Early Survival and Growth Plasticity of 33 Species Planted in 38 Arboreta across the European Atlantic Area

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Abstract: To anticipate European climate scenarios for the end of the century, we explored the climate gradient within the REINFFORCE (RÉseau INFrastructure de recherche pour le suivi et l'adaptation des FORêts au Changement climatiquE) arboreta network, established in 38 sites between latitudes 37° and 57°, where 33 tree species are represented. We aim to determine which climatic variables best explain their survival and growth, and identify those species that are more tolerant of climate variation and those of which the growth and survival future climate might constrain. We used empirical models to determine the best climatic predictor variables that explain tree survival and growth. Precipitation-transfer distance was most important for the survival of broadleaved species, whereas growing-season-degree days best explained conifer-tree survival. Growth (annual height increment) was mainly explained by a derived annual dryness index (ADI) for both conifers and broadleaved trees. Species that showed the greatest variation in survival and growth in response to climatic variation included *Betula pendula* Roth, *Pinus elliottii* Engelm., and *Thuja plicata* Donn ex D.Don, and those that were least affected included *Quercus shumardii* Buckland and *Pinus nigra* J.F.Arnold. We also demonstrated that provenance differences were significant for *Pinus pinea* L.,

Quercus robur L., and *Ceratonia siliqua* L. Here, we demonstrate the usefulness of infrastructures along a climatic gradient like REINFFORCE to determine major tendencies of tree species responding to climate changes.

1. Introduction

Predicted scenarios for the European climate at the end of the century point to a slight reduction in annual precipitation and an extension of rain seasons. Projected rise of global mean surface temperature by the end of the 21st century (2081–2100) relative to 1986–2005 is likely to be 0.3–1.7 °C for the lowest emission scenario (Representative Concentration Pathway—RCP 2.6) and 2.6–4.8 °C for the highest emission scenario (RCP8.5) [1]. The frequency of occurrence of extreme events is expected to increase, particularly the number of days with spring frost and periods of water stress for plants, leading to a decrease in productivity, and an increase in pest and disease activity [2–4]. Extreme events, such as drought and heat waves, have already been identified as a major cause of forest dieback [5–7]. In the future climate, trees will experience new biotic and abiotic environments and stresses, such as drought, temperature extremes, flooding, wildfire, and novel insect and disease pressures. The occurrence of extreme temperatures may be a relevant climatic indicator for plant stress. Physiologically, however, the effects of extreme heat or cold are confounded with other factors. For example, heat stress acts in conjunction with higher air humidity, wind speed, and radiation [8]. Higher temperatures are often associated with drought stress, which is dependent on water availability that varies seasonally in both temperate and Mediterranean climates. Regarding cold damage, temperate plants are particularly vulnerable to frost damage in spring, when leaves and flowers are developing after bud burst [9].

In the long term, evolutionary mechanisms can enable species to adapt to such changes, but it is likely that species and population responses will be too slow compared with the expected speed of climate change. Genetic diversity is, in this context, a tool that should be used and made available for forestry management. Providing forest-regeneration material with species–site–climate matching from appropriate provenance regions [10] is an opportunity to increase stand resilience and withstand the challenges that emerge with climate change. Production periods of forests are long, ranging from 20 to 80 years or longer, and a major concern is that planting stock originating from fixed contemporary seed zones will be growing in suboptimal conditions by the end of the century or sooner [2]. Patterns of genetic variation vary greatly among species; some species are climate specialists that exhibit strong differentiation over small geographic and climate scales, while others are generalists that show less differentiation across a wide range of environmental gradients [11,12]. Some species can also exhibit multiple adaptive strategies over different portions of their range [2]. Therefore, it is important to identify how different genetic material might respond to future climatic scenarios. As pointed out in Reference [13], we need to define which trade-offs between growth performance and sustainability are the most appropriate to cope with extreme events. In that sense, understanding and modeling tree-species response to climate change is a valuable tool to predict the consequences of climate change on forests and develop forest adaptation strategies. Several limitations apply when using climate models to understand the likely effects on forest ecosystems. Forests do not always linearly respond to changes in climate parameters such as annual temperature and precipitation. Many responses are to extremes rather than to means and, therefore, greater uncertainties in the projections of climate extremes cause considerable uncertainties when assessing the likely response of forest ecosystems towards the end of the current century. So, climate-model results diverge much more at the regional compared to the continental and global levels [10].

Although several species-distribution models have been studied, some aspects of plant responses have to be simplified because of incomplete information or understanding of mechanisms [4,5]. In particular, phenotypic plasticity fails to be considered by most models, mainly due to a lack of specific information. Typically, climate-envelope models of species distribution are based on species presence and absence records and do not identify population-level genetic variation in responses to environmental factors. However, with the migration of populations and species to outside their present distribution ranges, the environment and genetic interaction need to be considered [14]. On the other hand, models based on climate indicators, such as temperature and degree days, could fail to express physiological impacts on plants that have secondary growth, lignification, or thicker cell walls [15,16].

In order to study climate responses of trees within the Atlantic Region [17] of Europe, an infrastructure network of test sites was installed in four countries, involving 18 partner organizations in a project on forest adaptation to climate change. Established in 2012, this network, named the REINFFORCE Network (RÉseau INFrastructure de recherche pour le suivi et l'adaptation des FORêts au Changement climatiquE), extends from Scotland (North) to Lisbon (South), and from Bordeaux (East) to the Azores (West), taking advantage of very different climatic conditions. The north–south and east–west extent of this network allows responses such as survival and growth to be measured along gradients of climatic factors covering expected changes and the range of predicted future climate scenarios [18]. Each test site is planted with the same 33 species with three mandatory provenances each, with additional provenances selected by each partner [18].

The aim of the present work is to determine which climatic variables can best explain variation in survival and growth, and use the information to determine which species are likely to be more tolerant to climate variation, and those for which the future climate will bring higher constraints on growth and survival. This modeling work helps to understand how different species and provenances within species may respond differently to climate change.

2. Materials and Methods

2.1. REINFFORCE Arboreta Network

This network consists of 38 planting sites, called arboreta, each one of which contains a collection of exactly the same base material of 33 species ideally represented by three mandatory provenances selected from contrasting climate conditions within its current distribution range, in order to capture maximum species variability [18]. However, *Eucalyptus* spp. and *Quercus shumardii* Buckland are represented by only one provenance. Additional provenances were selected by each partner and installed locally; these are not included in the present analysis. The network was planted in the spring of 2012. The network's climatic gradient provides a variation of 9 °C for mean temperature and 900 mm for precipitation, and can be viewed in Supplementary Materials S1.

Growth and survival monitoring followed the REINFFORCE field protocol (reinfforce.iefc.net).

Species were selected through a joint literature review, specialist opinion, and decision-support methodology based on the PROMETHEE algorithm [19] (http://www.iefc.net/newsite/sitereinfforce/2012-processus-de-selection-des-especes-pour-les-arboretums-de-reinfforce), and availability on commercial suppliers (Figure 1). Seed was either sourced from commercial suppliers or, when important chosen provenances were unavailable, specifically collected from local populations within the provenance region.
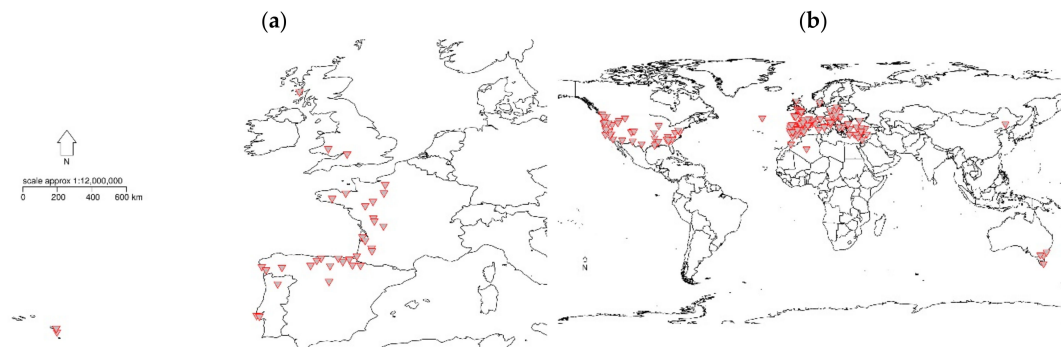
Figure 1. (**a**) Europe map showing the distribution of REINFFORCE (RÉseau INFrastructure de recherche pour le suivi et l'adaptation des FORêts au Changement climatiquE), arboreta network (red triangles). (**b**) World map showing distribution of material provenance regions used for the establishment of the REINFFORCE arboreta network (red triangles) [18].

Selected seed lots were sent to a centralized nursery in southeastern France for seedling production and preparation. Once plants reached their target sizes, they were then distributed to each arboretum.

A minimum of 36 trees of the same species (12 trees from each one of the 3 provenances) were established in all arboreta. Each provenance is represented by 12 trees planted together in a plot, but in heterogeneous sites the 12 trees were split in 2 plots of 6 trees. In each arboretum, 3 replications of 4 species (*Pinus pinaster* Aiton, *Betula pendula* Roth, *Cedrus atlantica* (Manetti ex. Endl.) Carrière, and *Quercus robur* L.) were planted randomly in order to assess site heterogeneity [18].

A list of species, provenance, and coding can be found in Supplementary Materials S2.

2.2. Plant Assessment Data

For all plants, data were recorded at planting and then annually at the end of the growing season as total shoot height (transformed to yearly growth) and survival over the period from 2012 to 2016.

Within the complete dataset, only one data point was excluded for growth, where the height of one plant was abnormally higher, probably due to recording error.

2.3. Climate Data

Daily weather data were recorded by local automatic weather stations, and recorded parameters were transformed to 2012–2016 period averages. There was minor occasional information missing on site weather due to difficulties with automatic weather stations, which represented no impact on analysis-period averages. An initial group of climatic variables considered relevant for modeling was selected from the available ones in both Worldclim [20], for the provenance site, and the local arboreta weather stations (Table 1). Growing season was standardized to the period from April to September, as in Reference [21]. Growing Season Degree Days (GSDD) was calculated as the sum of °C above 5 °C per day for each year and growing season. An Annual Dryness Index (ADI) was calculated as the square root of GSDD divided by annual precipitation (P) [21,22]. For a visualization of this index along the REINFFORCE arboreta network, see Supplementary Materials S10.

Table 1. Tested variables, units, and transformations.

Explanatory Variable	Code	Unit	Transformation
Mean daily air temperature	T_mean	°C	1/100
Mean Maximum daily temperature	T_max	°C	1/100
Mean Minimum daily temperature	T_min	°C	1/100
Extreme Minimum air temperature	Ext_T_min	°C	1/100
Extreme Maximum air temperature	Ext_T_max	°C	1/100
Annual Precipitation	*p*	mm	1/1000
Growing Season Precipitation	GSP	mm	1/1000
Summer Precipitation	SP	mm	1/1000
Growing Season Degree Days >5 °C	GSDD	°Cd	1/10,000
Degree Days >5 °C	DD5	°C	1/10,000
Annual Dryness Index	ADI	$\sqrt{°Cd}$/mm	
Growing Season Dryness Index	GSDI	$\sqrt{°Cd}$/mm	
Dependent Variable	**Code**	**Unit**	**Transformation**
Yearly Height Growth	Height	cm	Log
Survival	Survival	Alive/Dead binary	LOGIT

Provenance (seed origin) climate data for the 1970–2000 period were extracted from the Worldclim dataset [20], at 1 km² spatial resolution. Growing Degree Days were estimated using the Greer method [23].

In this study, we accounted for the effect of climatic distance [21,24,25] from provenance to arboreta-site conditions, as well for site-specific edaphoclimatic effect [26,27].

2.4. Statistical Analysis

Initial screening of the data using boxplots (Supplementary Materials S4–S9) identified that *Eucalyptus* 'Gundal' (EUGU-GUN), which is a hybrid *Eucalyptus gunnii* × *dalrympleana*, had a distinct growth-data variation (Supplementary Materials S8), and was modeled separately. From bibliographic analysis [28–31], it was decided that conifer and broadleaf species were to be analyzed as separate groups due to a possible differential response to environment variables.

Height growth and survival traits response to climate were modeled at the species level, with the genetic differences between the provenances included. Our approach was adapted from the methodology in References [21,25], using a mixed-effects model, separating fixed and random effects, and variation sources.

The fixed effects account for 3 levels of variation in plant responses:

1. The effect of meteorological conditions at the arboreta sites (Term A), expressing the plastic response of the genetic unit along the arboreta gradient.
2. The effect of climatic transfer distance, (Term D) expressed by the differential between climate at the arboreta site and climate at the provenance site, revealing the plasticity-linked plant adaptation to site conditions.
3. The interaction term A × D.

The full model is as follows:

$$Y_{ijkl} = \mu + \beta_0 + \beta_1 A_i + \beta_2 A_i^2 + \beta_3 D_{ij} + \beta_4 D_{ij}^2 + \beta_5 (A_i \times D_{ij}) + \beta_6 S_k + \beta_7 E_i + \beta_8 P_j (S_k) + e_{ijkl} \qquad (1)$$

where:

Y_{ijkl}—Individual tree height for the *l*th tree for the *j*th Provenance from the *k*th Species, on the *i*th arboretum, or log-odds for survival;

A_i and A_i^2—the value of a Climate variable observed at the *i*th Arboretum;

D_{ij} and D_{ij}^2—the value of Climate distance for a climate variable between the *i*th arboretum and *j*th provenance site;

$A_i \times D_{ij}$—the interaction between A and D terms;

S_k—Species effect of the *k*th species;

E_i—Site effect at the *i*th arboretum due to factors other than climate;

$P_j (S_k)$—Provenance effect of the *j*th provenance nested within the *k*th corresponding species;

e_{ijkl}—error term;

with A, D, A $\times$ D being fixed effects, and S, E, P(S) being random effects.

For the A and D terms, we tested both linear and quadratic climate-variable terms to account for nonlinearity in the response between species and climate conditions, as suggested in many studies [21,25,32–35]. As stated in Reference [21], this interaction is the expression of plasticity, and the ability to adjust to new environments experienced at the planting sites. The amplitude of the trait values associated with survival and growth shown in the different environments of the arboreta network demonstrates the adaptation capacity of the genotypes under evaluation. Phenotypic plasticity may contribute to the fitness of a genotype, especially if it is a long-lived species with a wide distribution encompassing many different site conditions. If this is the case, natural selection increases the frequency of genotypes with high phenotypic plasticity [36].

We fitted linear mixed effects models for height growth, and logistic regression through generalized linear mixed effects for the binary survival variable using the *lmer* and *glmer* functions from the *lme4* package in R [37]. The dependent Yearly Height Growth variable was log-transformed to ensure meeting normality assumptions, and Survival was modeled using the logit link function and binomial error distribution.

2.5. Selecting Variables

Some independent variables were transformed because the scale ratio between dependent and some independent variables was large enough to impact model convergence (Table 1). Temperature (Mean Monthly Maximum, Mean Monthly Minimum, Mean Yearly, Extreme Yearly Maximum, Extreme Yearly Minimum), Precipitation (Annual, Growing Season), Growing Degree Days [38], and Growing Season Growing Degree Days (April–September) were the independent variables tested for model fitting.

Each independent variable was fitted as its linear and its quadratic form, and considered as independent variables. Model's predictor variables were tested for multicollinearity magnitude by considering the size of the Variance Inflation Factor (VIF), excluding each one when VIF > 3 [39].

Models were firstly fitted using Maximum Likelihood (ML) estimation to allow for comparison between models with different fixed factors. Fixed-factor inclusion on the model was evaluated by running χ^2 Likelihood Ratio test and comparing the Akaike Information Criterion (AIC) between extended and reduced models. After model selection, the model was refitted with Restricted Maximum Likelihood (REML) and presented in the Results section.

2.6. Random Effects

Site term (E) accounts for all site effects other than climate (mainly edaphic). The Species (S) and Provenance nested within Species (P(S)) terms account for variation generated by evolutionary drivers [40,41] that are not captured by fixed-effect terms as selection due to factors other than climate.

Random intercepts and slopes on fixed effects were tested for species and provenance within Species. The significance of random-effect inclusion in the final model was evaluated by running an χ^2 likelihood ratio test and comparing the Akaike Information Criterion (AIC) between models with and without random effects, fitted through ML.

2.7. Model Selection

For linear model-fitting comparison, AIC was applied to models as an estimator of the relative quality of statistical models for a given dataset. The model or nested model with lower AIC represented the best fitting one.

Pseudo-R^2 with Marginal R^2 represented the variance explained by fixed factors, and Conditional R^2 interpreted as variance explained by the model (both fixed and random factors) [42,43]. For the logistic model, the Concordance index (C index) was used in order to verify a standard measure of the predictive accuracy of a logistic regression model [44]. For each dependent variable, the best fitting model was selected for each of the species groups (conifer and broadleaf).

3. Results

The best fitting model for Survival has site-linear GSDD for the conifer group (Table 2) and linear Annual Precipitation Climate Transfer Distance for the broadleaf species as significant explanatory variables (Table 3).

Table 2. Summary of selected mixed effect models for Survival, showing fixed-effect estimates, statistical significance, random effect on intercept and slope, and explained variance proportion for random parts, Akaike's Information Criterion (AIC), and Concordance index for mixed models. Summary for all species, grouped by conifer and broadleaf.

	Survival					
	Conifer			**Broadleaf**		
Fixed Part	**Estimate**	**% Variance**	***p* Value**	**Estimate**	**% Variance**	***p* Value**
Intercept	4.661		<0.001	1.918		<0.001
Precipitation Climate Distance/100				−0.022		0.001
Site Growing Season Degree Days >5 °C	−1.527		0.026			
Random Part						
Site *(Intercept)*		11.845			39.088	
Species *(Intercept)*		57.277			30.402	
Provenances within Species *(Intercept)*		4.352			30.510	
Species *(Slope)*		26.527				
AIC	12,497.9			10,932.6		
C Index	0.719			0.730		

Table 3. Summary of selected mixed-effect models for Yearly Height Growth, showing fixed-effect estimates, statistical significance, random effects on intercept and slope, and explained variance proportion for random part, AIC, and adjusted R^2 for mixed models. The table presents the summary for all species, conifer and broadleaf group d, except *Eucalyptus* 'Gundal', which can be found in Supplementary Materials S3.

	Yearly Height Growth (Log)					
	Conifer			**Broadleaf**		
Fixed Part	**Estimate**	**% Variance**	***p* Value**	**Estimate**	**% Variance**	***p* Value**
Intercept	3.339		<0.001	3.142		<0.001
Site ADI^2	−69.006		<0.001	−39.903		0.046
Random Part						
Site *(Intercept)*		0.007			0.012	
Species *(Intercept)*		0.019			0.031	
Provenances within Species *(Intercept)*		0.015			0.002	
Species *(Slope)*		99.933			99.933	
Residual		0.026			0.023	
AIC	17,370.589			21,208.356		
R^2 marginal	0.108			0.035		
R^2 conditional	0.651			0.641		

Both the A and the D terms appeared as significant explanatory variables, although for the selected model for Conifer group, the model included only the site-specific term (A). For growth, only site-specific (A) explanatory terms showed significance in the fitted models. The best fitting models for height growth included the quadratic Annual Dryness Index (ADI) term as an explanatory variable, for both species groups.

3.1. Random Effects

Species, Provenance (nested within Species), and Site random-factor inclusion significantly improved the model fit. The Species random effect captured most of the variance percentage, while the Site effect, representing other factors, such as edaphic features, had a lower expression except for Broadleaf survival. Species had significant intercept and slope random effects, with the random-slope component associated with ADI accounting for more than 99% of the growth-model random variance, revealing a species-specific response to the variable (Table 3). As for Survival, the random slope accounted for lower variation in the conifer group, and was not significant for the broadleaf (Table 2). For broadleaf Survival, the model's highest random-variance partition was allocated to site.

Provenance effects within Species account for a high percentage of Survival variance, but are much lower for height growth trait. Nevertheless, they proved to be significant for the selected models.

3.2. Survival

Increasing GSDD tends to decrease species survival in the conifer group (Figure 2, Table 2). However, species differences are apparent. Survival of *Pinus brutia* Tenore (PIBU) and *Cedrus libani* A.Rich (CELI) tends to increase with temperature, while survival of *Pinus elliottii* Engelm. (PIEL), *Sequoia sempervirens* (D. Don) Endl. (SESE), and *Thuja plicata* Donn ex D.Don (THPL) decreased greatly at GSDD above 1500.
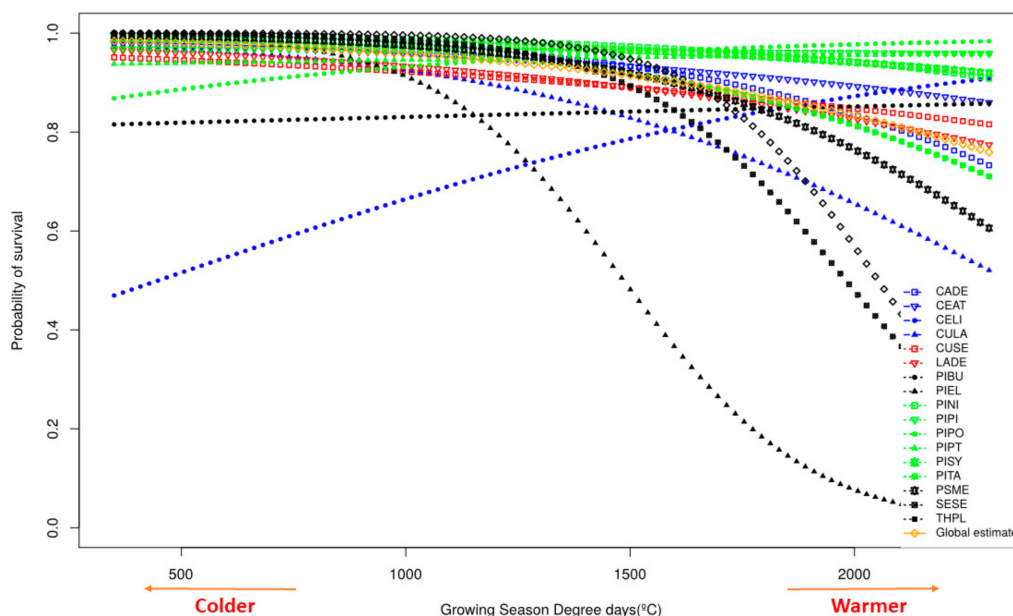

Figure 2. Estimated probability of survival plot for the explanatory variable "Growing Season Degree Days above 5 °C" in the conifer species group. The orange line shows the model's estimated response. Additional lines show the predicted variation from the global estimate for each conifer species.

The model fitted for Survival of broadleaved species shows a trend where transferring material to a site with lower precipitation than a provenance site had a negative impact on survival. It also shows that species' survival improves with transference to sites with higher precipitation than at a provenance location (Figure 3).
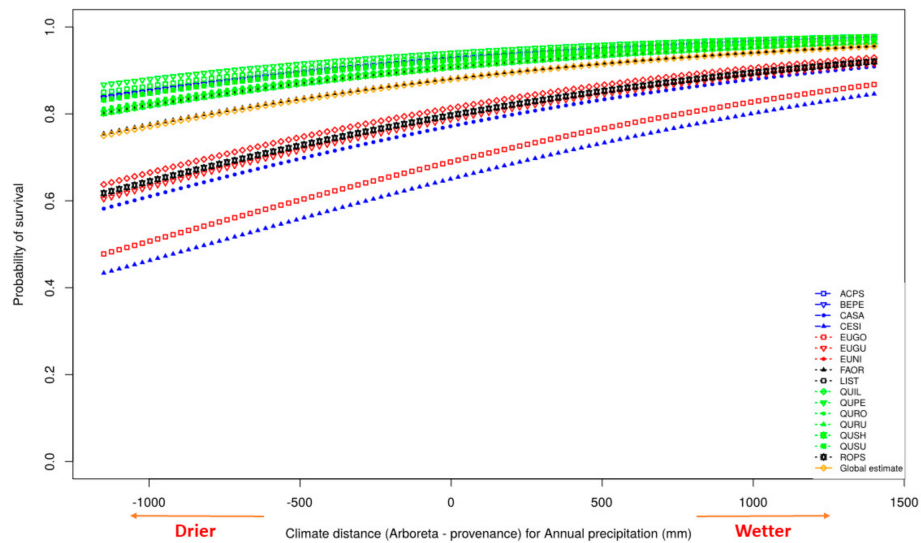
Figure 3. Estimated probability of survival for the explanatory variable "Climate distance for Annual Precipitation", in the broadleaf species group. Climate difference was calculated from "Climate variable at the test site-climate variable at a provenance site". The orange line shows the model's estimated response. Additional lines show the predicted variation from the global estimate for each broadleaf species.

The highest variation between provenances within species occurred in *Ceratonia siliqua* L. (CESI), *Quercus robur* (QURO), THPL, *Pinus pinea* L. (PIPI), PIEL, and *Calocedrus decurrens* Torrey (CADE) (Figures 4 and 5).
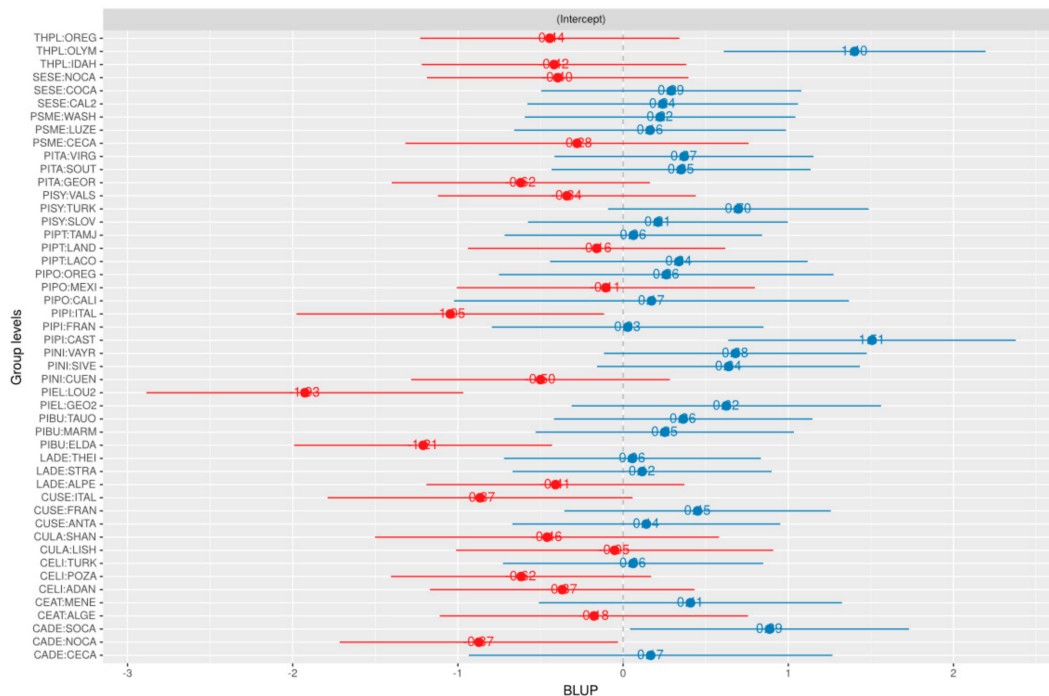
Figure 4. Best linear unbiased predictor for provenance nested within species random effects for survival within the conifer group. Dots represent variation from the global mean estimate, with 95% confidence intervals. Red dots and lines represent negative-effect differences; blue dots and lines represent positive-effect differences.
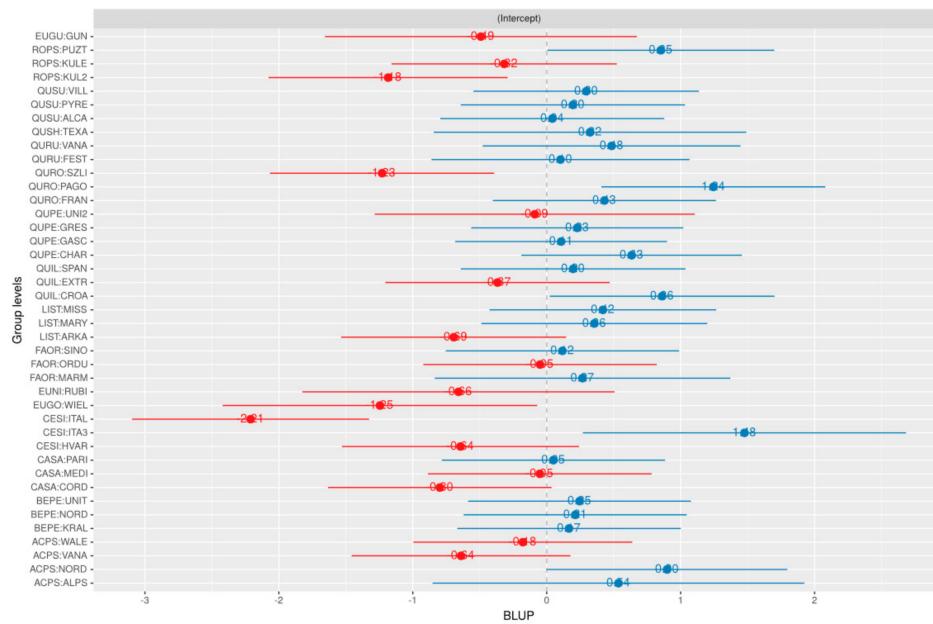
Figure 5. Best linear unbiased predictor for the provenance nested within species random effect for survival within the broadleaf group. Dots represent the variation from the global mean estimate, with 95% confidence intervals. Red dots and lines represent negative-effect difference; blue dots and lines represent positive-effect differences.

3.3. Growth

For height growth in both species groups, ADI was the climate variable that provided the best model fit. For nearly all species, height growth decreased as the index increased (Figures 6 and 7), that is, with decreasing precipitation and increasing accumulated temperature above 5 °C. This trend is particularly strong in the conifer group (Figure 6), in which CELI has the most constant growth along the ADI gradient, followed by PIPI, which exhibits higher growth values overall (Figure 6).
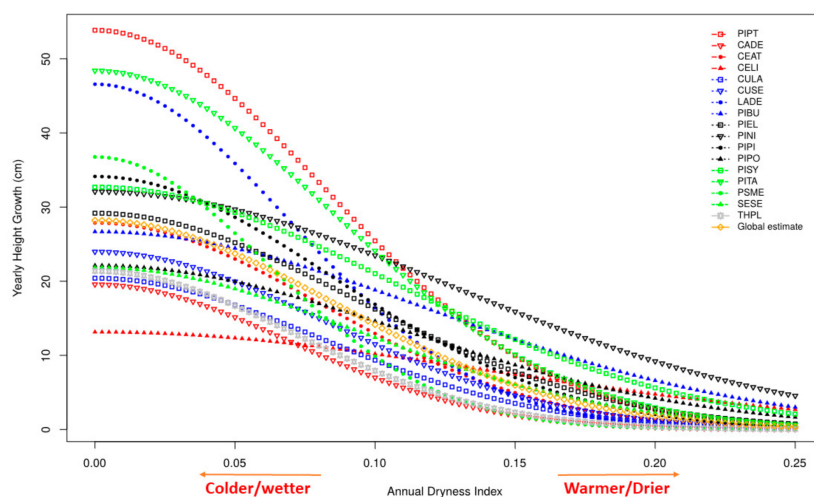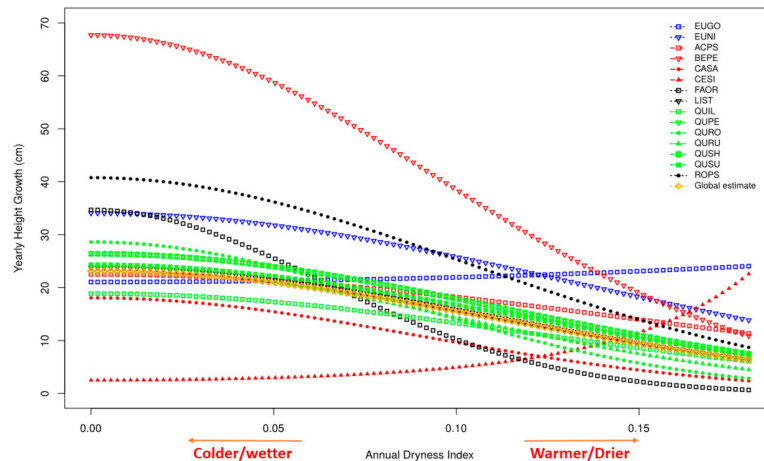

Figure 6. Estimated yearly height growth for explanatory variable ADI in the conifer species group. Orange line expresses the model's estimated response. ADI is calculated as $\sqrt{\text{degree days}}$ >5 °C/mean annual precipitation. Additional lines express the predicted variation from the global estimate for each conifer species.

The species with the greatest growth decrease with increasing ADI was *Betula pendula* (BEPE) (Figure 7). However, the trend was weaker in some other species. Height growth of *Eucalyptus globulus* Labill. (EUGO) was reasonably constant along the ADI gradient, with even a slight growth

increase at higher ADI values. CESI showed an opposite trend, with low growth at low ADI and increasing growth at higher ADI (Figure 7). The growth model for EUGU had the best fit using two predictor variables, "Mean Annual Temperature" and "Annual Precipitation"; although the first was not statistically significant, it was considered for the final model because it improved the AIC index. Higher growth was estimated for sites with high annual precipitation and mean temperature (Figure S1 in Supplementary Materials S3).

Figure 7. Estimated yearly height growth for explanatory variable ADI in the broadleaf species group. Orange line expresses the model's estimated response. ADI is calculated as $\sqrt{\text{degree days}} > 5\,°\text{C}/\text{mean}$ annual precipitation. Additional lines express the predicted variation from the global estimate for each broadleaf species.

Explained growth random variation by provenance effect was low, yet not negligible. The highest growth within species variation was found for *Acer pseudoplatanus* L. (ACPS), *Quercus ilex* L. (QUIL), THPL, *Pinus taeda* L. (PITA), and CADE (Figures 8 and 9).
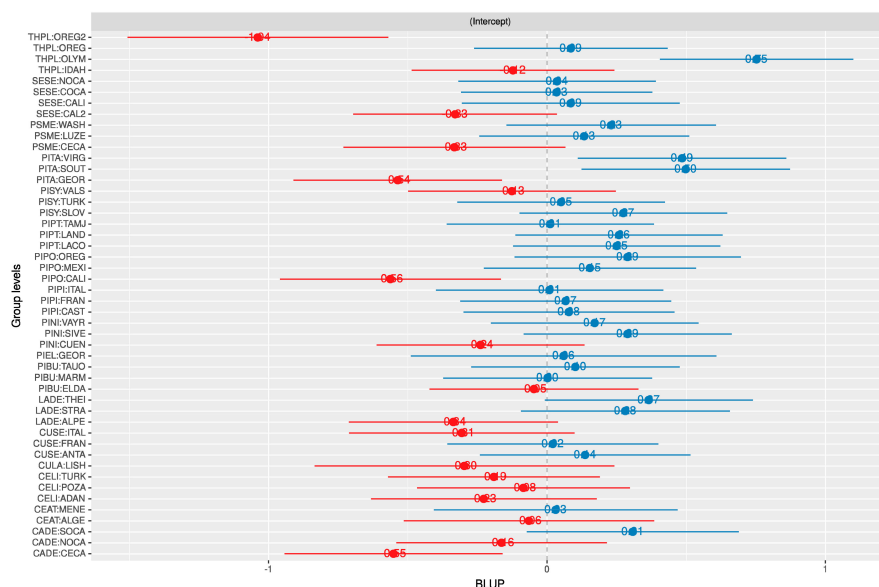

Figure 8. Best linear unbiased predictor for the provenance nested within species random effect, for yearly height growth on the conifer group. Dots represent the variation from the global mean estimate, with 95% confidence interval. Red dots and lines represent negative-effect differences, and blue dots and lines represent positive-effect differences.
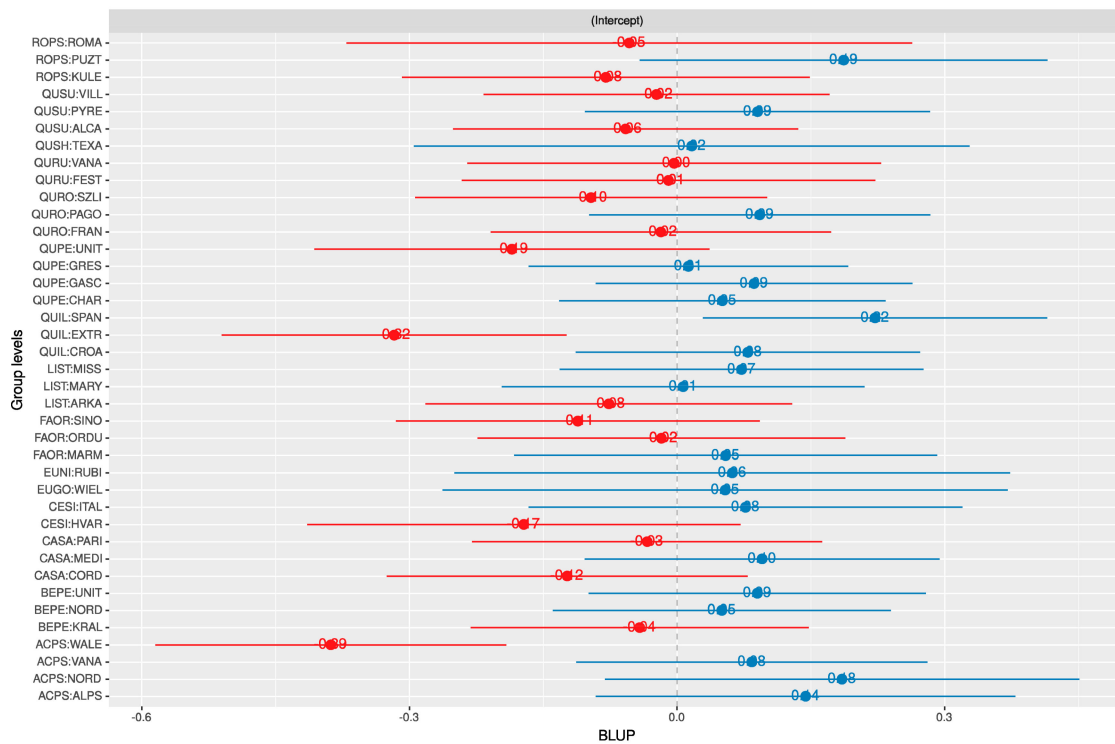
Figure 9. Best linear unbiased predictor for the provenance nested within species random effect for yearly height growth within the Broadleaf group. Dots represent the variation from the global mean estimate, with 95% confidence interval. Red dots and lines represent negative-effect differences; blue dots and lines represent positive-effect differences.

4. Discussion

As recognized in the Food and Agriculture Organization (FAO) of the United Nations [45], a further prerequisite for the use of adapted genetic resources in increasing the resilience of future production systems is improved knowledge of these resources: where they are found, what characteristics they have (e.g., resistance to drought or disease), and how they can best be managed. Within the present context, the REINFFORCE arboreta network has been established as an important tool for assessing species performance, and for supplying information for reducing uncertainty at short-, mid-, and long-term periods. Within this aim, we attempted to increase the knowledge about forest-tree responses to climatic conditions at the levels of functional groups, species, and within species variation, identifying the main drivers that would explain field performance along climate gradients. One of the advantages for this approach is the absence of assuming specific predicted scenarios, allowing an exploration of a multiplicity of conditions, and overcoming the uncertainty derived from these predictions, which may sometimes mislead management options [46].

The main functional basis for dividing species into two groups, broadleaves and conifers, is the overall differences in their leaf lifespans, and their individual phylogenetic histories that underlie differences in other phenotypic features such as leaf structure, crown architecture, and wood composition [47], all of which translate into different adaptation strategies and resilience capability. In our study, best-fit models differed between the conifer and broadleaf groups, particularly for survival. Transfer distance for annual precipitation (P) was the significant factor explaining broadleaf survival, and GSDD at the planting site was most significant for the conifer group. These results agree with the differential adaptability capacity by each group, higher for broadleaf, as water-use efficiency increase, or growth response to temperature increase [29,48].

EUGU required a separate explanatory model to be fitted with site temperature and precipitation included as the fixed effects (Supplementary Materials S3), differing in that way from the other

broadleaf and eucalyptus species. This naturally occurring hybrid, produced from selected material [49] does present very high growth capability, as already observed in other studies [50], and also considerable variability along the arboreta network (Supplementary Materials S8).

4.1. Growth

For both species groups, the site ADI was the most significant fixed-effect variable explaining variation in height growth. The significance of the quadratic term indicates that the response is nonlinear with higher ADI values, having the most negative impact on growth for both conifers and most broadleaved species. This means that a higher accumulated temperature, combined with lower precipitation, limits height growth of most of these species. This is consistent with Reference [51], where all coastal redwood (*Sequoia sempervirens*) provenances planted outside their natural range grew much more slowly at the xeric test site than the mesic test site, regardless of climate (dryness) at their provenance location. Typically, height growth is greatest and constant at low ADI, and then decreases with increasing ADI. For example, within the ADI range 0–0.02, there is only a slight inflection of the growth response curve for *Betula pendula*, meaning higher stability than in the 0.02–0.25 range, where there is a rapid decrease in growth response. Moreover, each species responds with a different magnitude to this climatic index. *Pinus pinaster* had the highest growth at ADI values close to 0, whereas PITA and *Larix decidua* Mill. (LADE) showed the highest plasticity for this trait, expressed by variability across the gradient. For higher ADI values (higher accumulated temperature, lower precipitation), these two species also showed the highest drop in estimated growth potential. Within the broadleaf group, BEPE, *Robinia pseudoacacia* L. (ROPS), and *Liquidambar styraciflua* L. (LIST) showed the greatest response to increasing ADI with a considerable drop in estimated growth potential at higher ADI values. *Quercus* species, as well as EUGO and *E. nitens* H. Deane & Maiden (EUNI) showed less variation along the ADI gradient. Overall, variation in height growth showed no significant relationship with climate transfer distance effects, so, apparently, growth appears to respond directly to site climate.

Overall, variation between provenances within species suggests that genetic variation within species was captured but had low expression in the model. Nevertheless, it is possible to identify those that differ positively or negatively to the climate index, relative to the global mean.

In general, site random effects explained a low percentage of variance (<1%), except for with *Eucalyptus* 'Gundal', which was >50%, and probably reflects very low or null genetic variation in this clone. This signifies the importance of selecting the appropriate site for establishment, as well as the genetic material [52].

For E. 'Gundal', estimated growth was positively influenced by increasing precipitation and temperature, with a greaterer response to temperature (higher fixed-effect estimate), and a high plasticity along the gradient. According to the Institut Technologique Forêt Cellulose Bois-construction Ameublement (FCBA) [49], this hybrid shows tolerance to moderate drought, and its productivity is directly dependent on water availability.

Despite the global and regional expected increase for forest growth under climate change [53] resulting from temperature increase and CO_2 fertilization, the current results reinforce that genetic-material selection needs to be considered as an adaptative management option in order to take advantage of the referred conditions.

4.2. Survival

For survival, the most significant fixed effect differed between the two species groups, with annual precipitation transfer distance being most significant for broadleaved species, and site GSDD for the Conifer. The fitted term for broadleaved species has a positive slope, indicating that survival increased at planting sites that are wetter than the provenance sites, and decreased where sites are drier. It has been suggested that greater survival should occur at sites with minimal transference distance values [21], but our results point to species' slightly suboptimal survival when grown at

sites with equivalent provenance climatic conditions, although these differences are expressed less in *Quercus* species. The decrease in survival at negative transfer distances was greatest for species that had lower overall survival, such as *Ceratonia siliqua* and *Eucalyptus globulus*. However, the random factor associated with slopes was not significant in the best-fitting model, which means that all species follow the same trend along the gradient, varying from the overall mean by the random intercept for site, species, and provenance. For the broadleaf group, site edaphic characteristics are highly relevant, agreeing with Reference [21], explaining over 39% of the model's variance, against less than 12% of the explained variance for conifers.

The best model for conifers showed an overall significant negative linear effect of growing-season degree days on survival, modified by different intercepts and slopes for species. In general, *Pinus* species showed less variation in survival along the gradient of accumulated temperature. The exception is *Pinus taeda* and *Pinus elliottii*, which seem to be consistent with References [54–56], where higher temperature at the beginning of summer seemed to constrain survival and growth. *Pinus elliotti* exhibited the largest decrease in survival as site growing-season degree days increased. Though conifers tend to be less responsive to temperature than broadleaved species, there is an indication that survival of species that originate in colder climates decreases more as temperature increases [48]. The significant influence of degree days is linked with temperature and duration of the growing season, which, for some species, represents early bud burst, taking advantage of water availability in drought-conditioned environments.

4.3. Trade-Offs for Adaptation

Should we focus on species with lower variation along a climate gradient in order to tackle the uncertainty issue? If we consider a *win-win* approach to the problem, we would select species that would perform better in an extended range of warmer and drier climates, and still additionally enhance forest productivity in current conditions. Nevertheless, we face some constraints for species performance, such as that introducing more drought-tolerant species in order to mitigate climate change might not necessarily be successful due to trade-offs between drought tolerance and growth plasticity [57].

Overall, there is a general response of species and species groups to temperature and precipitation variation. Higher temperature alone can result in decreasing survival and growth. Low annual precipitation, especially during the growing season, also negatively impacts survival and growth. Trait variation between provenances within species is significant, with higher expression for survival, supporting that a correct provenance selection can improve the species' response trend [58], as observable for *Pinus pinea*, *Quercus robur*, or *Ceratonia siliqua* (Figures 4 and 5). However, greater gains were achieved when selecting a more resilient or adaptable species because higher fitness corresponds to better performance. *Quercus shumardii* and *Pinus nigra* J.F.Arnold seem to be two species that present fewer trade-offs between survival and growth, and a less plastic response to climate gradient.

We do need to point out that this study is made on observations on four-year-old established seedlings, and although this is an extremely important phase for forest production, we cannot deduce a direct connection to mature-plant responses or forest-product quality. This preliminary work on the present material does present important information for species performance after establishment, improving existing basic knowledge for species selection as a base for more resilient and adapted forests. Further work will be conducted on the same material, expanding knowledge at the physiological level and in terms of productivity.

The arboretum design used in this study has the advantage of allowing side-by-side comparison of many species. However, there is an inevitable balance between the number of species studied, and the numbers of provenances within species and the numbers of individuals per plot that can be included. This implies that we cannot assure complete coverage of the entire species genetic variation, we can only assume to capture the variation based on selected material that originated from contrasting climatic

conditions. This design also generated constraints for data analysis, mainly due to the unbalanced experimental design caused by unequal mortality at the site, species, and provenance level.

5. Conclusions

In this study, we used empirical models to detect the best climatic-predictor variables explaining tree growth and survival. We used data from a network of 38 arboreta, each with 33 species and three provenances, established along a latitudinal range in the first four years following establishment. In the present climate range, we concluded that the best predictors for plant survival differed between conifer and broadleaf. Precipitation transfer distance was most important for broadleaf survival, whereas growing-season degree days mostly explained conifer tree survival. Growth performance was mainly explained by the ADI for both conifer and broadleaf. However, significant differences were found between species on growth and survival response to climatic variables. Moreover, provenance within species had a high expression in the variability of both traits, yet provenance variability was more expressive for survival, revealing the importance of considering this information on climate-response models. We identified species more prone to underperform within climatic variation, such as *Betula pendula*, *Pinus elliottii*, *Thuja plicata*, and the ones less affected, such as *Quercus shumardii* and *Pinus nigra;* we also demonstrated that provenance variation is more important for *Pinus pinea*, *Quercus robur*, and *Ceratonia siliqua*.

Here, we demonstrated the usefulness of infrastructures such as REINFFORCE along climatic gradient to determine major trends in the response of tree species to climate change. This information will be most useful for future forestry-adaptation management to climate change. Our work is based on the first four years after establishment. Future work is required to follow long-term tree growth and survival.

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