±0.4	1.1±0.4	0.9±0.3
Root	Dp	[0.5,14.2]3	2.6±1	5.3±2.1	1.7±0.7	2.5±0.6	2.6±0.6	3.5±1.1	3.8±0.9
	DW_r	[0.02,6.33]1.41	0.5±0.25	1.72±0.9	0.86±0.33	0.93±0.22	0.8±0.17	3.02±1.41	2.02±1.05
	QI	[0.01,4.66]0.45	0.23±0.18	0.92±0.74	0.22±0.15	0.26±0.13	0.3±0.18	0.63±0.31	0.75±0.39
	RAp	[53,404]193	175±56		222±44	188±45	249±53	172±78	163±56

Table 3.

Species traits	Values retrieved from authors' database (similar seedlings and stocktypes)							Values retrieved from the literature (averaged from table 6)			
	Total seedlings (Stocklots), n^{o}.	Plants with image analysis n^{o}.	SLA_sp	SRL	RTD	AD_r	Fib_r	cond_diam,	Ψ_{50},	Ψ_{md},	gs
ARUN	765(8)	15	47.6±14.3	695±517	.76±.32	.057±.01	71±9	35	3.1	4	20
FROR	298(3)	10	51.6±5.3	1122±74	.44±.11	.052±.01	69±13	35	3.3	1.8	40
JUPH	383(6)	18	19.9±9.3	954±385	.71±.71	.053±.01	66±5	22	8	6.5	30
PIHA	10660(64)	264	69.9±20.5	1315±461	.40±.23	.058±.02	55±19	20	4.8	0.75	13
PIPR	2470(16)	56	67.4±16.6	1138±153	.20±.05	.077±.01	50±9	19	3.7	1.65	28
QUFA	794(7)	15	84.2±7.9	288±37	.91±.47	.076±.02	75±6	70	3.4	3.4	65
QUIL	4194(34)	142	46.4±12.8	262±68	1.44±.52	.061±.01	70±5	80	4.0	2.85	65
Total	19564(520)	520									

Table 4.

Survival	N^{o}. of trees	Mean total deviance	Mean residual deviance	Estimated cross-Validation deviance (se)	Training data ROC score	Cross-Validation ROC score (se)
2008	2150	0.721	0.492	0.643(0.011)	0.908	0.763(0.013)
2009	4200	1.231	0.576	0.791(0.023)	0.949	0.873(0.008)
2018	8600	1.251	0.666	0.71(0.02)	0.920	0.910(0.007)

Table 5.

	No. trees	Mean total deviance	Mean residual deviance	Estimated cross-Validation deviance (se)	Training data correlation	Cross-Validation correlation (se)
Inc_D1	1450	0.042	0.020	0.025(0.001)	0.733	0.633(0.014)
Inc_D2	3350	0.023	0.018	0.022(0.003)	0.551	0.273(0.033)
Inc_H1	3650	3.210	1.643	2.122(0.204)	0.711	0.586(0.013)
Inc_H2	2050	1.205	0.929	1.115(0.250)	0.574	0.270(0.038)
Inc_Vol1	1050	0.056	0.024	0.034(0.003)	0.768	0.632(0.014)
Inc_Vol2	1300	0.048	0.036	0.045(0.011)	0.604	0.272(0.044)

Table 6

	ARUN	FROR	JUPH	PIHA	PIPR	QUFA	QUIL
Type of xylem	DP	RP	T	T	T	RP	DP
Mean diam. of early wood conduits, µm	20-50[a]	20-50[a]	22[b]	17[z], 22[b]	19[c]	70[d]	50-100[a], 80[e]
Vessels/mm^2	>200[a]	50-100[a]				90[a], 95[d]	5-20[a], 73[v]
Inter-conduit pit membrane diam, µm	>10[a]	4-7[a]		2[z] (0.6 torus to pit apert. overlap)	3.2[x]		4-7[a]

$\Psi50$, -MPa	3.1[f]	3.3[g]	> 8 [f,h(1)]	3.1-6.0[h,s,w,z]	3.7[h]	3.4[i]	2.0-6.0[f,j,ae]
Ψ_{md}, -MPa	4.0[k]	1.8[g]	3.6[q], 7.5[l]	0.7[q], 0.8[aa]	0.5[ab(2)], 1.5[t], 2.1-2.5[y,u]	3.4 [m]	1.9[q], 3.0[k], 3.5[n,m]
gs, mmol m^{-2} s^{-1}	≈ 20[f,k]	15[p], ≈40[o], 514[g]	≈27[q], ≈35[r]	≈15[q], ≈12[r]	≈20[t], 36[u]	≈ QUIL[m]	≈40[o], ≈50[q], ≈65[k], ≈75[r]
Rooting depth	Shallow[k]	Shallow[g]	Shallow[l]	Shallow[ac, ad]	Deep[ac,ad]	Deep[d]	Deep[k]
Intrazonal to this site (soil/ topography)	No	No	No	No	Yes (low soil pH)	Yes (N-facing slopes)	No

(a) Crivellaro and Schweingruber (2013); (b) Mohareb et al., (2016); (c) Vieira et al., (2014); (d) Corcuera et al., (2004); (e) Abrantes et al., (2013); (f) Martínez-Vilalta et al., (2003); (g) Petruzzelli et al., (2019); (h) Delzon et al., (2010); (i) Gil-Pelegrín et al., (2017); (j) Martin-StPaul et al., (2014); (k) Castell et al., (1994); (l) Castillo et al., (2002); (m) Mediavilla and Escudero (2004); (n) Garcia-Forner et al., (2016); (o) Fusaro et al., (2017); (p) Gortan et al., (2009); (q) Baquedano and Castillo (2006); (r) Martínez-Ferri et al., (2000); (s) Oliveras et al., (2003);(t) Picon et al., (1996); (u) Fernández et al., (2000); (v) Robert et al., (2017); (w) Froux et al., (2002); (x) Bouche et al., (2015); (y) Aussenac and Valette, (1982); (z) David-Schwartz et al., (2016); (aa) Melzack et al., (1985); (ab) del Campo et al., (2005); (ac) Ruiz de la Torre, (2006); (ad) Andivia et al., (2019); (ae) Peguero-Pina et al., (2014)

FIGURES

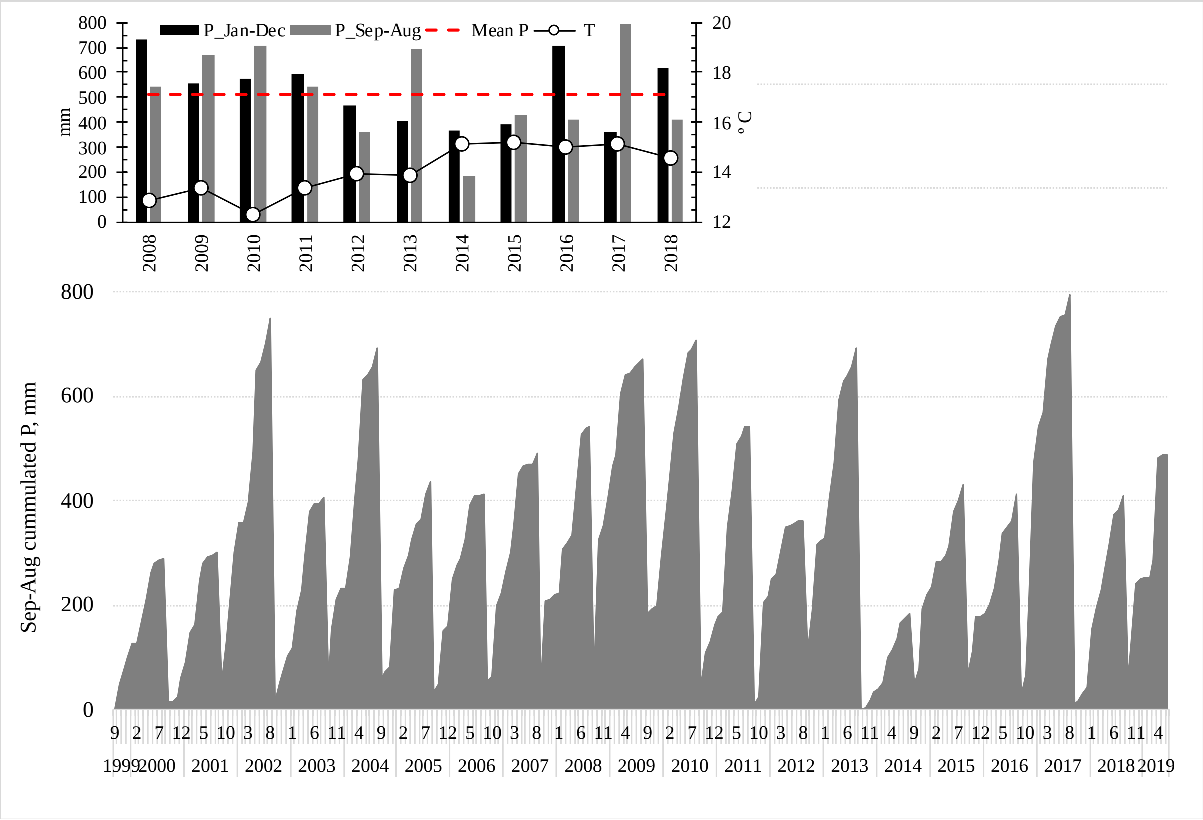

Figure 1. 12-moths (Sep-Aug) cumulated precipitation gathered at Cortes de Pallás-Casa del Barón weather station (CHJ, MITECO) for the last 20 years, showing the extreme meteorological drought in 2013-2014. The inset represents mean and total precipitation and average temperature values for the years in this study (2008-2018).

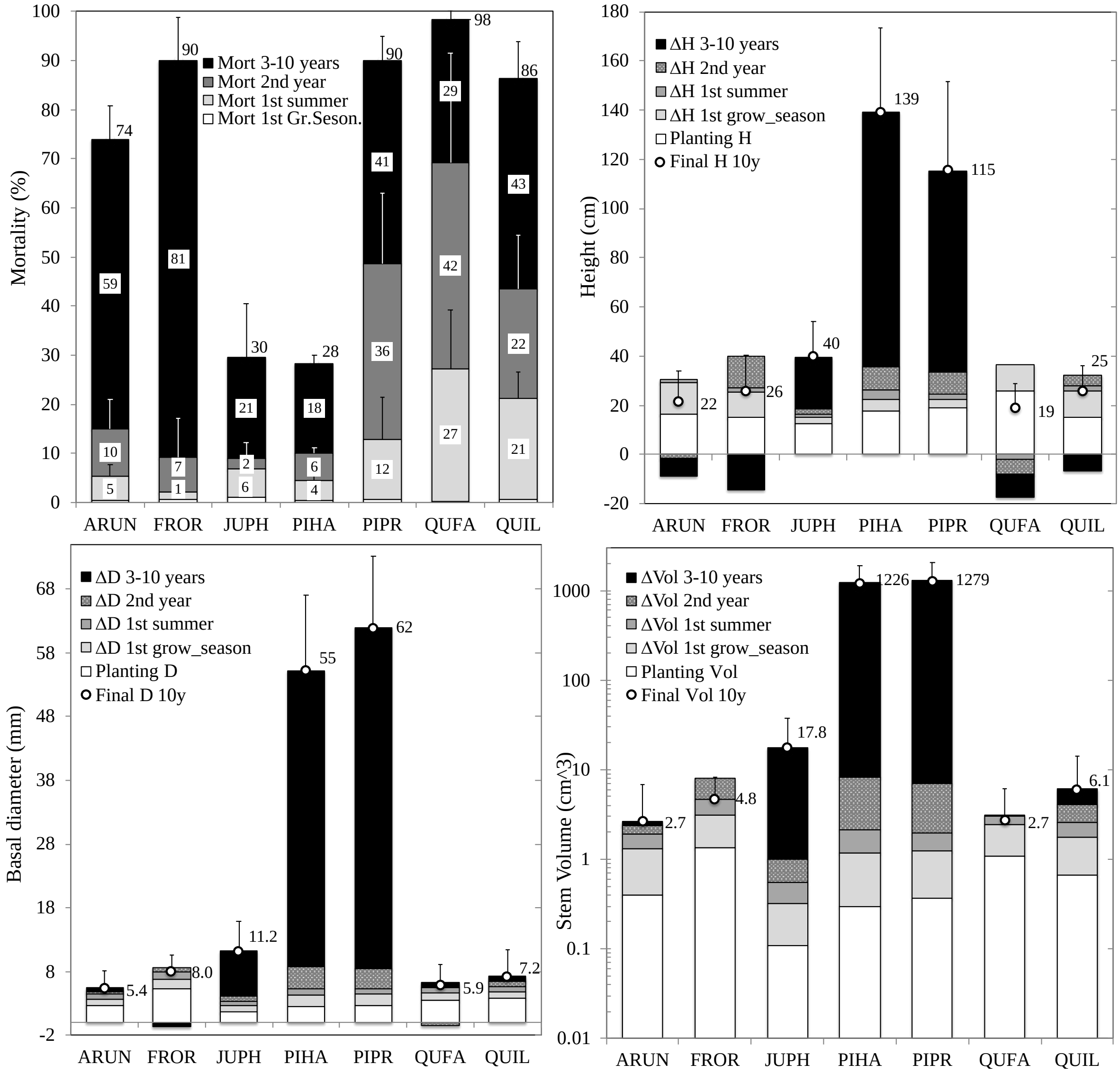

Figure 2. Mean species value of mortality (%), height (cm), diameter (mm) and stem volume (cm^3) along the 10-year period studied for field performance. In 2008 (planting year), both the spring and the summer performance values are shown. Figures outside the bars (open dots), indicate final (2018) values. Bars correspond to standard deviations.

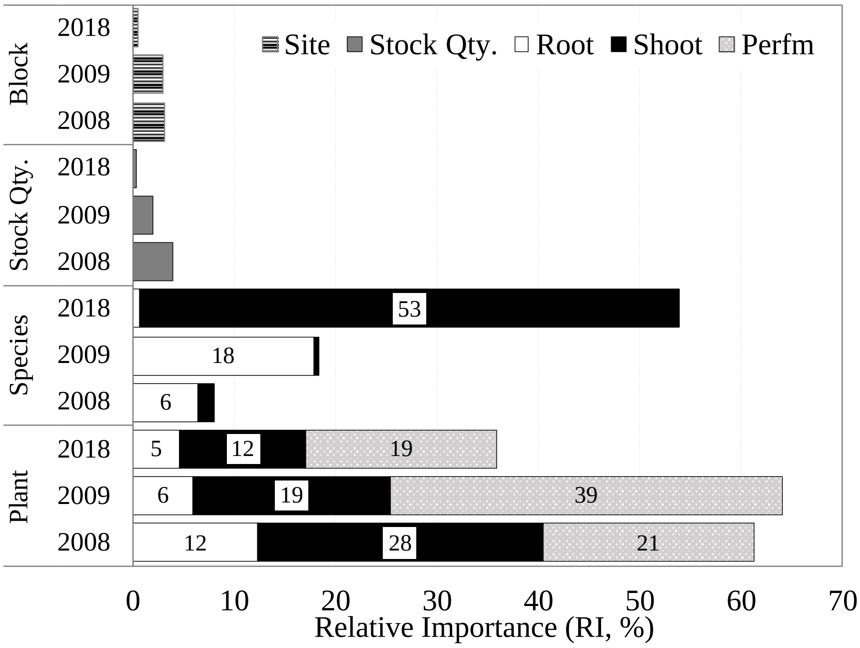

Figure 3. Relative importance (RI, %, obtained from BRT models) of the different sets of traits and independent variables on plantation survival (for 2008, 2009 and 2018). The set of predictors for survival are site (or experimental block), stock quality (stocklot), plant traits (grouped in shoot, root and early growth performance) and species traits (grouped in shoot and root). Partial dependence of the 4 highest-ranked predictors (higher relative importance in the BRT models) are presented in Figure 4.

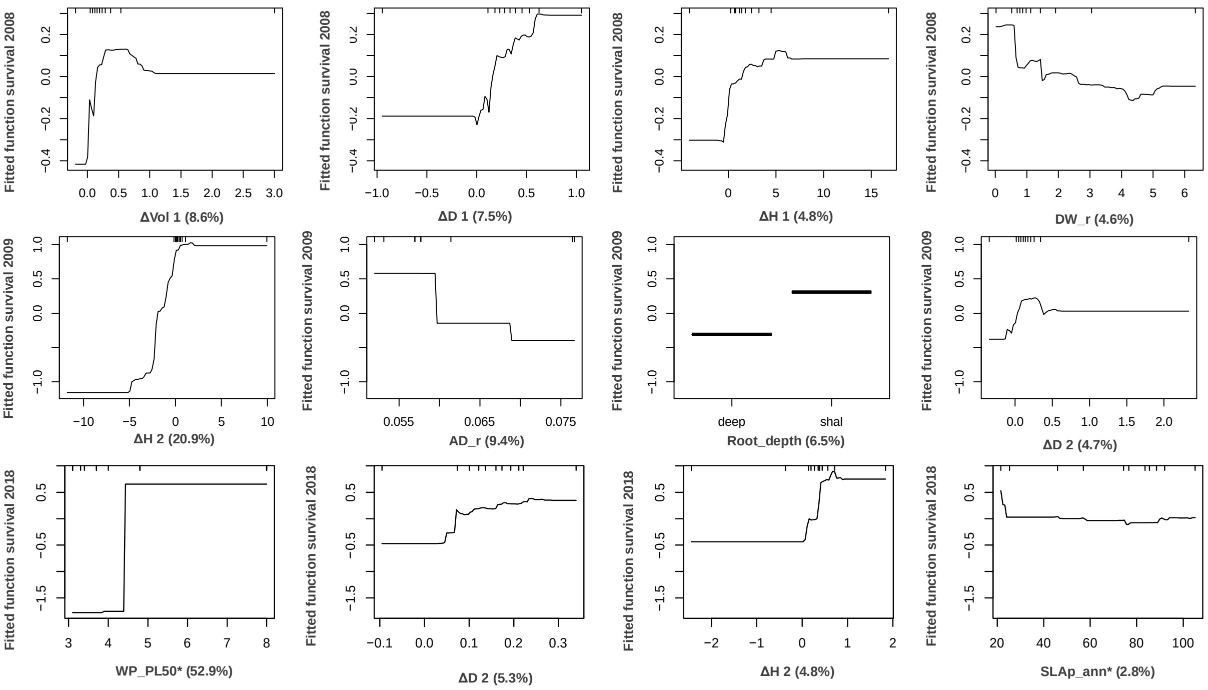

Figure 4. Partial dependence plots (PDP) of the 4 highest-ranked predictors (higher relative importance in the BRT models) on plantation survival performance (2008, 2009 and 2018). The Y axis is centered to have zero mean over the data distribution and spans the same range (in units of logit(p) from the mean predicted response value) across all plots to make the magnitude of the effects comparable among predictors. X-axes show rug plots that visualize the distribution of the respective data space in deciles, in order to avoid overinterpreting regions with almost no data. Note (*): WP_PL50* in -MPa; ann* = artificial neural network

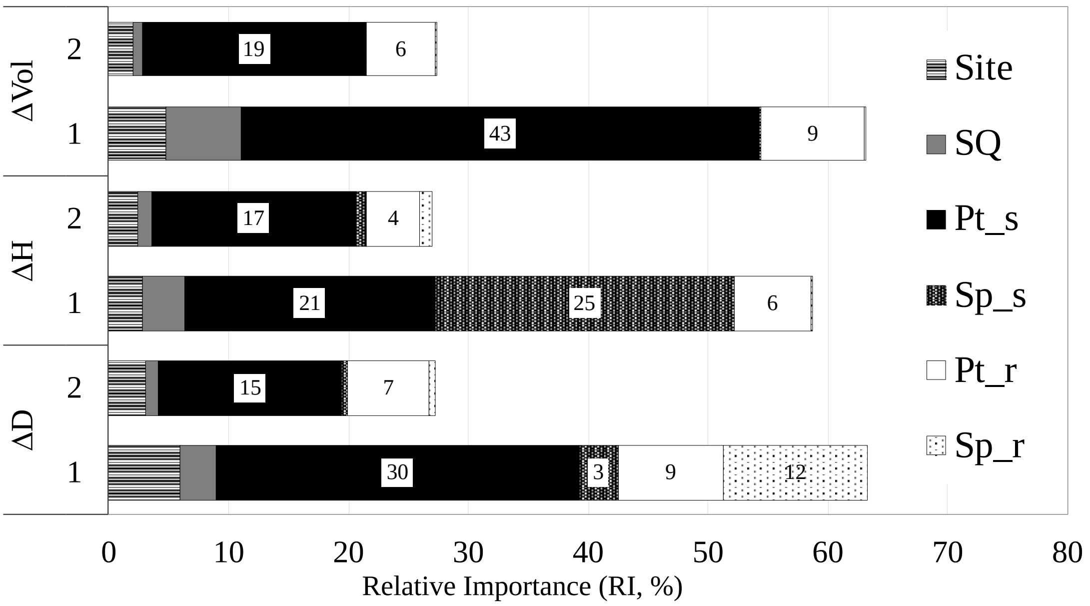

Figure 5. Relative importance (RI, %, obtained from BRT models) on the early-growth performance (increments in diameter, height and volume) in the first growing season (1) and in the first summer (2) after planting of the different sets of traits and independent variables. The set of predictors for the early growth response are site (or experimental block), stock quality (SQ, stocklot), plant traits (grouped in shoot and root, Pt_s and Pt_r respectively) and species traits (grouped in shoot and root, Sp_s and Sp_r respectively). Partial dependence for the most influential independent variables presented in Figure 6.

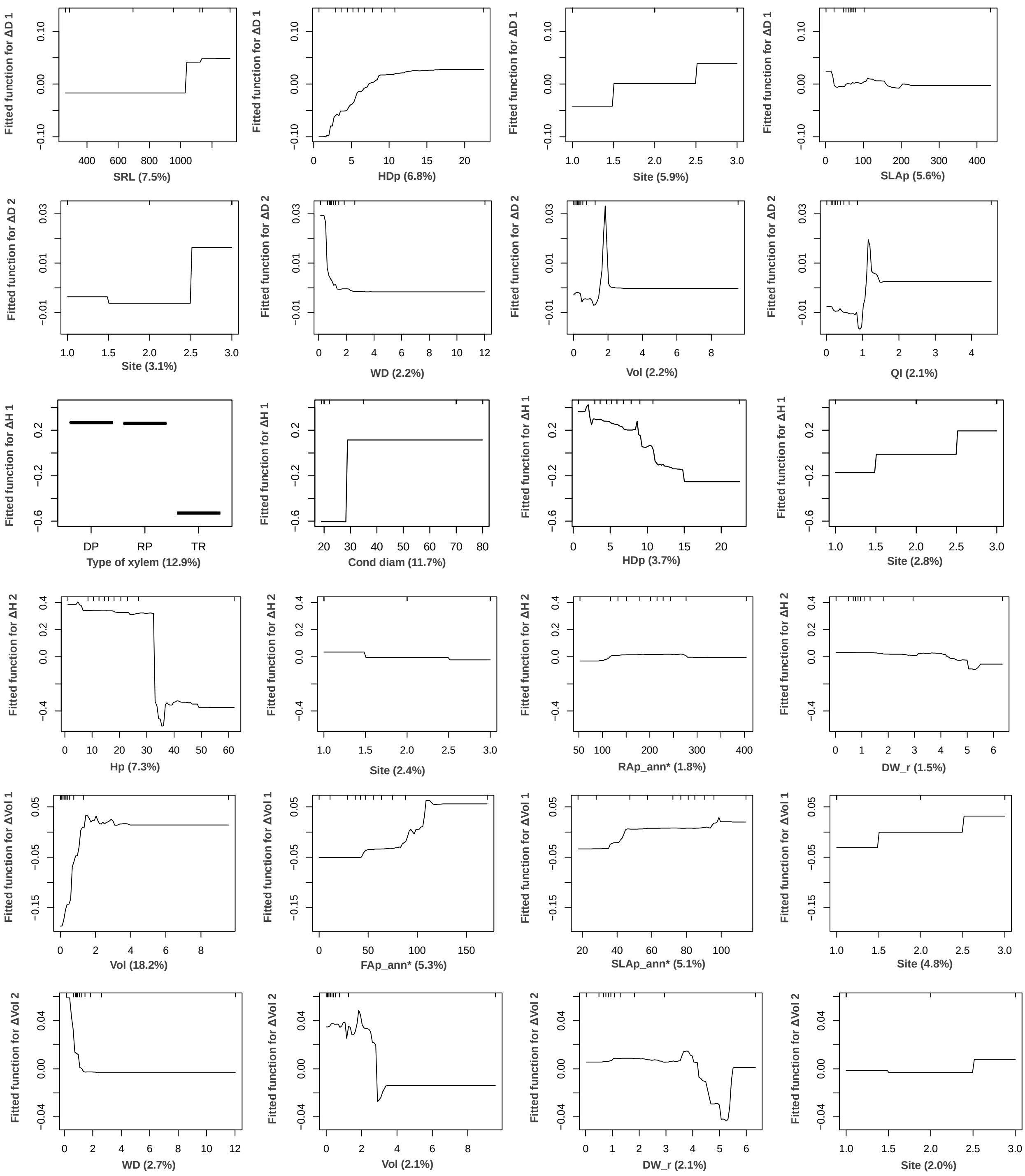

Figure 6. Partial dependence plots (PDP) of boosted regression tree (BRT) models showing the fitted functions of the 4 highest-ranked predictors (higher RI in the BRT models) on the early growth performance (monthly lapse): diameter growth (ΔD), height growth (ΔH) and volume increment (ΔVol), computed either in the first spring or in the first summer after planting (suffixes 1 and 2 respectively). The Y axis is centered to have zero mean over the data distribution and spans the same range (in units of standard deviation from the mean predicted response value) across all plots to make the magnitude of the effects comparable among predictors. X-axes show rug plots that visualize the distribution of the respective data space in deciles, in order to avoid overinterpreting regions with almost no data. Note (*): WP_PL50* in -MPa; ann* = artificial neural network.