forests

MDPI

Article

Variation in the Climate Sensitivity Dependent on Neighbourhood Composition in a Secondary Mixed Forest

Nere Amaia Laskurain [1,*], Arantza Aldezabal [1], Iñaki Odriozola [1] [iD], Jesús Julio Camarero [2] [iD] and José Miguel Olano [3]

[1] Department of Plant Biology and Ecology, University of the Basque Country (UPV/EHU), 48940 Leioa, Bilbao, Spain; arantza.aldezabal@ehu.es (A.A.); inaki.odriozola@ehu.eus (I.O.)
[2] Instituto Pirenaico de Ecología, Consejo Superior de Investigaciones Científicas (IPE-CSIC), Avda. Montañana 1005, 50080 Zaragoza, Spain; jjcamarero@ipe.csic.es
[3] Departamento de Ciencias Agroforestales, Área de Botánica, EUI Agrarias, Universidad de Valladolid, Los Pajaritos s/n, 42004 Soria, Spain; jmolano@agro.uva.es
* Correspondence: nereamaia.lascurain@ehu.eus; Tel.: +34-945-01-3023

Abstract: Understanding the vulnerability of individual trees to climate requires moving from population to individual level. This study evaluates individual tree response in a mixed forest by assessing how size and neighbourhood density modulated growth responses to climate among coexisting tree species. To understand the complete variation in growth responses to climate, it is necessary to consider intrapopulation variability. Trees respond as individual entities, and their response is modulated by their characteristics and neighbourhood context. To assess the individual climate sensitivity, all living Iberian birches, European beeches, and pedunculate oaks trees located in a temperate mixed forest were cored in four 40 m × 40 m plots. Standard ring-width chronologies were built at tree and species level for the 1977–2007 period. Chronologies were related to climatic variables (monthly precipitation, hailstorm and mean temperature, and summer (June–August) precipitation). Growth response to climate varied among species and individual trees. Differences in climate–growth relationship among species could be partially attributed to the different xylem anatomy, since secondary growth of ring-porous pedunculate oak (*Quercus robur* L.) was mainly dependent on the previous-winter climatic conditions (January temperature), while for the diffuse-porous Iberian birch (*Betula celtiberica* Rothm. and Vasc.) and European beech (*Fagus sylvatica* L.), spring temperature and summer precipitation were the major constraining factors of growth. Tree features and identity of neighbourhood modulated climatic response, especially for Iberian birch and pedunculate oak. Dominant trees in less crowded neighbourhoods responded more intensely to climate factors. Understanding the individual variability of growth responses to climate will provide more realistic predictions of forests response to climate change.

Keywords: European beech; Iberian birch; pedunculate oak; individual climatic sensitivity; mixed forests; tree size

1. Introduction

Annual tree rings encapsulate information about the factors that affect their formation during a time window before and during xylem development [1]. The cross-dating of tree rings has allowed using xylem features as proxies to reconstruct past environmental conditions [2,3], but also as tools to understand, predict, and model the tree responses to different environmental conditions [4–6].

These approaches share a similar population-based approach, regarding the individual variability as noise [7], and magnifying the common signal shared by coexisting trees [8–10].

The importance of individual context in shaping trees' response to the environment has been long recognized [7]. In the last decades, increasing evidence suggests that tree response to the climate is modulated by several endogenous factors, such as the genotype [11], age [12], size [13], and sex [14], in addition to exogenous factors of abiotic [15] and biotic nature [16,17]. Thus, population-based approaches might miss part of the wide range of individual responses that exist within a stand [18], obliterating different sources of variability that could contribute to more adequate management policies, or simply provide a better prediction of the individual growth responses to climate.

Tree growth depends on resource availability (i.e., light, water, nutrients), which is related to both abiotic factors, like soil type or climate [19], and biotic factors, like tree competition [7,20,21]. Climate and competition are the two major drivers that limit tree growth, but competition from neighbours may cause a greater reduction in growth than climate, at least in temperate forests [9,22–24]. However, competition for limiting resources and climatic stress, are interrelated factors [9,23,25]. Dense stands with high competition magnify the effect of extreme weather events (e.g., drought) on growth [20,23,24,26,27]. Thinning is therefore considered a valuable tool to improve the adaptation of forests to climate change [28]. Furthermore, tree size also modulates climate–growth relationships. In forests where asymmetric competition dominates, larger trees, that intercept a greater amount of resources, are more sensitive to climate, showing a higher growth-induced reduction in dry years [13,20,23]. At the same time, smaller and suppressed trees growing in highly competitive environments show a lower climatic signal [10,16]. Finally, growth responses to climate depend on species identity and the specific identity of the neighbourhood [29,30]. Differences in functional traits (e.g., crown architecture, leaf phenology, phenotypic plasticity, etc.) related to a plant shade tolerance can explain different climatic influences on radial growth across species [31]. Although, research on this topic yields heterogeneous results; in some studies, drought responses are lower for pioneer species [32], while in others, it is lower for shade tolerant species [33], and finally, in other cases, no relationship is found [34,35]. In addition, neighbourhood species composition with different traits, could result in positive (facilitation) or negative (competition) tree-to-tree interactions [25,36]. For example, interspecific facilitative effects in mixed forests improve the resilience to extreme climatic events, such as droughts [37,38].

These diverse results reflect that the tree growth response to climate is context-dependent, i.e., it depends on the neighbourhood settings, but it is also idiosyncratic for each tree species [19,29]. Forest ecosystems seem to be especially sensitive to climate change. Therefore, understanding how climate and competition interact and affect tree growth is crucial to predict how forests may respond to novel or no-analogue climatic conditions, to later adapt management to these new scenarios [16,20,39]. To test whether tree growth response to climate depends on the focal and neighbouring species characteristics, we analysed the climatic responses of individual trees from a mixed forest experiencing secondary succession [40]. The study forest experienced an almost complete felling of European beech trees, followed by the establishment of a low-density pine plantation which was logged, allowing the forest to undergo secondary succession. We analysed the climatic influences on radial growth for the three dominant species: early-successional Iberian birch, mid-successional pedunculate oak, and late-successional European beech. We evaluated the effect of precipitation, hailstorm, and mean temperature. Hailstorm was also included in the analyses because it has a strong effect on temperate forests canopies, and has previously received little attention [41].

The main objectives of this study were (i) to determine whether tree growth response to climate depends on the focal species identity and functional group (early- to late-successional species, i.e., shade intolerant to tolerant species), and (ii) to assess whether tree neighbourhood composition affects individual growth response to climate. We expected that in this secondary forest, in a stem-exclusion stage, climatic influences on radial growth would vary among the three study species in relation to their competitive ability (early- to late-successional species). Pioneer Iberian birch exploit

their resources faster that European beech and pedunculate oak, therefore, the climate impacts on growth will be greater in pioneer Iberian birch, while climatic variables that limit species growth will be more similar between European beech and pedunculate oak. Also, we expected that trees' features and neighbourhood would modulate climate–growth relationship at an individual level, and that climate impacts on growth will be greater in dominant trees than in less crowded neighbourhoods.

2. Materials and Methods

2.1. Site Description

The study site is a 4 ha large mixed forest located in the Urkiola Natural Park, (Basque Country, northern Spain, (43°86′ N, 28°39′ W), at about 550 m a.s.l. on a steep slope (21°–38°). Rock parent material is sandstone shales of the Supraurgonian complex (Cretaceous). The soil is acid with stony outcrops and shallow depth. Climate is temperate-oceanic with a high annual precipitation of 1655 mm, with a minimum during summer. Mean annual temperature is 11 °C (data from the Urkiola Pass station located 2 km from the study site). The forest is dense (854 live stems ha^{-1}), dominated by Iberian birch, European beech, and pedunculate oak, which together account for 89% of the total basal area (15 m^2 ha^{-1}). Other tree species present include Pyrenean oak (*Quercus pyrenaica* Willd.), chestnut (*Castanea sativa* Mill.), aspen (*Populus tremula* L.) and holm oak (*Quercus ilex* L.). A detailed dendrochronological study showed that this forest experienced two major perturbations in the 20th century: an almost complete felling of the trees followed by the establishment of a low-density Monterey pine (*Pinus radiata* D. Don) plantation in 1948, and its cutting in 1967, when the forest underwent a process of secondary succession [42]. At the sampling time, the stand was in the stem exclusion stage, characterized by a sharp growth decline and high mortality rates. Most of the Iberian birches were recruited in a short period after the 1967 perturbation, while pedunculate oak established during a larger window comprising the two decades after 1967 perturbation. The presence of a few European beech trees that survived the first forest cut, allowed European beech to establish shortly after the perturbation, maintaining a continuous establishment rate [40]. Therefore, the forest dynamics occurred according to competitive hierarchy of tree species (European beech > pedunculate oak > Iberian birch) matching classic pioneer-dominant successional theory for European temperate forests [40].

2.2. Study Species

European beech and pedunculate oak are the species that comprise the vegetation for most of the forested area of the North Iberian Peninsula. European beech forests are established in the montane belt from 500 to 1400 m, and pedunculate oak forests dominate from sea level to 600 m, while Iberian birch is a pioneer species that dominates secondary transitional forests to pedunculate oak or European beech forests. Iberian birch is a light-demanding, fast-growing pioneer species, and as is the case with many pioneer species, it is rather short-lived. Iberian birches are small to medium sized (about 15–20 m) trees that form a canopy, allowing a fair amount of light to pass. European beech is a long-lived and dominant shade-tolerant species. Finally, pedunculate oak is a mid-successional long-lived species, considered of intermediate shade tolerance.

2.3. Experimental Design and Field Sampling

In 1999, a 1.9 ha forest tract was selected to establish a permanent monitoring plot, where a complete spatial mapping of tree locations was realised. The stand was divided into 100 m^2 quadrats, on which the x and y coordinates to the centre of tagged stems were measured. In 1999 and 2005, the height and diameter at breast height (DBH) of all trees with DBH > 2 cm or height > 1.4 m were measured. In the 2006 and 2007 winters, four 40 m × 40 m plots (6400 m^2) were sampled (Figure 1). All living trees with a DBH > 5 cm diameter were cored at 1.3 m using a Pressler increment borer. To preserve the trees for further monitoring or re-sampling, each individual was cored only once.

This sampling design guaranteed the inclusion of a wide spectrum of environmental factors affecting the trees at the woodland scale, and was not biased by selecting trees with specific traits. The sampling was conducted in a single stand, because no opportunity was available to locate another site with similar features in terms of forest characteristics (i.e., a secondary Iberian birch forest that had not been disturbed during the last 40 years), stand size (4–5 ha), and land property designation (public use).

2.4. Core Preparation and Chronology Building

Once in the lab, cores were air-dried, glued in wooden mounts, and sanded until the rings were clearly visible for visual cross-dating. Age at 1.3 m was estimated by counting the rings in the core reaching the pith. Trees were visually cross-dated, and tree-ring widths were measured to the nearest 0.001 mm using a Velmex sliding-stage micrometer (Velmex, Bloomfield, USA). Cross-dating quality was checked using the program COFECHA which calculates moving correlations between each individual series and the mean series of each species [43]. The individual ring-width series were standardized, and detrended using the ARSTAN program [44]. The series were fitted to a spline function with a 50% frequency response of 21 years, which was flexible enough to maximise the high-frequency variability and minimise effects of other factors, such as ontogenetic trends and/or local disturbances [45]. The obtained values were pre-whitened by autoregressive modelling to remove temporal autocorrelation, giving dimensionless residual chronologies, which represent independent, normalized, and homogenised records of annual growth for each tree. These individual ring-width indexed series were averaged to calculate a mean chronology for each species considering the common 1977–2007 period. The chronology was characterised by calculating the first-order autocorrelation of raw ring widths (AC1), which measures the year-to-year persistence in growth, and the mean sensitivity of indices (MSx), which quantifies the relative growth changes among consecutive years. Also, it was estimated the common growth signal of trees by calculating the mean correlation coefficient among the individual series (Rbar), and the expressed population signal (EPS), which describes how well-replicated a chronology is when compared with an infinitely replicated chronology.
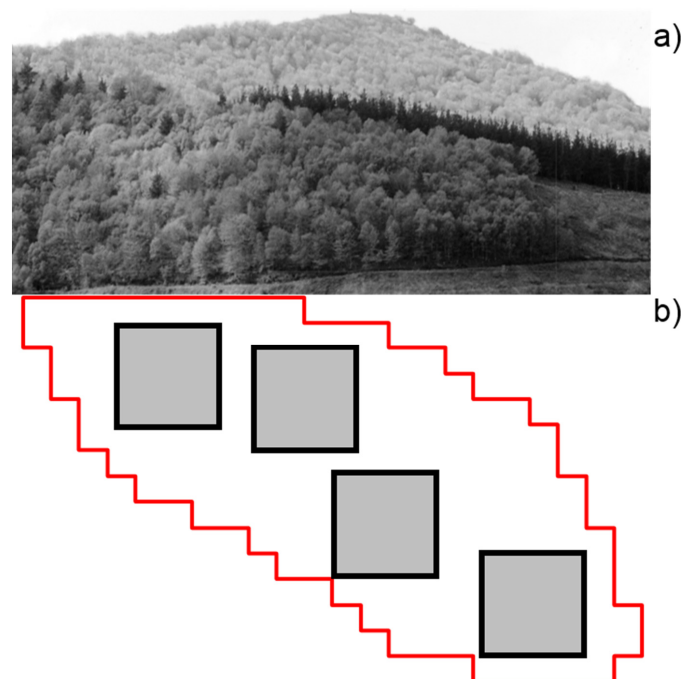

Figure 1. (**a**) View of the study area in northern Spain. (**b**) Experimental design with the spatial distribution of the four sampled 40 m × 40 m plots (6400 m^2).

2.5. Data Analyses

2.5.1. Assessing the Growth Response to Climate at the Species Level

Pearson correlations were used to identify the main climate parameters constraining secondary growth in the three species. The selected climatic factors were monthly precipitation, hailstorm and mean temperature, as well as summer (June–August) precipitation, since this period is critical for secondary growth in the study area. Temperature and precipitation data were obtained from the nearest meteorological station covering the study period (1977–2007), namely the Eibar station located 26 km away from the study site (43°11′07″ N, 2°28′15″ W, 121 m a.s.l.). Hail data were obtained from the Igeldo station located 59 km away (43°18′23″ N, 2°02′28″ W, 251 m a.s.l.), since this variable requires a permanent observation, and Igeldo fulfils that criterion. A time window from September, prior to the ring formation, to October from the year of growth, was used for temperature and precipitation correlations. For hail, the time window spanned from the previous December to the current April, as winter hail during this period is associated with large-scale cold fronts [46], and thus, meteorological data were reliable, in spite of the geographic distance. Significant climatic variables ($p < 0.05$) for each species were selected.

2.5.2. Assessing Individual Variation of Tree-Ring Growth Response to Climate

We selected within the significant climate–growth correlation obtained for the three species to carry out the individual analyses. Pearson's correlations were calculated for each tree by relating climatic variables and individual ring-width indexed series, resulting in a correlation coefficient per tree and selected climatic variable.

2.5.3. Calculating Individual and Neighbourhood Variables

For each tree, we considered individual traits (DBH and height) and several surrogates of neighbourhood-related tree-to-tree interactions. Neighbourhood was defined for a radius of 10 m from the focal tree. Canopy position (Cp) was estimated by counting the number of trees higher than the focal tree within this radius. A competition index for the focal tree was described using the competition index (If) [47]:

$$\text{If} = \Sigma \, (\text{dist}_{<10\text{m}}) \, \text{DBH}_m / \text{dist}_{n,f} \tag{1}$$

where DBH_m is the DBH of an individual neighbouring tree (n), and $\text{dist}_{n,f}$ is the distance between that tree and the focal tree (f). Four influence indices were calculated for each tree: an index including all tree species (If_T), and three indices considering only European beeches (If_F), Iberian birches (If_B), or pedunculate oaks (If_Q). An analysis of variance was performed to assess whether individual and neighbourhood variables differed among species.

2.5.4. Tree and Neighbourhood Effects on Growth

Multiple linear regressions were used to quantify the effects of tree-level variables (independent variables) on mean individual tree growth for the 1977–2007 period (dependent variable). The independent variables were the individual traits (DBH and height) and the different competition indices (Cp, If_T, If_F, If_B, and If_Q). Individual spatial position was also included to factor out spatially structured abiotic factors (topography, soil characteristic). Correlation analyses showed that there was a correlation only between If_T (influence indices based on the number of all tree species located within a 10 m radius) and the rest of the indices (If_B, If_Q, and If_F). This is an obvious result, since pedunculate oak, Iberian birch, and European beech dominate the forest composition. Therefore, to avoid the effect of multicollinearity between predictors, we assessed variance inflation factors (VIFs), and variables were excluded if VIFs exceeded 10, indicating strong multicollinearity. All potential models were compared, and the best model was selected using the Akaike information criterion corrected for finite sample sizes (AICc). When several models showed no significant differences, the model with the

smallest number of variables was selected [48]. Model residuals met the assumptions of homogeneity of the variance and normality of the errors. The inclusion of the spatial coordinates of the tree locations in the models allowed removing spatial autocorrelation in the residuals. To select the best model, we conducted an automated model selection using the glmulti package in R [48].

2.5.5. Assessing the Influence of Tree Level Factors on Climate–Growth Response

Multiple linear regressions were used to quantify the effects of tree-level variables (independent variables) on the individual climate–growth response for each climatic parameter (dependent variables). Models included individual traits (DBH and height), different indicators of competition (Cp, If_T, If_F, If_B, and If_Q), as well as tree spatial position. The best model was selected following the same procedure, described in the previous section.

3. Results

3.1. Sampled Tree Characteristics and Tree-Ring Chronologies

Overall, 228 trees were sampled (95 Iberian birches, 70 European beeches, and 63 pedunculate oaks). Average tree DBH and height did not differ among tree species, although there was a large variability in DBH within each species (Table 1). Radial growth was high (3 mm year^{-1}) for all species until 1989, when a decreasing trend started (Figure 2, upper plot). Decline was severe for pedunculate oak and Iberian birch, leading to growth rates lower than 0.5 mm year^{-1}, but moderate for European beech (2 mm year^{-1}).
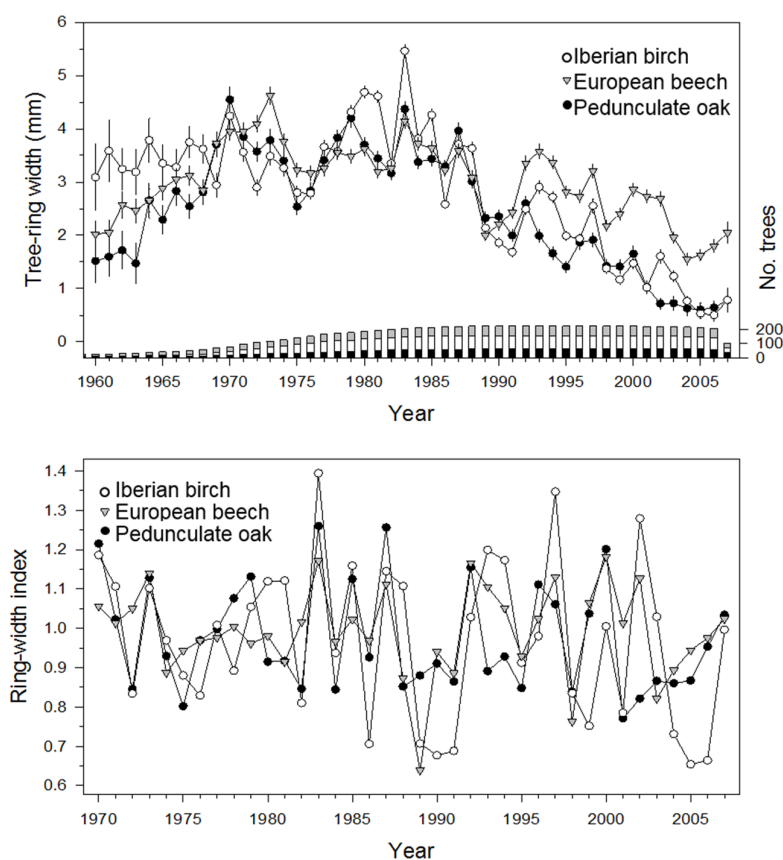

Figure 2. Temporal patterns of tree-ring width (**top**) and ring-width indices ((**bottom**), residual chronologies) calculated for the 1977–2007 period and the three species. In the upper plot, the values correspond to the mean ± standard error, and the right y-axis shows the sample size as bars, i.e., the number of trees considered each year.

Table 1. Number of sampled trees, diameter at breast height (DBH), height and age. Values are the mean ± standard deviation (with the range indicated between parentheses).

Species	No. Trees	DBH (cm)	Height (m)	Age at 1.3 m (Years)
Iberian birch	95	20.1 ± 5.8 (11.1–44.4)	15.0 ± 4.7 (6.5–31.8)	33 ± 6
European beech	70	23.0 ± 14.5 (6.0–59.7)	14.7 ± 5.4 (5.3–38.2)	38 ± 12
Pedunculate oak	63	20.0 ± 10.3 (6.6–47.5)	13.5 ± 5.0 (5.9–32.3)	35 ± 10

Pedunculate oak ring-width chronology presented the highest AC1, whereas Iberian birch chronology showed the highest MSx and Rbar (Table 2). EPS values for the three species were over 0.90 for 1977–2007, suggesting a satisfactory replication level. The chronologies of the three species were highly correlated, suggesting a high common signal (Iberian birch–pedunculate oak, $r = 0.541$; Iberian birch–European beech, $r = 0.535$; pedunculate oak–European beech, $r = 0.458$, $p < 0.01$ in all cases; Figure 2, lower plot).

Table 2. Dendrochronological statistics of the mean chronologies for the three studied trees. The residual chronology statistics correspond to the 1977–2007 common period. Abbreviations: SD = standard deviation, AC1 = first-order autocorrelation, MSx = mean sensitivity, Rbar = mean correlation coefficient among tree-ring series, and EPS = expressed population signal.

Tree species	Raw Data	Residual Chronology			
	Tree-ring width, mean ± SD (mm)	AC1	MSx	Rbar	EPS
Iberian birch	2.78 ± 1.75	0.62	0.21	0.29	0.97
European beech	3.03 ± 1.26	0.63	0.19	0.23	0.91
Pedunculate oak	2.46 ± 1.59	0.74	0.13	0.16	0.94

3.2. Tree-Ring Growth Response to Climate

Iberian birch and European beech responded positively to current April temperature and summer (June–August) precipitation, whilst pedunculate oak showed a weaker, but close to significant response to these variables (Figure 3). Pedunculate oak responded negatively to January temperature and positively to September temperature. The frequency of April hail was negatively correlated with the Iberian birch ($r = -0.508$, $p < 0.01$) and European beech ($r = -0.523$, $p < 0.01$) ring-width chronology, but had no significant association with pedunculate oak chronology.

We selected April temperature, April hail, and summer precipitation for individual sensitivity analyses. All these variables were significant for European beech and Iberian birch, and April temperature and summer precipitation were marginally significant for pedunculate oak. Individual tree chronologies showed lower correlation coefficients with climatic variables than species level chronologies, except for April hail and temperature for pedunculate oaks, which showed similar responses at the individual and species levels (i.e., species value was similar individual values median) (Figure 4). Therefore, species level analysis magnified climate–growth associations compared with the individual analysis. Moreover, individual responses were very scattered for all species, although Iberian birch showed more grouped correlation values, whereas pedunculate oak correlations were more dispersed (Figure 4).
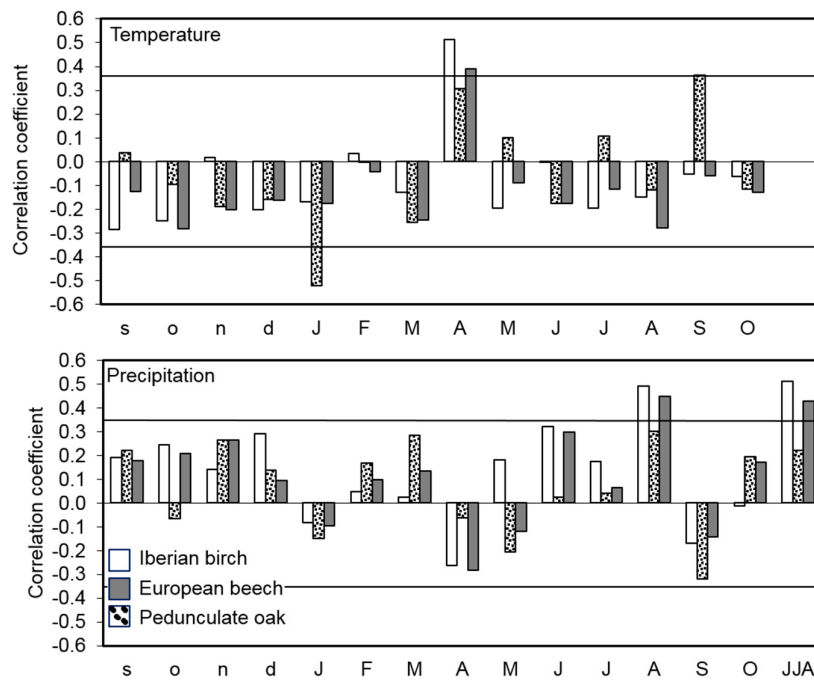
Figure 3. Pearson correlations between the indexed ring-width residual chronologies and monthly mean temperature and precipitation for the period between previous September and October of the growth year. Lowercase letters indicate the months before tree-ring formation, and the uppercase letters indicate months of the year of tree-ring formation. JJA (June-July-August) indicates summer precipitation (from June to August). The horizontal lines indicate the significance level ($p < 0.05$).
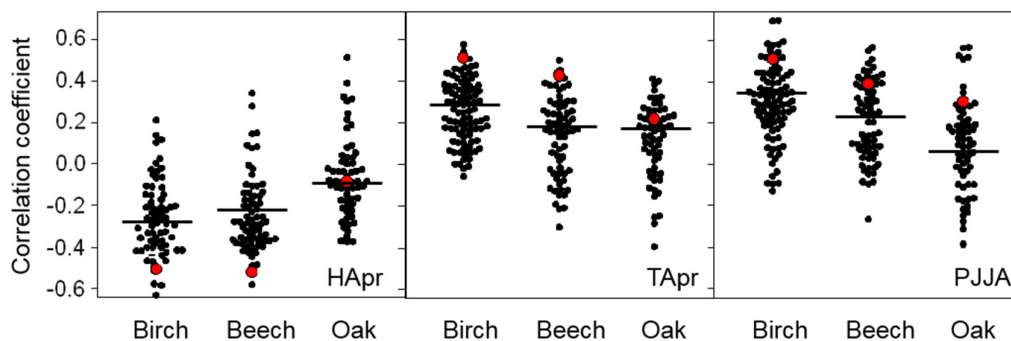

Figure 4. Individual tree climate–growth correlation coefficients calculated for the three tree species and considering selected significant climatic variables. Significant climatic variables: April hail (HApr) and mean temperature (TApr), and summer precipitation (PJJA, June-July-August precipitation). The red dots represent the species climate–growth correlations, the black dots show individual climate–growth correlations, and the horizontal lines indicate the medians of individual correlations.

3.3. Individual Growth Response

The differences in tree size (DBH and height) among the studied species were not significant (Table 1). Nevertheless, there were differences between the characteristics of the neighbourhoods. Iberian birch occupied less competitive neighbourhoods than European beech and pedunculate oak, in other words, Iberian birches were often surrounded by fewer trees (particularly fewer European beeches) and smaller trees in relation to the focal one (Table 3).

Table 3. Summary of the neighbourhood characteristics for the three species.

Species	If$_B$	If$_F$	If$_Q$	Cp	If$_T$
Iberian birch	38.2 ± 14.9	15.5 ± 12.5 [a]	11.6 ± 8.8	8.2 ± 4.7 [a]	68.2 ± 16.2
European beech	32.7 ± 16.0	20.8 ± 12.2 [b]	13.5 ± 9.7	10.9 ± 9.0 [b]	70.0 ± 20.6
Pedunculate oak	36.3 ± 15.0	17.9 ± 13.2 [a,b]	12.4 ± 10.3	11.4 ± 7.3 [b]	69.8 ± 20.2

If$_B$, If$_Q$, If$_F$, and If$_T$ are the influence indices based on the number of Iberian birch, pedunculate oak, European beech, and all tree species located within a 10 m radius from each focal tree, and Cp is the canopy position estimated by the number of trees higher than the focal tree within that same radius. Values are means ± standard deviation. The *a* and *b* superscripts show statistically significant differences (*p* < 0.05) among species based on analysis of variance.

Neighbourhood and tree size had substantial effects on tree growth, but these relationships varied among tree species. In Iberian birch, secondary growth depended on the presence of European beech and Iberian birch, as well as the number of trees higher than the focal, whereas in the pedunculate oak, only individual traits (height and diameter) showed significant influences on tree growth. Finally, both of the factors competition (European beech presence and the number of trees higher than the focal) and tree DBH modulated secondary growth in European beeches (Table 4). The models explain a large part of the radial growth variability in European beech and pedunculate oak (Table 4), but little in Iberian birch (10.7%).

Table 4. Selected multiple regression models of tree growth for the 1977–2007 common period and the three species.

Species Selected	x	y	DBH	H	If$_B$	If$_F$	Cp	Adjusted r^2
Iberian birch					−	−	−	0.107
European beech	+	+	+			−	−	0.543
Pedunculate oak			+	+				0.395

The symbols show the sign (+, positive; −, negative) of the factors included in each model. x and y are the spatial coordinates of the tree positions, DBH is the diameter at breast height (1.3 m) and H the tree height. If$_B$ and If$_F$ are the influence indices based on the number of Iberian birches or European beeches located within a 10 m radius from each focal tree, and Cp is the canopy position estimated by the number of trees higher than the focal tree within that same radius.

3.4. Effect of Environmental Factors on the Climate–Growth Response

Neighbourhood characteristics and tree individual traits modulated climate–growth relationship in the studied species (Table 5). Iberian birches surrounded by more conspecifics showed a lower growth response to April temperature, whereas Iberian birch response to April hail was higher (less negative) in neighbourhoods with higher European beech density and lower (more negative) in areas with higher pedunculate oak densities. European beech had a negative effect on the Iberian birch growth response to summer precipitation, thus, Iberian birches surrounded by more European beeches were less responsive to summer precipitation. In pedunculated oak, growth response to climate was associated to tree size and conspecific presence. Pedunculate oaks with a larger diameter, and in neighbourhoods with more conspecifics, showed stronger growth responses to April temperature, whereas response to summer precipitation depended on tree height and the presence of conspecifics. Thicker and taller pedunculate oaks were also more exposed to the deleterious effect of April hail. Finally, the best-fitted models for European beech included the tree height and DBH for April hail growth relationship (stronger negative effect for taller trees) and summer precipitation (higher response for larger diameters). Overall, the spatial position of the trees within the forest had a strong effect on their response to climate. Models for European beech showed the lowest explained variances (2%–9%) in climatic response, Iberian birch models explained 9%–16% of the variation, and, finally, pedunculate oak showed the best models, accounting for 16%–20% of the variation (Table 5).

Table 5. Selected multiple regression models explaining the variability in climate–growth relationships at the individual tree level.

Climatic Variable	Species	x	y	DBH	H	If$_B$	If$_F$	If$_Q$	Adjusted r^2
April mean temperature	Iberian birch	+				−			0.087
	European beech	+				−			0.036
	Pedunculate oak	+	+	+	+			+	0.177
April hail	Iberian birch	−					+	−	0.163
	European beech		+		−				0.088
	Pedunculate oak	−		−	−				0.156
June–August precipitation	Iberian birch	+					−		0.126
	European beech			+	+				0.017
	Pedunculate oak	+	+	+	+			+	0.198

The symbols show the sign (+, positive; −, negative) of the factors included in each model. Independent variables are x and y as the spatial coordinates of the tree positions, DBH is the diameter at breast height (1.3 m), H the tree height, If$_B$, If$_Q$, and If$_F$ are the influence indices based on the number of Iberian birch, pedunculate oak, or European beech trees located within a 10 m radius from each focal tree. The dependent variables were the correlation coefficients obtained by relating the ring-width indices and selected climatic variables at the tree level.

4. Discussion

4.1. Species-Dependent Growth Response to Climate

Growth response to climate differed among species. Secondary growth was controlled by April temperature and summer precipitation, with this effect being stronger in diffuse-porous species (Iberian birch and European beech). A higher spring temperature is associated with an earlier leaf flushing [49,50] and start of xylogenesis, determining longer periods for carbon gain and wood formation [51,52]. Summer water availability limits growth in European beech [13], and summer drought may be particularly relevant for Spanish European beech forests, forming the southernmost limit of distribution of the species in Europe [53,54]. Pedunculate oaks possess a deeper root system and forms ring-porous wood, which enables them to access deeper soil water [55], and to transport it rapidly to the crown, potentially reducing its dependence on summer precipitation and providing an advantage over Iberian birches and European beeches during dry growing seasons. However, summer drought and winter frosts cause the embolism of most previous-year earlywood vessels in pedunculate oaks, leading to a dependence on newly formed vessels, which concentrate up to 90% of the hydraulic conductivity. In contrast, species with diffuse-porous wood retain most of the conductive potential in the outer xylem layers, due to the small size of their vessels [56,57]. This difference poses a limitation to pedunculate oaks, since first earlywood row must be performed prior to leaf unfolding, with this formation being controlled by previous winter climate conditions [58,59]. This fact has an additional implication that earlywood and leaf formation in pedunculate oak is more dependent on the previous carbohydrates pools than in European beech [60]. Therefore, an increase in stem respiration associated with higher winter temperatures might reduce the carbohydrate pools available for cambial reactivation in pedunculate oaks, negatively affecting earlywood formation and leaf formation, and leading to narrower rings [61].

Although hail has a strong impact on agriculture production [52,62], its effect on tree growth has received little attention in forest sciences [41]. This may result from the scarcity of climatic stations with long-term records for hail [63], and from its spatial heterogeneity [62]. Hail events during leaf flushing in spring may severely damage bursting buds and tender leaves, leading to a reduction of the photosynthetic area and draining carbon pools, to the formation of new leaves and epicormic shoots. We showed that the impact of hail on tree growth was of similar magnitude to summer drought or low spring temperatures. Furthermore, we speculate that if climate warming leads to earlier bud breaks, some deciduous tree species (e.g., Iberian birch, European beech) might become more vulnerable to hail damage in early spring, as observed for spring frosts [64]. Our results suggest that the different

responses to climate among species were not related to competitive ability (early- to-late successional species), and that they can be attributed to different xylem anatomy.

4.2. Individual Tree Responses to Climate

Secondary growth depended on the characteristics of the focal trees and their neighbourhoods in the three studied species. Tree size was an important factor in pedunculate oak and European beech, controlling growth responsiveness to climate, whereas neighbourhood was a more relevant driver of growth reactions to climate in Iberian birch. Secondary growth and climate–growth relationship were modulated by similar tree and neighbourhood characteristics. Therefore, trees showing the highest growth rates presented the highest sensitivity to climate, as previously reported [9]. The effect of tree-level factors on climate–growth relationship could be related to each species' traits. For example, Iberian birch, pedunculate oak, and European beech show different leaf unfolding timing [65]. Iberian birches showed an earlier leaf flush than European beeches and pedunculate oak, thus gaining a time window with higher light levels. This relative advantage of an earlier canopy development in warm April might be minimised in environments where most neighbours show the same response pattern, so, where conspecific Iberian birches dominate [26]. Furthermore, European beech cover protected Iberian birches from the harmful April hailstorms, probably because of its branching architecture (horizontal and high branching) with higher interception rates, while less dense pedunculate oak neighbourhoods increased this damage. However, the European beech presence reduced the Iberian birch response to summer precipitation [26]. This is probably related to the presence of similar root systems, with shallow roots in Iberian birch and European beech, but the root system of European beech shows the highest efficiency in capturing soil water [66,67]. Rooting depth is considerably influenced by the soil character, and in soils with stony outcrops, birch develops shallow and superficial root systems [68]. Pedunculate oaks showed the largest variation in the individual growth responses, and the best individual climate–growth relationships models (accounting for a greater proportion of the total variation). Thicker and taller pedunculate oaks, with access to more resources and higher growth rates, showed higher sensitivity to the April temperature and summer precipitation [9]. The same factors enhanced the negative effect of April hail because of the increased exposure of the dominant large canopy trees. As shown in an earlier study in this forest, pedunculate oak mortality was related to pedunculate oak size and neighbourhood identity, since European beech presence increased pedunculate oak mortality, and Iberian birch presence decreased the mortality rate [40]. Surprisingly, pedunculate oak growth and individual climate sensitivity only depended on the size of the pedunculate oaks and the presence of conspecific trees in the neighbourhood. In pedunculate oak, competition for resources among individuals with similar traits (conspecific trees) results in an increase of the asymmetric competition [9]. Larger pedunculate oaks intercept a greater amount of resources, grow more, and are more sensitive to climate, and create the microclimatic conditions reducing the climate sensitivity of the suppressed trees [13,69]. Furthermore, neighbourhoods dominated by pedunculate oaks could favour the hydraulic lift, leading to soil water redistribution and growth enhancement [70]. Recent findings show that intraspecific facilitation is more frequent than it seems and e.g., McIntire and Fajardo show that conspecific plants benefit from clustering in mature *Nothofagus pumilio* forests. Finally, European beech response to climate show little dependence on tree size and neighbourhood identity, with individual climate–growth models explaining the small proportion of the total variation. European beeches are tolerant to low light levels, and very efficient in capturing soil water [60,61], which makes them good competitors that are less sensitive to the presence of other tree species [30,37]. European beeches in mixed stands, especially in presence of sessile oak, show a competition reduction that improves their climate resistance [37]. Therefore, the second hypothesis is accepted, trees' features and identity of neighbourhood modulated the climatic response of dominant trees in less competitive environments, showing greater climate sensitivity.

5. Conclusions

We showed that climate impacts on growth were not associated with variation in shade tolerance in this secondary forest. Differences in climate–growth relationship among species could be partially attributed to the different xylem anatomy, since secondary growth of ring-porous pedunculate oak was mainly dependent on the January temperature, while for the diffuse-porous Iberian birch and European beech, April temperature and summer precipitation were the major constraining factors.

We showed that individual traits (DBH and height) and neighbourhood modulate individual growth and growth–climate relationship. The effect of tree neighbourhood on climatic influences on radial growth was species dependent: early- and mid-successional species showed a stronger response to neighbourhood context than late-successional European beech. This species is tolerant to low light levels, and very efficient in capturing soil water, showing a competition reduction in this forest that improves their climate resistance. Nevertheless, in Iberian birch, climatic sensitivity was modulated by European beech and Iberian birch competition. Although European beeches protects Iberian birches from spring hail, its presence reduced the Iberian birch response to summer precipitation. We consider that the overall effect was negative, and therefore, European beeches worsen Iberian birches' climate resistance. Finally, pedunculate oaks showed the largest variation in the individual growth responses, but this variation only depended on the size of the pedunculate oaks, and the presence of conspecific trees in the neighbourhood. Neither the presence of Iberian birch nor European beech modulated growth response to climate. We can say that in this mixed forest, European beech was the only species that improves their climate resistance.

Forest ecosystems may be strongly affected by changing climate, and mixed forests may increase resilience to climate change through facilitation and competitive reduction. In the context of an expansion of secondary mixed forests, as result of traditional land use abandonment, there is a need to acquire better knowledge of climatic influences on radial growth in these mixed environments. Unveiling the highly heterogeneous responses of tree individuals to climate warming and extreme climate events might provide hints for adaptive forest management.

Author Contributions: Nere Amaia Laskurain, contributed in the design of the experiment, analyzed data, and wrote and edited the paper, Arantza Aldezabal and Iñaki Odriozola edited and wrote the paper Jesús Julio Camarero and José Miguel Olano contributed in the design of the experiment, analyzed data, and wrote and edited the paper.

Conflicts of Interest: The authors declare no conflict of interest.

References

1.　Cook, E.R. The decomposition of tree-ring series for environmental studies. *Tree-Ring Bull.* **1987**, *47*, 37–59.

2.　Swetnam, T.W.; Allen, C.D.; Betancourt, J.L. Applied historical ecology: Using the past to manage for the future. *Ecol. Appl.* **1999**, *9*, 1189–1206. [CrossRef]

3.　Yang, F.; Wang, N.; Shi, F.; Ljungqvist, F.C.; Wang, S.; Fan, Z.; Lu, J. Multi-proxy temperature reconstruction from the West Qinling Mountains, China, for the past 500 years. *PLoS ONE.* **2013**, *8*, e57638. [CrossRef] [PubMed]

4.　Batllori, E.; Gutiérrez, E. Regional tree line dynamics in response to global change in the Pyrenees. *J. Ecol.* **2008**, *96*, 1275–1288. [CrossRef]

5.　Olano, J.M.; Arzac, A.; García-Cervigón, A.I.; Arx, G.; Rozas, V. New star on the stage: Amount of ray parenchyma in tree rings shows a link to climate. *New Phytol.* **2013**, *198*, 486–495. [CrossRef] [PubMed]

6.　Pieper, H.; Heinrich, I.; Heußner, K.U.; Helle, G. The influence of volcanic eruptions on growth of central European lowland trees in NE-Germany during the last millennium. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2014**, *411*, 155–166. [CrossRef]

7.　Fritts, H.C. *Tree Rings and Climate*; Academic Press: London, UK, 1976.

8.　Carrer, M. Individualistic and time-varying tree-ring growth to climate sensitivity. *PLoS ONE* **2011**, *6*, e22813. [CrossRef] [PubMed]

9.　Rozas, V. Individual-based approach as a useful tool to disentangle the relative importance of tree age, size and inter-tree competition in dendroclimatic studies. *iForest* **2014**, *8*, 187–194. [CrossRef]

10.　Rozas, V.; Olano, J.M. Environmental heterogeneity and neighbourhood interference modulate the individual response of *Juniperus thurifera* tree-ring growth to climate. *Dendrochronologia* **2013**, *31*, 105–113. [CrossRef]

11.　Jump, A.S.; Hunt, J.M.; Martínez-Izquierdo, J.A.; Peñuelas, J. Natural selection and climate change: Temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. *Mol. Ecol.* **2006**, *15*, 3469–3480. [CrossRef] [PubMed]

12.　Carrer, M.; Urbinati, C. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* **2004**, *85*, 730–740. [CrossRef]

13.　Mérian, P.; Lebourgeois, F. Size-mediated climate–growth relationships in temperate forests: A multi-species analysis. *For. Ecol. Manag.* **2011**, *261*, 1382–1391. [CrossRef]

14.　Rozas, V.; DeSoto, L.; Olano, J.M. Sex specific, age dependent sensitivity of tree-ring growth to climate in the dioecious tree *Juniperus thurifera*. *New Phytol.* **2009**, *182*, 687–697. [CrossRef] [PubMed]

15.　Galván, J.D.; Camarero, J.J.; Gutiérrez, E. Seeing the trees for the forest: Drivers of individual growth responses to climate in *Pinus uncinata* mountain forests. *J. Ecol.* **2014**, *102*, 1244–1257. [CrossRef]

16.　Martin-Benito, D.; Kint, V.; Del Rio, M.; Muys, B.; Cañellas, I. Growth responses of West-Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity: Past trends and future perspectives. *For. Ecol. Manag.* **2011**, *262*, 1030–1040. [CrossRef]

17.　Magruder, M.; Chhin, S.; Monks, A.; O'Brien, J. Effects of initial stand density and climate on red pine productivity within Huron National Forest, Michigan, USA. *Forests* **2012**, *3*, 1086–1103. [CrossRef]

18.　Castagneri, D.; Motta, R. A research gap in the interactive effects of climate and competition on trees growth. In *Tree Growth: Influences, Layers and Types*; Karam, W.P., Ed.; Nova Science Publisher: New York, NY, USA, 2010; pp. 93–102.

19.　Sánchez-Gómez, D.; Zavala, M.A.; Van Schalkwijk, D.B.; Urbieta, I.R.; Valladares, F. Rank reversals in tree growth along tree size, competition and climatic gradients for four forest canopy dominant species in Central Spain. *Ann. For. Sci.* **2008**, *65*, 1. [CrossRef]

20.　Linares, J.C.; Camarero, J.J.; Carreira, J.A. Competition modulates the adaptation capacity of forests to climatic stress: Insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *J. Ecol.* **2010**, *98*, 592–603. [CrossRef]

21.　Tenzin, J.; Tenzin, K.; Hasenauer, H. Individual tree basal area increment models for broadleaved forests in Bhutan. *Forestry* **2017**, *90*, 367–380. [CrossRef]

22.　Gómez-Aparicio, L.; García-Valdés, R.; Ruíz-Benito, P.; Zavala, M.A. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: Implications for forest management under global change. *Glob. Chang. Biol.* **2011**, *17*, 2400–2414. [CrossRef]

23.　Sánchez-Salguero, R.; Linares, J.C.; Camarero, J.J.; Madrigal-González, J.; Hevia, A.; Sánchez-Miranda, Á.; Ballesteros-Cánovas, J.A.; Alfaro-Sánchez, R.; García-Cervigón, A.I.; Bigler, C.; et al. Disentangling the effects of competition and climate on individual tree growth: A retrospective and dynamic approach in Scots pine. *For. Ecol. Manag.* **2015**, *358*, 12–25. [CrossRef]

24.　Zhang, J.; Huang, S.; He, F. Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 4009–4014. [CrossRef] [PubMed]

25.　Zambrano, J.; Marchand, P.; Swenson, N.G. Local neighbourhood and regional climatic contexts interact to explain tree performance. *Proc. R. Soc. B* **2017**, *284*. [CrossRef] [PubMed]

26.　Lebourgeois, F.; Eberlé, P.; Mérian, P.; Seynave, I. Social status-mediated tree-ring responses to climate of *Abies alba* and *Fagus sylvatica* shift in importance with increasing stand basal area. *For. Ecol. Manag.* **2014**, *328*, 209–218. [CrossRef]

27. Gleason, K.E.; Bradford, J.B.; Bottero, A.; D'Amato, A.W.; Fraver, S.; Palik, B.J.; Battaglia, M.A.; Iverson, L.; Kenefic, L.; Kern, C.C. Competition amplifies drought stress in forests across broad climatic and compositional gradients. *Ecosphere* **2017**, *8*, e01849. [CrossRef]

28. González de Andrés, E.; Camarero, J.J.; Blanco, J.A.; Imbert, J.B.; Lo, Y.-H.; Sangüesa-Barreda, G.; Castillo, F.J. Tree-to-tree competition in mixed European beech–Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions. *J. Ecol.* **2017**, *106*, 59–75. [CrossRef]

29. Lebourgeois, F.; Gomez, N.; Pinto, P.; Mérian, P. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *For. Ecol. Manag.* **2013**, *303*, 61–71. [CrossRef]

30. Mölder, I.; Leuschner, C. European beech grows better and is less drought sensitive in mixed than in pure stands: Tree neighbourhood effects on radial increment. *Trees* **2014**, *28*, 777–792. [CrossRef]

31. Valladares, F.; Niinemets, Ü. Shade tolerance, a key plant feature of complex nature and consequences. *Annu. Rev. Ecol. Evol. Syst.* **2008**, *39*, 237–257. [CrossRef]

32. Bolte, A.; Eisenhauer, D.R.; Ehrhart, H.P.; Groß, J.; Hanewinkel, M.; Kölling, C.; Profft, I.; Rohde, M.; Röhe, P.; Amereller, K. Klimawandel und Forstwirtschaft—Übereinstimmungen und Unterschiede bei der Einschätzung der AnpassungsnotwendigkeitenundAnpassungsstrategien der Bundesländer. *Landbauforsch. vTI Agric. For. Res.* **2009**, *59*, 269–278.

33. Vanoni, M.; Bugmann, H.; Nötzli, M.; Bigler, C. Quantifying the effects of drought on abrupt growth decreases of major tree species in Switzerland. *Ecol. Evol.* **2016**, *6*, 3555–3570. [CrossRef] [PubMed]

34. Weemstra, M.; Eilmann, B.; Sass-Klaassen, U.G.; Sterck, F.J. Summer droughts limit tree growth across 10 temperate species on a productive forest site. *For. Ecol. Manag.* **2013**, *306*, 142–149. [CrossRef]

35. Walentowski, H.; Falk, W.; Tobias, M.; Kunz, J.; Bräuning, A.; Meinardus, C.; Zang, C.; Sutcliffe, L.; Leuschner, C. Assessing future suitability of tree species under climate change by multiple methods: A case study in southern Germany. *Ann. For. Sci.* **2017**, *60*, 101. [CrossRef]

36. Pretzsch, H.; Schutze, G. Effect of tree species mixing on the size structure, density, and yield of forest stands. *Eur. J. For. Res.* **2016**, *135*, 1–22. [CrossRef]

37. Pretzsch, H.; Schütze, G.; Uhl, E. Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter specific facilitation. *Plant Biol.* **2013**, *15*, 483–495. [CrossRef] [PubMed]

38. Chhin, S.; Wang, G. Climatic Sensitivity of a Mixed Forest Association of White Spruce and Trembling Aspen at Their Southern Range Limit. *Forests* **2016**, *7*, 235. [CrossRef]

39. Hartmann, H.; Messier, C. Interannual variation in competitive interactions from natural and anthropogenic disturbances in a temperate forest tree species: Implications for ecological interpretation. *For. Ecol. Manag.* **2011**, *261*, 1936–1944. [CrossRef]

40. Olano, J.M.; Laskurain, N.A.; Escudero, A.; De La Cruz, M. Why and where do adult trees die in a young secondary temperate forest? The role of neighbourhood. *Ann. For. Sci.* **2009**, *66*, 1–8. [CrossRef]

41. Hohl, R.; Schweingruber, F.H.; Schiesser, H.H. Reconstruction of severe hailstorm occurrence with tree rings: A case study in central Switzerland. *Tree-Ring Res.* **2002**, *58*, 11–22.

42. Herrera, J.; Laskurain, N.A.; Loidi, J.; Escudero, A.; Olano, J.M. Sucesión secundaria en un abedular-hayedo en el Parque Natural de Urquiola. Vizcaya. *Lazaroa* **2001**, *22*, 59–66.

43. Grissino-Mayer, H.D. Evaluating crossdating accuracy: A manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* **2001**, *57*, 205–221.

44. Cook, E.R.; Holmes, R.L. Guide for computer program ARSTAN. In *The International Tree-Ring Data Bank Program Library, Version 2.0.*; University of Arizona: Tucson, AZ, USA, 1996; Volume 2, pp. 75–87.

45. Helama, S.; Lindholm, M.; Timonen, M.; Eronen, M. Detection of climate signal in dendrochronological data analysis: A comparison of tree-ring standardization methods. *Theor. Appl. Climatol.* **2004**, *79*, 239–254. [CrossRef]

46. De Castro, M.D.; Martín-Vide, J.; Alonso, S. *El clima de España: Pasado, Presente y Escenarios de Clima Para el Siglo XXI*; Impactos del Cambio Climatico en España; Ministerio Medio Ambiente: Madrid, Spain, 2005.

47. Woods, K.D. Dynamics in late-successional hemlock-hardwood forests over three decades. *Ecology* **2000**, *81*, 110–126.

48. Calcagno, V. *Glmulti: Model Selection and Multimodel Inference Made Easy*; R Package Version, 1.7; R Package Vignette: Madison, WI, USA, 2013.

49. Bunn, A.G.; Goetz, S.J.; Fiske, G.J. Observed and predicted responses of plant growth to climate across Canada. *Geophys. Res. Lett.* **2005**, *32*, L16710. [CrossRef]

50. Chmielewski, F.M.; Rötzer, T. Response of tree phenology to climate change across Europe. *Agric. For. Meteorol.* **2001**, *108*, 101–112. [CrossRef]

51. Čufar, K.; Prislan, P.; de Luis, M.; Gričar, J. Tree-ring variation, wood formation and phenology of beech (*Fagus sylvatica*) from a representative site in Slovenia, SE Central Europe. *Trees* **2008**, *22*, 749–758. [CrossRef]

52. Lupi, C.; Morin, H.; Deslauriers, A.; Rossi, S. Xylem phenology and wood production: Resolving the chicken or egg dilemma. *Plant Cell Environ.* **2010**, *33*, 1721–1730. [CrossRef] [PubMed]

53. Piovesan, G.; Biondi, F.; Filippo, A.D.; Alessandrini, A.; Maugeri, M. Drought driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Glob. Chang. Biol.* **2008**, *14*, 1265–1281. [CrossRef]

54. Rozas, V.; Camarero, J.J.; Sangüesa-Barreda, G.; Souto, M.; García-González, I. Summer drought and ENSO-related cloudiness distinctly drive *Fagus sylvatica* growth near the species rear-edge in northern Spain. *Agric. For. Meteorol.* **2015**, *201*, 153–164. [CrossRef]

55. Scharnweber, T.; Manthey, M.; Wilmking, M. Differential radial growth patterns between beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) on periodically waterlogged soils. *Tree Physiol.* **2013**, *33*, 425–437. [CrossRef] [PubMed]

56. Essiamah, S.; Eschrich, W. Water uptake in deciduous trees during winter and the role of conducting tissues in spring reactivation. *IAWA J.* **1986**, *7*, 31–38. [CrossRef]

57. Hacke, U.; Sauter, J.J. Drought-induced xylem dysfunction in petioles, branches, and roots of *Populus balsamifera* L. and *Alnus glutinosa*. L. Gaertn. *Plant Physiol.* **1996**, *111*, 413–417. [CrossRef] [PubMed]

58. Alla, A.Q.; Camarero, J.J. Contrasting responses of radial growth and wood anatomy to climate in a Mediterranean ring-porous oak: Implications for its future persistence or why the variance matters more than the mean. *Eur. J. For. Res.* **2012**, *131*, 1537–1550. [CrossRef]

59. González, I.G.; Eckstein, D. Climatic signal of earlywood vessels of oak on a maritime site. *Tree Physiol.* **2003**, *23*, 497–504. [CrossRef] [PubMed]

60. Barbaroux, C.; Bréda, N.; Dufrêne, E. Distribution of above-ground and below-ground carbohydrate reserves in adult trees of two contrasting broad-leaved species. *Quercus petraea* and *Fagus sylvatica*. *New Phytol.* **2003**, *157*, 605–615. [CrossRef]

61. Rozas, V.; Lamas, S.; García-González, I. Differential tree-growth responses to local and large-scale climatic variation in two *Pinus* and two *Quercus* species in northwest Spain. *Ecoscience* **2009**, *16*, 299–310. [CrossRef]

62. Saa Requejo, A.; García Moreno, R.; Diaz Alvarez, M.C.; Tarquis, A.M.; Burgaz, F. Analysis of hail damages and temperature series for peninsular Spain. *Nat. Hazards Earth Syst. Sci.* **2011**, *11*, 3415–3422. [CrossRef]

63. Intergovernmental Panel on Climate Change (IPCC). *2013 Climate Change: The Physical Science Basis*; Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change; Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M., Eds.; IPCC: Cambridge, UK; New York, NY, USA, 2013.

64. Augspurger, C.K. Spring 2007 warmth and frost: Phenology, damage and refoliation in a temperate deciduous forest. *Funct. Ecol.* **2009**, *23*, 1031–1039. [CrossRef]

65. Fu, Y.H.; Campioli, M.; Deckmyn, G.; Janssens, I.A. Sensitivity of leaf unfolding to experimental warming in three temperate tree species. *Agr. For. Meteorol.* **2013**, *181*, 125–132. [CrossRef]

66. Grossiord, C.; Gessler, A.; Granier, A.; Berger, S.; Bréchet, C.; Hentschel, R.; Hommel, R.; Scherer-Lorenzen, M.; Bonal, D. Impact of interspecific interactions on the soil water uptake depth in a young temperate mixed species plantation. *J. Hydrol.* **2014**, *519*, 3511–3519. [CrossRef]

67. Leuschner, C.; Coners, H.; Icke, R. In situ measurement of water absorption by fine roots of three temperate trees: Species differences and differential activity of superficial and deep roots. *Tree Physiol.* **2004**, *24*, 1359–1367. [CrossRef] [PubMed]

68. Mauer, O.; Palátová, E. The role of root system in silver birch (*Betula pendula* Roth) dieback in the air-polluted area of Krušné hory Mts. *J. For. Sci.* **2003**, *49*, 191–199.

69. Piutti, E.; Cescatti, A. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. *Can. J. For. Res.* **1997**, *27*, 277–284. [CrossRef]
70. Zapater, M.; Hossann, C.; Bréda, N.; Bréchet, C.; Bonal, D.; Granier, A. Evidence of hydraulic lift in a young beech and oak mixed forest using 18O soil water labelling. *Trees* **2011**, *25*, 885–894. [CrossRef]