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Original Article

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Temperature more strongly influences Douglas-fir radial growth than precipitation under European temperate conditions

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Abstract

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has been introduced in Europe due to its high productivity. Although it is considered a relatively drought tolerant species, its ability to cope with climate change remains uncertain. This study aims to investigate the growth response of Douglas-fir to climate under European temperate conditions. A total of 720 bore cores were taken from 360 trees in 24 mature Douglas-fir stands in the Belgian Ardennes, spanning a range of annual climatic water balance (368–700 mm), estimated maximal soil extractable water reserve, and stand basal area (30–53 m^2/ha). Climate-growth relationships over the period 1976–2020 were investigated by calculating Bootstrapped Correlation Coefficients (BCCs) on detrended chronologies. Principal Component Analysis was computed on the BCCs to explore how growth response might be modulated according to the site and stand characteristics mentioned above. The results revealed (i) a consistent positive effect of higher February temperatures and precipitation on radial growth; (ii) a consistent negative effect of higher maximum temperatures in October of the current year; and (iii) a consistent positive effect of prior-year October minimum temperatures on radial growth, with these last two relationships becoming stronger in recent decades. These findings suggest that in these environments, Douglas-fir likely photosynthesizes through the winter period, and its growing season extends into October. The general lack of significant correlations between growth and precipitation except in February also suggests that temperatures are a more important driver than precipitation in influencing Douglas-fir productivity in this region. The site and stand conditions studied did not significantly influence these climate-growth relationships.

Keywords *Pseudotsuga menziesii*, dendroecology, climate response, tree ring, european forest

Introduction

Temperatures in Europe are projected to keep rising rapidly, while summer precipitation is expected to decrease globally (IPCC 2021). These changes, accompanied by an increase in the frequency and intensity of extreme events such as droughts and heatwaves, could threaten the growth and survival of forest ecosystems as we know them today (Lindner et al. 2014). In this context, *P. menziesii* (Mirb.) Franco or Douglas-fir is regularly cited as a species that could help sustain forest ecosystems services (e.g. Eilmann and Rigling 2012, Vitali et al. 2017, Mihai et al. 2022). Indeed, its high growth rate, valuable wood, high ecological plasticity, and lower susceptibility to pathogens and droughts than spruce (Thomas et al. 2022) are at the basis of its still growing economic success.

Douglas-fir is a species native to North America that was first introduced in Europe for its exceptional productivity. The species includes a coastal variety (var. menziesii) and a Rocky Mountain variety (var. glauca). The coastal variety, from the area between Washington and Oregon, has been most widely introduced in Europe (Lavender and Hermann 2014, Thomas et al. 2022). In its native range, this variety can grow under a wide range of climatic conditions. Average temperatures vary between 20 and 30°C in July and between −9 and 2.5°C in January. Mean annual precipitation is between 600 and 3000 mm, most of which occurs during winter (Lavender and Hermann 2014).

In Europe, Douglas-fir covers more than 820 000 ha, representing 0.4 per cent of the European forest area. It is best adapted to the temperate oceanic climate which is characterized by milder winters and wetter summer months than in its native region (Nicolescu 2019). The species is most productive when the mean annual temperature is between 7 and 11°C and when annual precipitation exceeds 750 mm (Nicolescu et al. 2023). Growth is limited when the average summer temperature (June to August) exceeds 18°C, and precipitation during the same period drops below 270 mm (Eckhart et al. 2019).

Douglas-fir grows best in deep, well-drained, silty to sandy-silty soils with a pH (H2O) of 4.5–7.2 (Eckhart et al. 2019). Its wide trophic range and its ability to cope with dry conditions also allow it to adapt very well to shallow, sandy or stony soils with lower water and nutrient reserves (Thomas et al. 2022). On the other hand, it is quite sensitive to anaerobiosis and soil compactness (Lavender and Hermann 2014).

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Even in sites where Douglas-fir has so far benefited from optimal climatic and edaphic conditions, the ongoing changes in Europe's climate may have an impact on the growth and vitality of the species. Some studies have revealed that the species has become more sensitive to hot and dry summer conditions and that it has experienced a recent growth decline (Gauli et al. 2022, Gribbe et al. 2024, Vejpustková and Čihák 2019). Moreover, significant biotic attacks on Douglas-fir have been reported in the past few years in regions that were part of the optimal climatic zone for Douglas-fir up to now, such as the Belgian Ardennes. These attacks have been observed primarily in young stands and are mainly associated with the insect *Contarinia pseudotsugae* Condrashoff, and two fungal pathogens: the Swiss needle cast (*Phaeocryptopus gaeumannii* (T.Rohde) Videira, C.Nakash., U.Braun & Crous) and *Sirococcus conigenus* (Pers.) P.F.Cannon & Minter (André et al. 2023). These biotic attacks may be related to an increased sensitivity of the trees to the changing climate. Therefore, questions remain as to how Douglas-fir will respond to climate in the future.

In its native range, the climatic drivers of Douglas-fir growth (coastal variety) depend on elevation: at low and mid elevations, higher precipitation and lower temperatures during summer promote growth (Dagley et al. 2023, Lee et al. 2016, Restaino et al. 2016), whereas at higher elevation, warmer winter conditions becomes increasingly beneficial (Lee et al. 2016). Precipitation seems to positively influence growth even at the northernmost and highest sites (Griesbauer and Scott Green 2010). In the European temperate oceanic climate (Beck et al. 2018), similar patterns to those at low and mid elevation in the native range have been observed (Castaldi et al. 2019, Gauli et al. 2022, Vitali et al. 2018). Milder winter and early spring temperatures can also have a positive influence on growth (Castaldi et al. 2019, Chen et al. 2010). The negative influence of drier and warmer summer conditions was found to increase over time (Enderle et al. 2024, Gauli et al. 2022) while the influence of other climatic variables overall remains stable (Vejpustková and Čihák 2019).

Several factors are likely to influence the growth response of Douglas-fir to climate. One important factor is a given site's water availability shaped by local climate and soil characteristics (Carnwath et al. 2012). Some studies showed indeed an increased climate sensitivity on sites with low water availability, due to an exacerbated water deficit (Carnwath et al. 2012, Gazol et al. 2022, Griesbauer et al. 2019). Other studies have shown the opposite effect, which was explained by the possible local acclimation of the trees to the site's low water availability (Castaldi et al. 2019; Chen et al. 2010). Lévesque et al. (2014) found no significant effect of climatic water balance.

Stand density may also impact the relationship between growth and climate through its effects on water availability (Aussenac 2000). Ford et al. (2016) showed that climate sensitivity is lower at higher densities and hypothesized that competition limits the ability of trees to take advantage of favourable climatic conditions. Lebourgeois et al. (2014) showed that sensitivity to dry conditions tends to increase with density. Carnwath and Nelson (2016) further showed that competition increases climate sensitivity in wet years, but has no effect when water availability is below average.

The aim of this study is to characterize the radial growth responses of Douglas-fir to climate in the Belgian Ardennes, taking into account environmental factors that may influence climate-growth relationships and recent drought events such as the one that occurred in central Europe in 2018. Up to now, the climate of the Belgian Ardennes has been among the most favourable in Europe for Douglas-fir growth (Nicolescu et al. 2023). However, recent declines in growth and increased sensitivity to dry conditions suggest that these optimal conditions may be changing (Gauli et al. 2022, Gribbe et al. 2024). In this context, we want to answer the following questions: (i) What are the main climatic drivers of Douglas-fir radial growth in the Belgian Ardennes? (ii) How do site water availability and stand density modulate growth response to climate? (iii) Are the climate-growth relationships stable over time? We assumed that Douglas-fir radial growth would be poorly responsive to hot and dry conditions on average (H1), but that it might be more sensitive on drier sites (climate × soil water reserve) and under conditions of higher stand density (H2). Given ongoing climate change, we also expected climate-growth relationships to evolve over time (H3). To verify these hypotheses, we applied a dendrochronological approach to wood cores extracted from dominant and co-dominant trees located in stands covering a wide range of site water availabilities and densities found in the Belgian Ardennes.

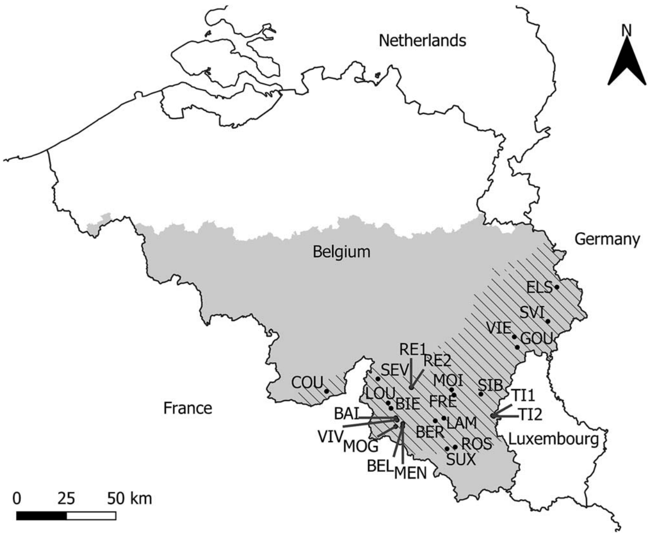

Figure 1 Location of the 24 study sites in Belgium. In grey the Walloon region and in hatched lines the Belgian Ardennes. The labels indicate the site code (see Table 1 for details).

Material and methods

Study sites and sampling design

We selected 24 study sites in the Belgian Ardennes (Fig. 1). The climate in this region is well representative of the temperate oceanic climate i.e. most favourable for Douglas-fir growth in Europe: mean annual temperature between 7 and 9°C (14–16°C for the summer), and mean annual precipitation between 980 and 1300 mm (240–300 mm in summer) for the period 1961–2020 (data from Royal Meteorological Institute of Belgium—RMI, described in the following section). Over this period, the mean annual temperature increased by 1.8°C and the mean summer temperature by 2.0°C (average climatic data for all sites). Annual and summer precipitation have tended to decrease in recent years, but these changes are not significant for the period 1961–2020 (Supplementary Material Fig. S1; Table S1).

All sites are located on a plateau, at an elevation between 340 and 600 m and on well drained stony loam soils (Cambisols in the WRB classification), like most of the Douglas-fir stands in Wallonia (more than 90 per cent of the area) (Alderweireld et al. 2015). The 24 selected sites are equally distributed into two zones with contrasting climatic water balance (CWB), crossed by two groups of soils differing in their maximal extractable soil water (MEW) (Table 1). CWB, defined as P-ET0, the difference between precipitation and reference potential evapotranspiration, was calculated from the daily climatic data described in the following section. When P-ET0 is <575 mm per year in average (median for all sites), the CWB is referred to as 'Low P-ET0,' and when it is >575 mm as 'High P-ET0.' Two MEW groups were delimited based on soil depth and stoniness derived from the detailed 1:20000 scale Belgian soil map (Dudal et al. 2005), and further checked in the field: more than 80 cm deep with stoniness below 15 per cent for high MEW, and less than 80 cm deep with stoniness greater than 15 per cent for low MEW. Based on detailed assessment carried out in similar soils in Wallonia, our sampling is expected to cover a range of MEW between 65 and 205 mm (Manise and Vincke 2014, Renard 2023).

The stands are even-aged, ranging from 48 to 67 years old at the time of sampling (2021). They cover a broad density gradient with a stand basal area (SBA) between 30 and 53 m^2/ha, of which at least 80 per cent is Douglas-fir (Table 1). The SBA corresponds to the basal area (BA) at half of the silvicultural thinning interval, computed from the BA measured at the sampling time, the average annual increment (Perin et al. 2016), and the year of the last thinning. For the analyses that follow, the stands are classified into three groups of contrasting densities: high (H) when SBA is greater than 44 m^2/ha, medium (M) when it is between 38 and 44 m^2/ha, and low (L) when it is below 38 m^2/ha. Stand density, mean diameter, and dominant height were obtained from measurements in 4 circular sample plots per stand. Most stands belong to the average yield class with a site index (SI, i.e. dominant height at some reference age) of 36 m at 50 years old, except SUX, COU and SIB which show higher productivity (SI = 40 m at 50 years old), and TI2, GOU and SEV which show lower productivity (SI = 32 m at 50 years old) (Perin et al. 2016).

Climatic data and indicators

Daily climatic data were obtained from the Royal Meteorological Institute of Belgium (RMI, https://opendata.meteo.be/) for the period 1961–2020. RMI provides gridded data with a spatial resolution of 5 × 5 km from which we selected the geographically closest point for each site. The data consist of daily minimum, maximum and mean temperatures, cumulative daily precipitation, and daily reference evapotranspiration (ET0). ET0 was calculated from radiation, air temperature, air humidity and wind speed data using the FAO Penman-Monteith method (Allen et al. 1998) and mean daily temperature from the average of daily minimum and maximum temperatures.

These data were aggregated into monthly and seasonal variables. Seasons were defined by three calendar months (i.e. winter = previous year Dec.–current year Feb., spring = Mar.–May, summer = June–Aug., autumn = Sept.–Nov.), or by eight calendar months for the growing season (Mar.–Oct.). Monthly/seasonal precipitation and evapotranspiration were calculated by summing daily data. Monthly minimum and maximum temperatures were defined as the absolute minimum and maximum of daily temperatures.

Drought and temperature stress indicators were also calculated: (i) the seasonal climatic water balance in mm (Wb) as the difference between precipitation and reference evapotranspiration over the corresponding period; (ii) the number of days with a minimum temperature below zero between April and June (late frost days) and between September and October (early frost days); (iii) the absolute value of the sum of daily minimum temperatures below zero between April and June (Late frost temperatures) and between September and October (early frost temperatures); (iv) the number of days with a mean temperature below −5°C (cold days); (v) the number of days with a maximum temperature above 30°C (hot days) (Raspe et al. 2020).

Dendroecological approach

Sampling and crossdating

In each of the 24 stands, 15 dominant or co-dominant trees were selected for sampling from May to November 2021. These trees were dominant in diameter (diameter greater than the minimum diameter of the 6 largest trees measured in each sample plot), and spaced at least 10 m apart, with independent crowns. Heavily defoliated trees (>20 per cent defoliation), and trees at the edge of the stand were avoided. Two cores per tree were taken at 1.3 m height with a 5 mm Pressler borer, from both the eastern and northern side of the selected trees, resulting in a total of 720 cores. The height and the circumference at 1.3 m of each sampled tree was also measured.

The wood cores were cut with a microtome along the transverse plane and air-dried before being scanned at 2400 dpi. Ring widths were then measured using CooRecorder (Maxwell and Larsson 2021). The last ring measured was the 2020 ring because the 2021 ring was not yet fully formed at the time of sampling. The chronologies were visually cross dated and then statistically checked using the COFECHA programme (Holmes 1983).

Average chronologies, standardization, and statistics

Individual tree-ring series were obtained by averaging the ring width of the two cores of each tree. These individual tree-ring series were then aggregated into site-level chronologies (master series) by calculating a bi-weighted robust mean for each site (Fig. S2). The study period (1976–2020; 44 years) was chosen to have a common interval for at least six trees per chronology (Cook and Kairiukstis 1991). Because our focus is on the short-term response of growth to interannual climate variations, individual tree-ring series were detrended using first a negative exponential, and then a 20 years cubic smoothing spline with a 50 per cent frequency response cut-off (Cook and Peters 1981). This method was chosen over the Regional Standardization Curve (RSC) method (Becker 1989, Esper et al. 2003), which selectively removes the age-related low-frequency signal, since our sampling targets only one age class. We did not remove the residual first-order autocorrelation from the obtained standardized chronologies, as it was low (<0.3) for almost all study sites.

Several statistics were calculated to characterize the ring width chronologies at each site: (i) mean ring width and standard deviation; (ii) coefficient of variation (ratio between the mean ring width and its standard deviation); (iii) mean sensitivity, which quantifies the interannual variability in the width of consecutive rings (Biondi and Qeadan 2008); (iv) first order serial autocorrelation, which measures the influence of previous year's conditions on ring formation (Lebourgeois and Mérian 2012). To assess the signal strength, two additional statistics were calculated from the detrended chronologies: (i) the inter-series correlation which is the mean of the correlation between each individual tree ring series and a master series calculated by averaging all individual series except the one under study; (ii)

Table 1 Site characteristics according to climatic water balance (P-ET0), maximal extractable soil water (MEW) and stand density groups (H = high, M = medium and L = low). T, P and P-ET0 are respectively the mean annual temperature, precipitation sum and difference between P and reference potential evapotranspiration (ET0) over the period 1961–2020.

				Climate				**Soil**		**Stand characteristics**				
				Altitude (m)	**T (°C)**	**P (mm)**	**P-ET0 (mm)**	**Depth (cm)**	**Stoniness (%)**	**Age (years)**	**Diameter (cm)**	**Height (m)**	**Density (Nb/ha)**	**SBA (m^2/ha)**
Low P-ET0	Low MEW	H	TI1	475	8.1	1075	468	40–80	15–50	55	46.2	40.8	314	52.7
		M	VIE	500	7.8	1070	468	40–80	15–50	47	47.4	33.1	300	41.7
			RE2	416	8.5	1066	462	40–80	15–50	55	52	37.9	176	39.3
		L	RE1	403	8.5	1066	462	40–80	15–50	53	52.1	38.1	161	35.9
			TI2	466	8.1	1075	468	40–80	15–50	57	48.9	35.1	200	35.8
			COU	347	8.8	1036	431	40–80	15–50	48	50	39.4	182	35.1
	High MEW	H	FRE	475	7.9	1139	550	> 80	0	67	60.5	43.9	179	51.0
			SEV	348	8.9	984	368	> 80	5–15	57	52	37.6	238	50.2
			SIB	541	7.7	1008	414	> 80	5–15	54	52.6	41.1	218	48.8
		M	MOI	547	7.8	1101	518	> 80	5–15	63	61.4	40.6	143	39.2
		L	GOU	483	8.0	1016	411	> 80	5–15	52	47.1	34.7	225	37.4
			SVI	492	7.7	1050	456	> 80	5–15	61	57.5	39.9	154	37.2
High P-ET0	Low MEW	H	VIV	402	8.2	1286	684	40–80	15–50	55	49.2	38.7	236	44.9
			ROS	451	8.5	1210	593	40–80	15–50	62	62.9	40.8	150	44.8
		M	MOG	391	8.5	1298	690	40–80	15–50	51	44.1	36.7	252	41.1
			ELS	591	7.0	1270	700	40–80	15–50	55	57.6	37.8	182	38.6
		L	BEL	431	8.5	1298	690	40–80	15–50	63	61.1	41.8	129	33.2
			SUX	405	8.5	1239	623	40–80	15–50	56	63.4	41.5	103	30.3
	High MEW	H	LAM	439	8.2	1216	615	> 80	5–15	58	50.3	40.8	239	50.0
			BER	460	8.2	1233	634	> 80	0	62	57.2	43.2	189	48.4
			BAI	422	8.2	1286	684	> 80	5–15	52	52.9	37	211	46.0
		M	LOU	396	8.3	1225	622	> 80	5–15	63	61	42.4	136	41.0
			BIE	395	8.2	1278	677	> 80	5–15	55	51.2	39.4	196	39.1
		L	MEN	401	8.2	1286	684	> 80	0	50	48	37.9	193	33.9

The soil depth and stoniness are estimated from the Belgian soil map and should therefore be interpreted as indicative values. The mean diameter was measured at 1.3 m high. The height is the dominant height, defined here as the average height of the tree in each plot that is closest to the dominant diameter. The density corresponds to the number of trees per hectare. The SBA is the Stand Basal Area.

the expressed population signal, which indicates the strength of the common signal compared to the total signal.

The calculation of average chronologies and dendrochronological statistics, as well as the standardisation procedure, was carried out using the dplR package (Bunn 2008) in R software (R Core Team 2022).

Climate-growth relationships

Climate-growth relationships over the 44-years common period for all sites (1976–2020) were investigated through the calculation of Bootstrapped Correlation Coefficients (BCCs; Guiot 1991) with the treeclim R package (Zang and Biondi 2015). Detrended master chronologies per site were used as dependent variable. Climatic explanatory variables were of three types: (i) monthly indicators: average temperature (Tavg), minimal minimum temperature (Tmin), maximum temperature (Tmax), and precipitation sum (P) organized from March of the previous growing season, to October of the current growing year; (ii) water stress indicators: seasonal climatic water balance (Wb) from the spring of the previous growing season to the autumn of the current growing year; (iii) temperature related indicators: late and early frosts days (FrostD), late and early frosts temperatures (FrostT), cold days (ColdD), and hot days (HotD). The significance of the coefficients was evaluated by generating 1000 bootstrap resamples of the data and calculating the confidence level at 95 per cent.

Principal Component Analysis (PCA) was computed on the BCCs for P and Tavg obtained for each site for the whole period (1976–2020) to evaluate the influence of three environmental factors on the growth response to climate: the mean climatic water balance (P-ET0; $\leq$ 575 mm vs $>$ 575 mm), the maximal extractable soil water (low, high), and the stand density (SBA; $>$ 44 m^2/ha, between 38 and 44 m^2/ha, $\leq$ 38 m^2/ha). These factors were introduced in the PCA as additional qualitative variables. The PCA was performed with the ‘FactoMineR’ package (Lê et al. 2008), using the variance–covariance matrix since the descriptors (the BCCs) were of the same type and had similar magnitudes.

Correlation functions on 30-years moving windows were also computed with the same climatic regressors to assess the change in growth response through time. This window length corresponds to at least 1.5 times the number of predictors tested, which makes it possible to maintain sufficient degrees of freedom (Biondi 1997). Each moving window is offset by one year from the previous one. Two successive windows are therefore overlapping over 29 years. Since no major differences were found when calculating BCC per site over the entire period, this analysis was realized with a master chronology calculated for all sites together and with climatic data and indicators averaged for all sites.

Results

Characteristics of tree-ring chronologies

Mean annual radial growth (RW) ranged from 4.54 to 6.24 mm per year, with values between 5 and 6 mm/year for most of the study sites regardless of stand basal area level. The coefficient of variation which allows the comparison of the dispersion of ring width values varied between 0.11 and 0.25. Mean sensitivity (MS) varied between 0.12 and 0.20. The four highest values were observed for sites with a low climatic water balance (TI1, TI2, SEV and SIB). No major difference in MS values was observed between sites with low and high maximal extractable soil water. First order autocorrelation (AC1) ranged between 0.56 and 0.78. The interseries correlation (cor.ser) varied between 0.49 and 0.73, which indicates a correct crossdating. All chronologies had EPS values above 0.85, indicating a strong common signal i.e. presumably climate signal (Wigley et al. 1984). All the dendrochronological statistics are listed in Table 2.

Effect of climate on Douglas-fir growth

In general, more significant correlations were observed for a larger number of sites in the current year than in the year preceding ring formation, and for temperatures rather than precipitation (Fig. 2). The correlations with temperature and precipitation were mostly positive, except for the maximum temperature in October of the current year for which negative correlations were observed for most of the sites (17 out of 24). Late winter-early spring (February–March) of the current year seemed to be a crucial period for growth, with many positive correlations observed for precipitation, mean temperature and minimum temperature. The end of the growing season of the previous year (September–October), and the month of December also seemed to affect growth with the positive influence of the temperatures. To a lesser extent, precipitation in early summer of the current year (June and July) influenced Douglas-fir growth with significant positive correlations for 7 (June) and 9 (July) out of 24 sites.

The temperature-related indicators that most negatively influence growth were the cold days of February and the early frosts (days and temperatures) of the current year (22, 16 and 15 sites out of 24, respectively). Late frosts and hot summer temperatures had no significant influence. Concerning the water balance, most positive correlations were observed for the current growing season and the current summer. Some correlations were also observed with the winter water balance, but no significant correlations were observed for the spring.

Effect of climatic water balance, maximal extractable soil water and density on climate—growth relationships

The first two axes of the Principal Component Analysis (PC1 and PC2) performed on the bootstrapped correlation coefficients (BCCs) for the monthly precipitation sum (P) and mean temperature (T) explained 25.1 per cent and 15.2 per cent of the total variance, respectively (Fig. 3a). The BCCs for late winter-early spring precipitation (December of the previous year, January and March of the current year), and of the end of the growing season (September and October) showed strong correlations with PC1 scores. PC2 scores were mainly positively correlated with the BCCs for temperatures of the previous and current summer (June, July and August), and negatively correlated with the BCCs for precipitation of the current summer (June, July and August).

PC1 and PC2 did not allow a clear separation of sites according to the level of climatic water balance (low and high P-ET0), maximal extractable soil water (low and high MEW) and stand density (low, medium and high BAs) (Figs 3b–d).

Temporal evolution of climate-growth relationships and climate

The positive correlations observed with precipitation (P), mean temperature (Tavg) and minimum temperature (Tmin) during late winter-early spring remained stable over time (Fig. 4). This is not the case for the positive influence of Tmin at the end of the growing season of the previous year (September–October) which became significant only from the 1982–2011 window. Positive correlations with precipitation

Table 2 Chronologies statistics for the common period 1976–2020.

				RW	±	sd	CV	MS	AC1	cor.ser	EPS
Low P-ET0	Low MEW	H	TI1	4.54	±	1.10	0.24	0.19	0.62	0.71	0.94
		M	VIE	5.67	±	1.44	0.25	0.13	0.78	0.68	0.94
			RE2	4.96	±	0.62	0.13	0.15	0.58	0.60	0.91
		L	RE1	5.45	±	0.78	0.14	0.14	0.66	0.52	0.87
			TI2	5.35	±	1.15	0.21	0.20	0.58	0.71	0.95
			COU	6.24	±	1.56	0.25	0.16	0.70	0.73	0.95
	High MEW	H	FRE	5.23	±	0.71	0.14	0.14	0.56	0.67	0.93
			SEV	5.64	±	1.32	0.23	0.17	0.70	0.68	0.94
			SIB	5.00	±	1.10	0.22	0.17	0.63	0.51	0.87
		M	MOI	5.56	±	0.80	0.14	0.15	0.58	0.65	0.92
		L	GOU	5.81	±	1.48	0.25	0.14	0.78	0.55	0.89
			SVI	5.23	±	0.91	0.17	0.16	0.66	0.64	0.92
High P-ET0	Low MEW	H	VIV	5.32	±	0.93	0.17	0.14	0.67	0.54	0.88
			ROS	5.46	±	1.15	0.21	0.16	0.65	0.62	0.92
		M	MOG	5.63	±	1.34	0.24	0.14	0.73	0.54	0.88
			ELS	5.69	±	0.83	0.15	0.14	0.63	0.65	0.93
		L	BEL	5.46	±	0.75	0.14	0.12	0.65	0.60	0.91
			SUX	5.81	±	0.99	0.17	0.14	0.68	0.67	0.94
	High MEW	H	LAM	5.09	±	0.92	0.18	0.15	0.66	0.65	0.93
			BER	4.87	±	0.78	0.16	0.16	0.67	0.62	0.92
			BAI	5.59	±	1.11	0.20	0.14	0.68	0.68	0.94
		M	LOU	5.10	±	0.56	0.11	0.12	0.69	0.51	0.86
			BIE	5.59	±	1.30	0.23	0.16	0.71	0.52	0.88
		L	MEN	5.82	±	0.71	0.12	0.15	0.62	0.49	0.85

The study sites are classified according to climatic water balance (P-ET0), maximal extractable soil water (MEW) and stand density (H = high, M = medium and L = low). RW = mean ring width in millimeters, sd = standard deviation, CV = coeff. of variation (sd/RW), MS = mean Sensitivity, AC1 = first autocorrelation, cor.ser = interseries cor., EPS = Expressed Population Signal.

during the early summer of the current year (June and July) were only significant for a few time windows from 1983 onwards. The negative correlation with Tmax in October of the current year observed for most of the sites increased with time and became significant only for the last time windows (1991–2020).

Concerning the stress indicators, the positive correlations with summer and growing season water balance (Wb) for the current year were significant starting from the 1980s. The same was true for the negative correlation with early frosts (FrostT and FrostD in September–October). In contrast, the correlation with the cold days in February (ColdD.FEB) remained stable throughout the whole period studied). This is consistent with the results obtained for Tmin in February of the current year.

The temporal evolution of the climatic regressors (P, Tmin, Tmax and Tavg) was calculated by season for the period 1961–2020 (Supplementary Material Fig. S1; Table S1) to understand the temporal evolution of the climate-growth relationships. Spring and autumn were the periods during which all the climatic regressors were the most stable. Only the mean temperature increased significantly during these seasons (+1.93 and + 1.12°C respectively). In winter, in addition to the increase in temperature (+3.68, +2.43 and + 2.13 for Tmin, Tmax and Tavg respectively), precipitation rose by 113 mm. In summer, precipitation seemed to be decreasing since the 2000s, but this decrease was not significant. The summer temperature increased significantly (+1.84, +3.56 and + 2.04 for Tmin, Tmax and Tavg respectively).

Discussion

Major climatic drivers of Douglas-fir radial growth

The results indicate that late winter to early spring (February–March) plays a key role in the radial growth dynamics of Douglas-fir. Warmer and wetter conditions during this period favoured current year's growth, irrespective of the climatic water balance, maximal extractable soil water and stand density level. Similar positive effects of spring temperatures have been reported by other European studies in temperate oceanic climates (Castaldi et al. 2019, Gauli et al. 2022, Gazol et al. 2017). The importance of this period has also been highlighted in Central Europe (Charlet de Sauvage et al. 2023, Feliksik and Wilczyński 2009, Levanič and Štraus 2022, Vejpustková and Čihák 2019), as well as in the native range of Douglas-fir in the United States (Chen et al. 2010).

One possible explanation is linked to the early start of cambial activity when conditions are favourable (Begum et al. 2013, Rossi et al. 2016). On average, Douglas-fir growth starts in mid-April (Miller et al. 2022), but it can start sooner when temperature rises (Huang et al. 2020, Miller et al. 2022). This was indeed the case in the study area over the period 1961–2020.

Like other evergreen conifers, Douglas-fir can show photosynthetic activity under mild winter conditions (>5°C) (Guehl et al. 1985), leading to improved growth and carbon storage for the following year (Chen et al. 2010, Lebourgeois et al. 2010). Indeed, in Wallonia, eddy covariance measurements showed that, on average, Douglas-fir trees start their main period of photosynthetic activity in February and end it in November (Aubinet et al. 2016). The positive correlations with the maximum temperature in December of the previous year could therefore also be explained by the extension of the period with favourable conditions (temperature, radiation) for winter photosynthesis.

Another possible explanation for the positive influence of warmer temperatures in winter and early spring could be the reduced exposure to late frost and winter desiccation (Vejpustková and Čihák 2019). Low night temperatures, large short-term temperature fluctuations, and high irradiation can together induce drought stress in trees that

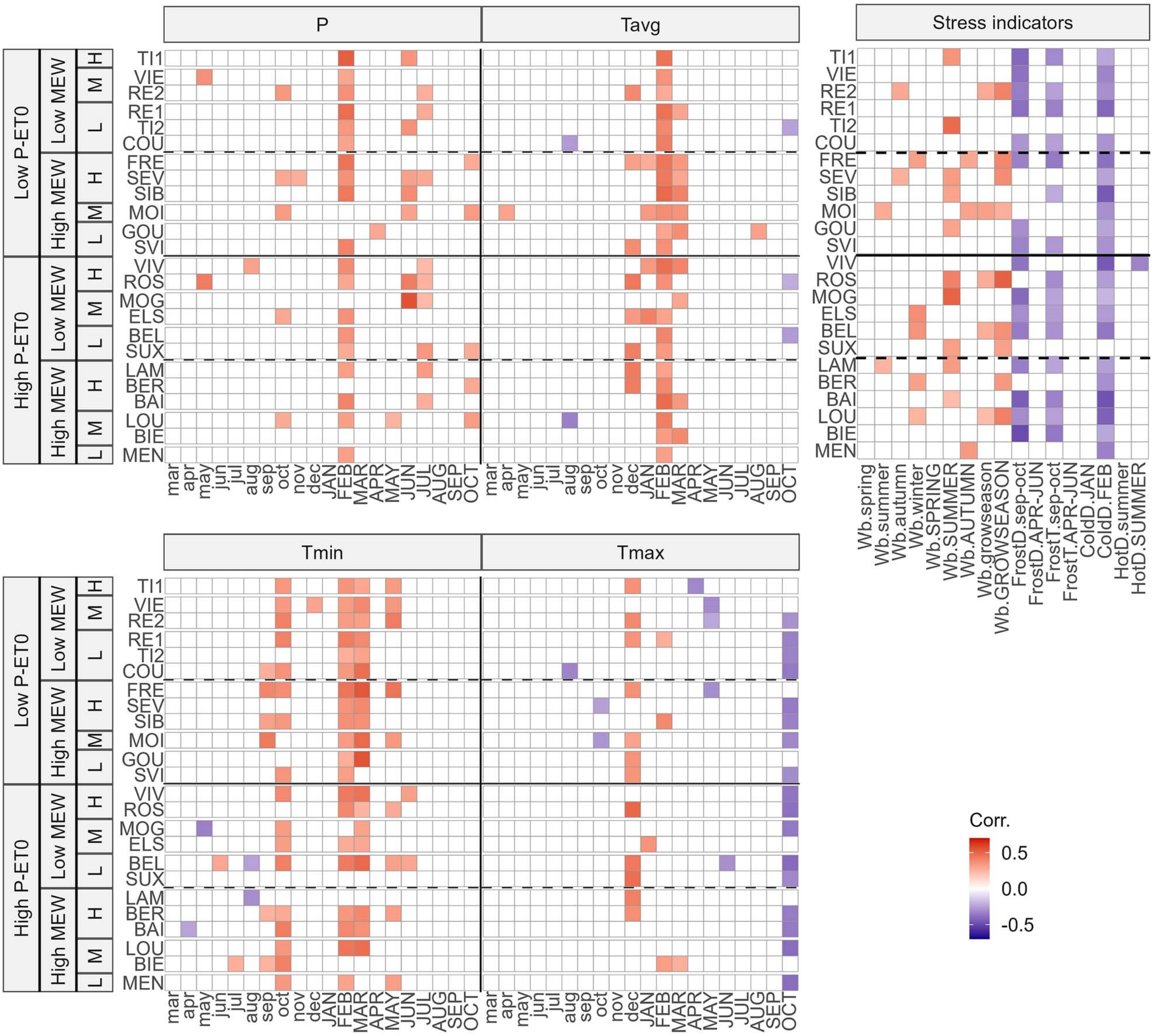

Figure 2 Significant bootstrapped correlation coefficients (BCCs) with radial growth for the 24 study sites classified according to climatic water balance (P-ET0), maximal extractable soil water (MEW), and stand density (H = high, M = medium and L = low). The significant correlations ($P < .05$) are represented with coloured squares. P = monthly precipitation sum, Tavg = monthly mean temperature, Tmax and Tmin = maximum and minimum temperatures. Months in full caps refer to current year (previous year otherwise). ColdD = cold days, FrostD = frost days, HotD = hot days, Wb = water balance.

can no longer meet the evaporative demand (Malmqvist et al. 2018). This phenomenon is often observed on Douglas-fir in France, mainly in young individuals (less than 15 years) (Saintonge et al. 2023).

Radial growth of Douglas-fir was enhanced by warmer temperatures and the absence of frost at the end of the previous growing season (September–October). Similar results were obtained in western Romania with a positive effect of warmer autumn temperatures (Mihai et al. 2022). This may be related to a delayed growth cessation, allowing the trees to improve carbon storage and growth for the following year (Ford et al. 2017). Douglas-fir dormancy can be induced by cool autumn temperatures where temperature is a limiting factor, while it is more controlled by the photoperiod where it is warmer (Ford et al. 2017). The positive correlations observed with the minimum temperatures at the end of the previous growing season suggest that temperature is indeed a limiting factor. Vejpustková and Čihák (2019) observed the opposite relationships with temperatures in September of the previous year, and explained it by the possible delay in cold hardening which increases cold injury (Bansal et al. 2015). The study by Bansal et al. (2015) focused on young trees, which may therefore be more sensitive to this phenomenon. However, Noordermeer et al. (2021) also studied young trees and showed no disruption in cold acclimation for the coastal variety of Douglas-fir when the carbon uptake period was extended by autumn warming. In our study, Douglas-fir appears sensitive to early frost (September–October), but the effect of warmer temperatures during this period remains positive.

As we expected, Douglas-fir radial growth was not very sensitive to hot and dry summer conditions (H1). It did not respond to summer temperatures (Tavg, Tmax, hot days) despite their significant increase during the studied period. Positive effects on growth were

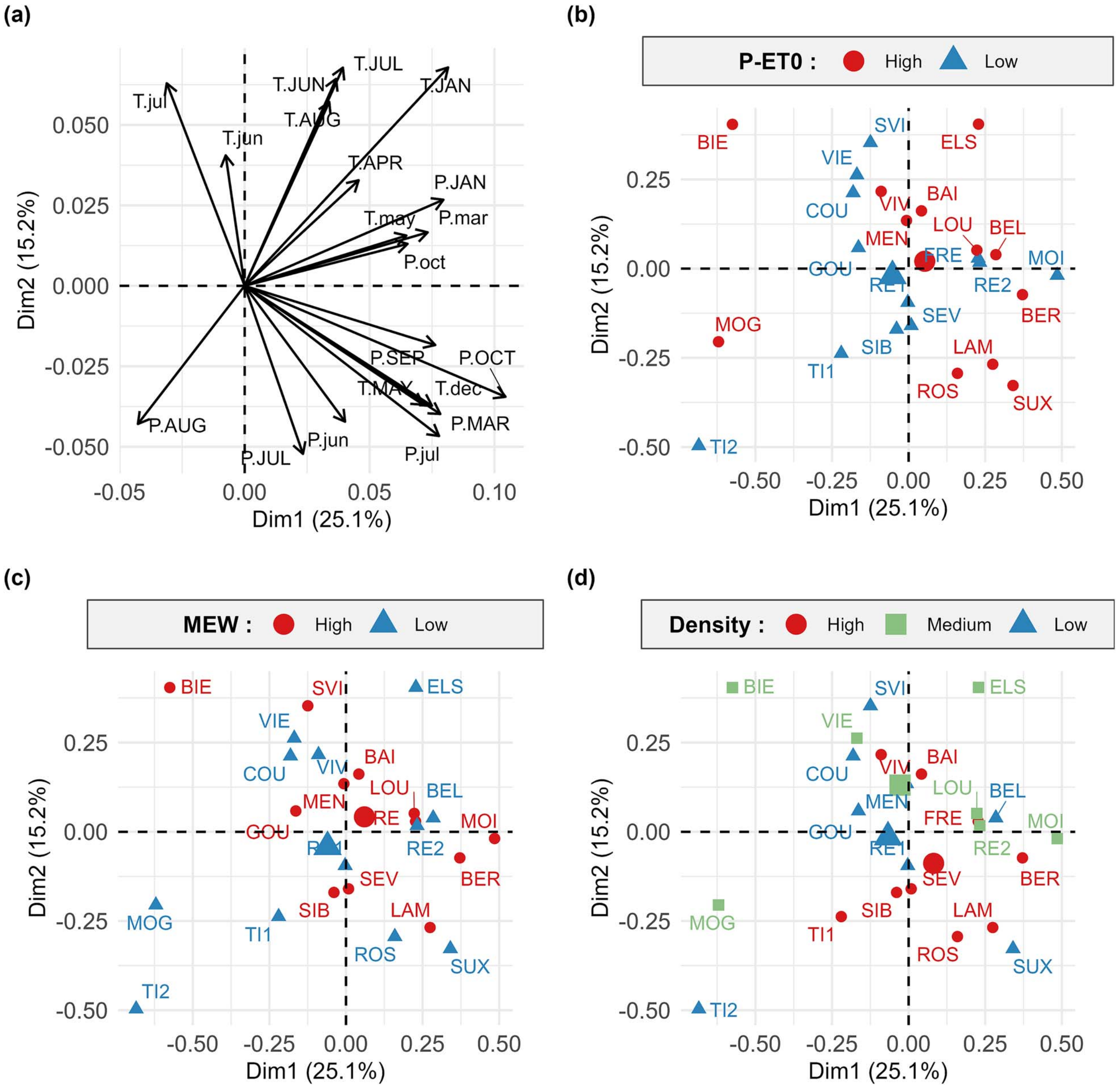

Figure 3 Principal component analysis of the bootstrapped response coefficients between the standardized ring-width chronologies and the monthly mean temperatures (T) and precipitation sums (P). (a) The 20 most influential climate variables. Months in full caps refer to the current year (previous year otherwise). Vectors pointing in the same direction indicate a high positive correlation, whereas opposite direction indicates negative correlation. (b) the 24 sites are coloured according to the climatic water balance (high and low P-ET0); (c) according to the maximal extractable soil water; (d) according to the stand density level. For each group, in the same colour but larger size, the centre of gravity of the ellipses of point concentration (ellipses not shown because too much overlap).

nevertheless observed at a limited number of study sites when early summer precipitation was higher, and the water balance was favourable. This positive effects of wetter summer conditions is frequently observed both in the native range of Douglas-fir (e.g. Littell et al. 2008, Chen et al. 2010, Jarecke et al. 2024) and in Europe (e.g. Vejpustková and Čihák 2019, Levanič and Štraus 2022, Charlet de Sauvage et al. 2023), but unlike what we observed in our study, it is often associated with a reduction in growth when summer conditions are warmer (Castaldi et al. 2019, Gauli et al. 2022, Mihai et al. 2022, Trouvé et al. 2014, Vitali et al. 2018). These effects on radial growth can be explained by the fact that a lack of water or very high temperatures in summer can induce an early cessation of cambial cell division (Eilmann et al. 2011, Ford et al. 2017, Miller et al. 2022), which slows down on average in the first half of September (Miller et al. 2022). Warmer summer temperatures can also have an indirect effect on growth by favouring the development of pathogens such as Swiss needle cast (*Nothophaeocryptopus gaeumannii*) when combined with wet conditions (Lee et al. 2013).

An increase in maximum temperatures in October of the year of ring formation resulted in radial growth reduction of Douglas-fir for most of the study sites. This result does not appear in other studies, which generally investigate the relationship between growth and climate until September (e.g. Vitali et al. 2018, Castaldi et al. 2019, Levanič and Štraus 2022, Charlet de Sauvage et al. 2023). It suggests

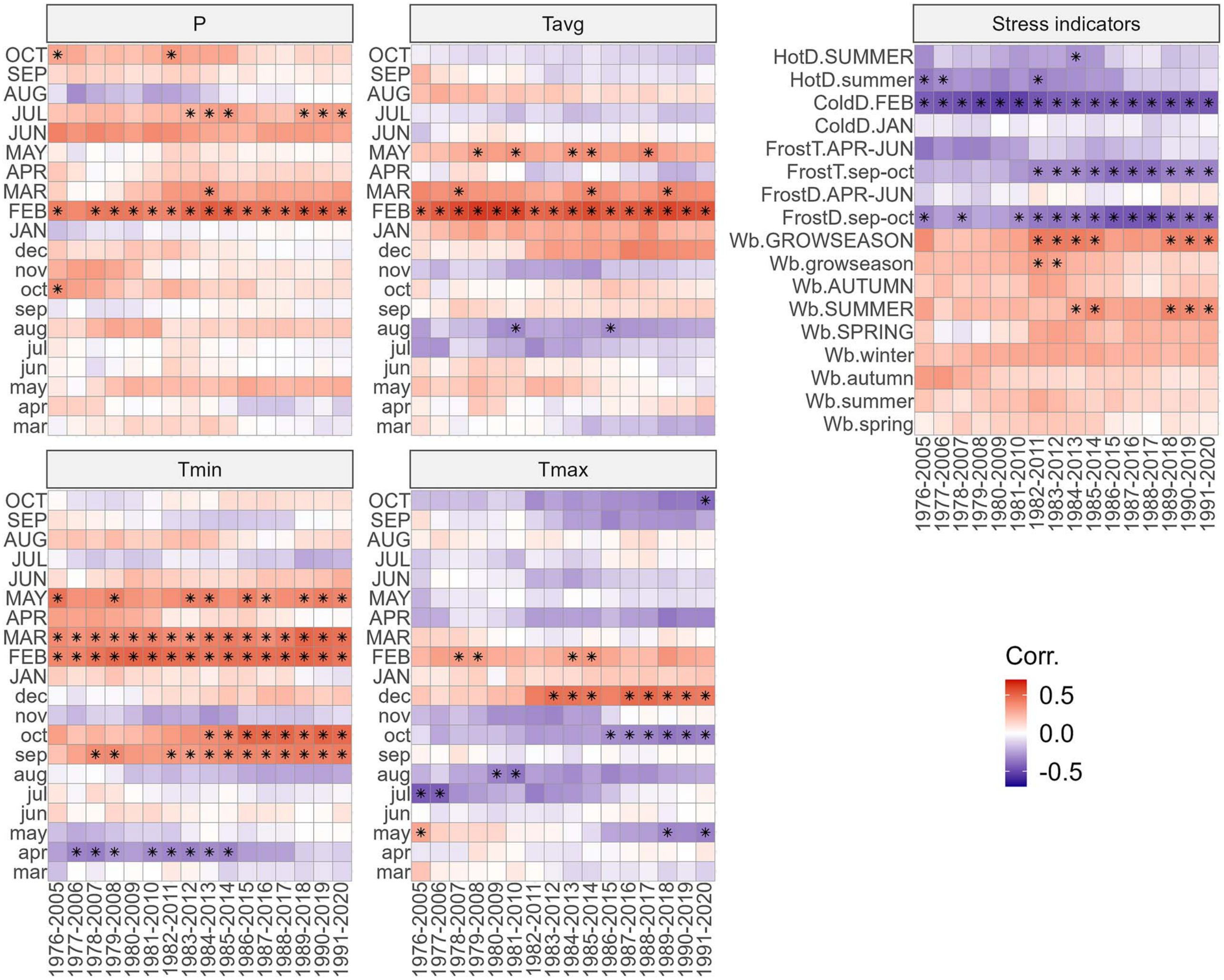

Figure 4 Moving correlations with radial growth on 30-year moving windows at regional level (all sites together). The monthly climatic variables P, Tavg, Tmin and Tmax correspond respectively to precipitation sum, average temperature, minimum temperature, and maximal temperature. Months in full caps refer to the current year (previous year otherwise). Significant correlations ($P < .05$) are marked with black asterisks.

that Douglas-fir growth can continue beyond September in the Belgian Ardennes. Emmingham (1977) also observed cambial growth until the end of October in western Oregon (USA). An increase in temperature during this period could reduce growth by increasing the vapour pressure deficit which could affect growth even in the presence of sufficient soil moisture (Jarecke et al. 2023, Restaino et al. 2016). This could also exacerbate the effects of water shortages in soils that have not yet been recharged by winter precipitation. The few positive correlations observed with October precipitation support this hypothesis. Another possible explanation is related to respiration which, like water availability, limits the net primary productivity (NPP) (Girardin et al. 2016). Both photosynthesis and respiration increase during autumn warming, but the increase in respiration is greater (Krishnan et al. 2009, Piao et al. 2008).

Environmental factors influence on climate-growth relationships

Contrary to our expectations (H2), principal component analysis shows no clear differences in response to climate as a function of the mean climatic water balances (P-ET0), maximal soil extractable water (MEW) and stand densities covered by the study sites.

The lack of P-ET0 effect is consistent with the good adaptation of Douglas-fir to the temperate oceanic climate of the Belgian Ardennes. Even the study site with the most restrictive climatic conditions (SEV, Table 1) remains within the range of optimal growing conditions for Douglas-fir (Nicolescu et al. 2023). Lévesque et al. (2014) studied the influence of the same factor over a wider climatic gradient in Central Europe. They did not detect any effect on climate growth sensitivity and explained it by the buffering role played by the soil at the site level.

Concerning the influence of soil on the growth-climate relationship, we might have expected an increase in climate sensitivity, especially to dry conditions, at low MEW (Lebourgeois et al. 2010, Weber et al. 2013). Here the lack of effect of MEW could be related to its use as a qualitative variable, estimated using simple soil descriptors (stoniness and depth) as proxies for water availability. This could have resulted in insufficient contrast between MEW groups. A more precise measurement of the MEW at a greater depth would be required to confirm or not its influence. Douglas-fir is indeed able to extend its roots into rock crevices deep in the soil, and has a root biomass mostly located between 0 and 125 cm depth (Thomas et al. 2015).

Higher stand density implies higher competition for nutrient, water and light resources (Aussenac 2000). This can have an influence on climate sensitivity, which can be positive or negative depending on the context (Carnwath and Nelson 2016, Ford et al. 2016). The results here did not show any differences in climate response according to this parameter. This may indicate that, on average, water availability was sufficient regardless the stand density in the range sampled (SBA between 30 and 53 m^2/ha). It should also be remembered that SBA was defined here as the stand basal area at half the silvicultural thinning interval estimated at the time of sampling. However, we have very little information on the management history of the stands.

Despite the wide range of stands sampled in terms of average climatic water balance, maximum water reserve and stand density within the study area, the response of Douglas-fir to climate appears to be relatively homogeneous. This may suggest that under the optimal growing conditions of the temperate oceanic climate, radial growth is more influenced by the climatic sensitivity of the Douglas-fir species than by site-specific characteristics such as stand density modulated by the silviculture interventions. This may also suggest that the study did not span a sufficiently wide gradient of ecological and stand conditions to identify patterns in BCC variability. However, differences in growth response could appear during extreme climatic events such as drought. This issue was addressed in a complementary study based on the same data (Guisset et al. 2024) and in several other studies, which produced divergent results (e.g. Sergent et al. 2012, Carnwath and Nelson 2017, Charlet de Sauvage et al. 2023).

Climate-growth relationships stability through time

Moving correlation functions (MCFs) were calculated at the regional level which is justified by the homogeneity of the growth response to climate across the study sites. Although the influence of some climatic parameters remained stable over the study period, the MCFs confirmed that Douglas-fir's sensitivity to climate evolved over time (H3).

The positive influence of mild, wet late winters-early springs remained stable over the whole period studied (1976–2020). The stability of the temperature influence over the same period has been shown in another study in a temperate oceanic climate (Gauli et al. 2022). In contrast, the influence of temperatures in winter (December), and at the end of the growing season (September and October) tended to increase. This could be related to the significant increase in temperature in the study area for all seasons, and particularly in winter which shows the strongest increase in the minimum temperature (+3.7°C over the period 1961–2020, Table S1 in the Supplementary Material).

As in several other studies (e.g. Castaldi et al. 2019, Gribbe et al. 2024, Levanič and Štraus 2022, Vejpustková and Čihák 2019), the influence of summer water availability (P and Wb) was increasing, with significant correlations only for the last decades. This increase may be related to the decrease in summer precipitation since the early 2000s, although this increase was not significant when considering the whole study period. We might have expected a similar increase in the influence of summer temperatures, since they can have an impact on soil water and are also rising, but this has not been observed. Their influence remained insignificant throughout the study period.

It has been assumed here that the relationship between growth and climate does not vary with age once the low-frequency signal has been removed with standardisation. However, several authors have shown that age can have an influence on the sensitivity of growth to climate, and that this can vary between species (Carrer and Urbinati 2004, Konter et al. 2016, Mašek et al. 2021). The age effect could therefore be another explanation for the observed change in the growth-climate relationships. However, these studies generally show an effect at a much older ages (>200 years) than the Douglas-fir trees studied here (max 67 years at the time of sampling).

Conclusion

We investigated the radial growth response of Douglas-fir in the Belgian Ardennes, under European temperate oceanic climate. Our study showed that radial growth of Douglas-fir is favoured by mild and wet late winters-early springs, warmer temperatures at the end of the previous growing season and in winter, and lower maximal temperatures during October of the current year. Temperatures had an overall dominant role in influencing radial growth compared to precipitation.

Despite the diversity of climatic water balance, estimated soil water reserve, and stand basal area covered by the study sites, these factors did not significantly modulate climate-growth relationships, indicating a broadly uniform response of Douglas-fir within this temperate environment.

Over the next few decades, the global increase in temperatures could have a positive effect on Douglas-fir growth due to its ability to take advantage of higher late growing season and winter temperatures. This effect could be offset by a decrease in summer precipitation as our study showed a recent increase in the sensitivity of Douglas-fir to summer water deficits. However, the lack of influence of summer temperatures despite their increase suggests that this result should be interpreted with caution.

Further studies exploring additional indicators of growth sensitivity to climate, such as wood anatomical traits, and comparing the climatic responses of Douglas-fir with those of other native and non-native tree species established in Europe, would provide deeper insights into the adaptability of Douglas-fir to the ongoing climate change.

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Author contributions

C.G., C.V and Q.P. designed the study and defined the methods; C.G. conducted the field work, performed the tree ring measurements, and analysed the data; all authors contributed to the interpretation of the results. C.G. wrote the manuscript, with the contributions of C.V. and Q.P. C.V. and Q.P. co-supervised the research.

Supplementary data

Supplementary data are available at *Forestry* online.

Conflicts of interest

None declared.

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Data availability

The data underlying this article are available in Zenodo repository, at https://doi.org/10.5281/zenodo.16736962.

References

Alderweireld, M., Burnay, F., Pitchugin, M., *et al.* 2015 Inventaire Forestier Wallon. Résultats 1994–2012. SPW, DGO3, DNF, Namur, Belgium, p. 246.

Allen, R.G., Pereira, L.S., Raes, D., *et al.* 1998 Crop evapotranspiration-guidelines for computing crop water requirements-FAO irrigation and drainage paper 56. *Rome Food Agric Organ U N* **300**, D05109.

André, A., Bay, E., Bologna, A., *et al.* 2023 *La Lettre d’info de L’OWSF n° 10. Données 2022*. Observatoire Wallon de la Santé des Forêts, Gembloux, Belgium.

Aubinet, M., Vincke, C., Heinesch, B., *et al.* 2016 Vingt ans de mesures des échanges de CO2 et de vapeur d’eau à l’Observatoire Terrestre de Vielsalm. *For Nat* **139**, 17–28.

Aussenac, G. 2000 Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Ann For Sci* **57**, 287–301. https://doi.org/10.1051/forest:2000119.

Bansal, S., St. Clair, J.B., Harrington, C.A., *et al.* 2015 Impact of climate change on cold hardiness of Douglas-fir (Pseudotsuga menziesii): environmental and genetic considerations. *Glob Change Biol* **21**, 3814–3826. https://doi.org/10.1111/gcb.12958.

Beck, H.E., Zimmermann, N.E., McVicar, T.R., *et al.* 2018 Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Sci Data* **5**, 180214. https://doi.org/10.1038/sdata.2018.214.

Becker, M. 1989 The role of climate on present and past vitality of silver fir forests in the Vosges mountains of northeastern France. *Can J For Res* **19**, 1110–1117. https://doi.org/10.1139/x89-168.

Begum, S., Nakaba, S., Yamagishi, Y., *et al.* 2013 Regulation of cambial activity in relation to environmental conditions: understanding the role of temperature in wood formation of trees. *Physiol Plant* **147**, 46–54. https://doi.org/10.1111/j.1399-3054.2012.01663.x.

Biondi, F. 1997 Evolutionary and moving response functions in dendroclimatology. *Dendrochronologia.* **15**, 139–150.

Biondi, F. and Qeadan, F. 2008 Inequality in paleorecords. *Ecology.* **89**, 1056–1067. https://doi.org/10.1890/07-0783.1.

Bunn, A.G. 2008 A dendrochronology program library in R (dplR). *Dendrochronologia.* **26**, 115–124. https://doi.org/10.1016/j.dendro.2008.01.002.

Carnwath, G. and Nelson, C. 2017 Effects of biotic and abiotic factors on resistance versus resilience of Douglas fir to drought. *PloS One.* **12**, e0185604. https://doi.org/10.1371/journal.pone.0185604.

Carnwath, G.C. and Nelson, C.R. 2016 The effect of competition on responses to drought and interannual climate variability of a dominant conifer tree of western North America. *J Ecol* **104**, 1421–1431. https://doi.org/10.1111/1365-2745.12604.

Carnwath, G.C., Peterson, D.W. and Nelson, C.R. 2012 Effect of crown class and habitat type on climate–growth relationships of ponderosa pine and Douglas-fir. *For Ecol Manage* **285**, 44–52. https://doi.org/10.1016/j.foreco.2012.07.037.

Carrer, M. and Urbinati, C. 2004 Age-dependent tree-ring growth responses to climate in Larix decidua and Pinus cembra. *Ecology.* **85**, 730–740. https://doi.org/10.1890/02-0478.

Castaldi, C., Marchi, M., Vacchiano, G., *et al.* 2019 Douglas-fir climate sensitivity at two contrasting sites along the southern limit of the European planting range. *J For Res* **31**, 2193–2204. https://doi.org/10.1007/s11676-019-01041-5.

Charlet de Sauvage, J., Bugmann, H., Bigler, C., *et al.* 2023 Species diversity and competition have minor effects on the growth response of silver fir, European larch and Douglas fir to drought. *Agric For Meteorol* **341**, 109664. https://doi.org/10.1016/j.agrformet.2023.109664.

Chen, P.-Y., Welsh, C. and Hamann, A. 2010 Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. *Glob Change Biol* **16**, 3374–3385. https://doi.org/10.1111/j.1365-2486.2010.02166.x.

Cook, E.R. and Kairiukstis, L.A. 1991 *Methods of Dendrochronology: Applications in the Environmental Sciences*. Springer Science & Business Media, Dordrecht, The Netherlands, p. 403.

Cook, E.R. and Peters, K. 1981 The smoothing spline: a new approach to standardizing Forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bull* **41**, 45–53.

Dagley, C.M., Berrill, J.-P. and Fraver, S. 2023 Forest restoration mitigates drought vulnerability of coast Douglas-fir in a Mediterranean climate. *Can J For Res* **53**, 210–216. https://doi.org/10.1139/cjfr-2022-0119.

Dudal, R., Deckers, J., Van Orshoven, J., *et al.* 2005 *Soil Survey in Belgium and its Applications (No. 9)*. European Soil Bureau, Office for Official Publications of the European Communities, Luxembourg city, Luxembourg.

Eckhart, T., Pötzelsberger, E., Koeck, R., *et al.* 2019 Forest stand productivity derived from site conditions: an assessment of old Douglas-fir stands (Pseudotsuga menziesii (Mirb.) Franco var. menziesii) in Central Europe. *Ann For Sci* **76**, 19. https://doi.org/10.1007/s13595-019-0805-3.

Eilmann, B. and Rigling, A. 2012 Tree-growth analyses to estimate tree species’ drought tolerance. *Tree Physiol* **32**, 178–187. https://doi.org/10.1093/treephys/tps004.

Eilmann, B., Zweifel, R., Buchmann, N., *et al.* 2011 Drought alters timing, quantity, and quality of wood formation in Scots pine. *J Exp Bot* **62**, 2763–2771. https://doi.org/10.1093/jxb/erq443.

Emmingham, W.H. 1977 Comparison of selected Douglas-fir seed sources for cambial and leader growth patterns in four western Oregon environments. *Can J For Res* **7**, 154–164. https://doi.org/10.1139/x77-022.

Enderle, L., Gribbe, S., Muffler, L., *et al.* 2024 A warmer climate impairs the growth performance of Central Europe’s major timber species in lowland regions. *Sci Total Environ* **941**, 173665. https://doi.org/10.1016/j.scitotenv.2024.173665.

Esper, J., Cook, E.R., Krusic, P.J., *et al.* 2003 Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies. *Tree-Ring Res* **59**, 81–98.

Feliksik, E. and Wilczyński, S. 2009 The effect of climate on tree-ring chronologies of native and nonnative tree species growing under homogenous site conditions. *Geochronometria.* **33**, 49–57. https://doi.org/10.2478/v10003-009-0006-4.

Ford, K.R., Breckheimer, I.K., Franklin, J.F., *et al.* 2016 Competition alters tree growth responses to climate at individual and stand scales. *Can J For Res* **47**, 53–62. https://doi.org/10.1139/cjfr-2016-0188.

Ford, K.R., Harrington, C.A. and St. Clair, J.B. 2017 Photoperiod cues and patterns of genetic variation limit phenological responses to climate change in warm parts of species' range: modeling diameter-growth cessation in coast Douglas-fir. *Glob Change Biol* **23**, 3348–3362. https://doi.org/10.1111/gcb.13690.

Gauli, A., Neupane, P.R., Mundhenk, P., *et al.* 2022 Effect of climate change on the growth of tree species: dendroclimatological analysis. *Forests.* **13**, 496. https://doi.org/10.3390/f13040496.

Gazol, A., Camarero, J.J., Anderegg, W.R.L., *et al.* 2017 Impacts of droughts on the growth resilience of northern hemisphere forests. *Glob Ecol Biogeogr* **26**, 166–176. https://doi.org/10.1111/geb.12526.

Gazol, A., Valeriano, C., Cantero, A., *et al.* 2022 Douglas fir growth is constrained by drought: delineating the climatic limits of timber species under seasonally dry conditions. *Forests.* **13**, 1796. https://doi.org/10.3390/f13111796.

Girardin, M.P., Hogg, E.H., Bernier, P.Y., *et al.* 2016 Negative impacts of high temperatures on growth of black spruce forests intensify with the anticipated climate warming. *Glob Change Biol* **22**, 627–643. https://doi.org/10.1111/gcb.13072.

Gribbe, S., Enderle, L., Weigel, R., *et al.* 2024 Recent growth decline and shifts in climatic growth constraints suggest climate vulnerability of beech, Douglas fir, pine and oak in northern Germany. *For Ecol Manage* **566**, 122022. https://doi.org/10.1016/j.foreco.2024.122022.

Griesbauer, H.P., Klassen, H., Saunders, S.C., *et al.* 2019 Variation in climate-growth relationships for Douglas-fir growth across spatial and temporal scales on southern Vancouver Island, British Columbia. *For Ecol Manage* **444**, 30–41. https://doi.org/10.1016/j.foreco.2019.04.014.

Griesbauer, H.P. and Scott Green, D. 2010 Assessing the climatic sensitivity of Douglas-fir at its northern range margins in British Columbia, Canada. *Trees.* **24**, 375–389. https://doi.org/10.1007/s00468-009-0407-z.

Guehl, J.M., Clerc, B. and Desjeunes, J.M. 1985 Etude comparée des potentialités hivernales d'assimilation carbonée de trois conifères de la zone tempérée (Pseudotsuga menziesii Mirb., Abies alba mill. Et Picea excelsa link.). *Ann Sci For* **42**, 23–38. https://doi.org/10.1051/forest:19850102.

Guiot, J. 1991 The bootstrapped response function. *Tree-Ring Bull* **51**, 39–41.

Guisset, C., Dendoncker, M., Vincke, C., *et al.* 2024 Drought timing, intensity, and consecutiveness have more influence on Douglas fir response than site conditions and stand density in European temperate climate. *For Ecol Manage* **569**, 122177. https://doi.org/10.2139/ssrn.4804994.

Holmes, R.L. 1983 Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull* **43**, 69–78.

Huang, J.-G., Ma, Q., Rossi, S., *et al.* 2020 Photoperiod and temperature as dominant environmental drivers triggering secondary growth resumption in northern hemisphere conifers. *Proc Natl Acad Sci* **117**, 20645–20652. https://doi.org/10.1073/pnas.2007058117.

IPCC 2021 In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. V., Masson-Delmotte, P., Zhai, A., Pirani, S.L., Connors, C., Péan, S., Berger, *et al.* (eds). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jarecke, K.M., Bladon, K.D., Meinzer, F.C., *et al.* 2024 Impact of rainfall and vapor pressure deficit on latewood growth and water stress in Douglas-fir in a Mediterranean climate. *For Ecol Manage* **551**, 121529. https://doi.org/10.1016/j.foreco.2023.121529.

Jarecke, K.M., Hawkins, L.R., Bladon, K.D., *et al.* 2023 Carbon uptake by Douglas-fir is more sensitive to increased temperature and vapor pressure deficit than reduced rainfall in the western Cascade Mountains, Oregon, USA. *Agric For Meteorol* **329**, 109267. https://doi.org/10.1016/j.agrformet.2022.109267.

Konter, O., Büntgen, U., Carrer, M., *et al.* 2016 Climate signal age effects in boreal tree-rings: lessons to be learned for paleoclimatic reconstructions. *Quat Sci Rev* **142**, 164–172. https://doi.org/10.1016/j.quascirev.2016.04.020.

Krishnan, P., Black, T.A., Jassal, R.S., *et al.* 2009 Interannual variability of the carbon balance of three different-aged Douglas-fir stands in the Pacific northwest. *J Geophys Res Biogeosciences* **114**, G04011. https://doi.org/10.1029/2008JG000912.

Lavender, D.P. and Hermann, R.K. 2014 *Douglas-Fir: The Genus Pseudotsuga.* Oregon Forest Research Laboratory, Oregon State University, Corvallis, USA, p. 378.

Lê, S., Josse, J. and Husson, F. 2008 FactoMineR: an R package for multivariate analysis. *J Stat Softw* **25**, 1–18. https://doi.org/10.18637/jss.v025.i01.

Lebourgeois, F., Eberlé, P., Mérian, P., *et al.* 2014 Social status-mediated tree-ring responses to climate of Abies alba and Fagus sylvatica shift in importance with increasing stand basal area. *For Ecol Manage* **328**, 209–218. https://doi.org/10.1016/j.foreco.2014.05.038.

Lebourgeois, F., Rathgeber, C.B.K. and Ulrich, E. 2010 Sensitivity of French temperate coniferous forests to climate variability and extreme events (Abies alba, Picea abies and Pinus sylvestris). *J Veg Sci* **21**, 364–376. https://doi.org/10.1111/j.1654-1103.2009.01148.x.

Lebourgeois FF, Mérian P. 2012 Principes et méthodes de la dendrochronologie, AgroParis Tech-ENGREF, Nancy, France, p. 85.

Lee, E.H., Beedlow, P.A., Waschmann, R.S., *et al.* 2013 Tree-ring analysis of the fungal disease Swiss needle cast in western Oregon coastal forests. *Can J For Res* **43**, 677–690. https://doi.org/10.1139/cjfr-2013-0062.

Lee, E.H., Beedlow, P.A., Waschmann, R.S., *et al.* 2016 Douglas-fir displays a range of growth responses to temperature, water, and Swiss needle cast in western Oregon, USA. *Agric For Meteorol* **221**, 176–188. https://doi.org/10.1016/j.agrformet.2016.02.009.

Levanič, T. and Štraus, H. 2022 Effects of climate on Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) growth southeast of the European Alps. *Plants.* **11**, 1571. https://doi.org/10.3390/plants11121571.

Lévesque, M., Rigling, A., Bugmann, H., *et al.* 2014 Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. *Agric For Meteorol* **197**, 1–12. https://doi.org/10.1016/j.agrformet.2014.06.001.

Lindner, M., Fitzgerald, J.B., Zimmermann, N.E., *et al.* 2014 Climate change and European forests: what do we know, what are the uncertainties, and what are the implications for forest management? *J Environ Manage* **146**, 69–83. https://doi.org/10.1016/j.jenvman.2014.07.030.

Littell, J.S., Peterson, D.L. and Tjoelker, M. 2008 Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. *Ecological monographs* **78**, 349–368. https://doi.org/10.1890/07-0712.1.

Malmqvist, C., Wallertz, K. and Johansson, U. 2018 Survival, early growth and impact of damage by late-spring frost and winter desiccation on Douglas-fir seedlings in southern Sweden. *New For* **49**, 723–736. https://doi.org/10.1007/s11056-018-9635-7.

Manise, T. and Vincke, C. 2014 Impacts du climat et des déficits hydriques stationnels Sur la croissance radiale du hêtre, du chêne, de l'épicéa et du Douglas en Wallonie. *For Wallonne* **129**, 48–57.

Mašek, J., Tumajer, J., Rydval, M., *et al.* 2021 Age and size outperform topographic effects on growth-climate responses of trees in two central European coniferous forest types. *Dendrochronologia.* **68**, 125845. https://doi.org/10.1016/j.dendro.2021.125845.

Maxwell, R.S. and Larsson, L.-A. 2021 Measuring tree-ring widths using the CooRecorder software application. *Dendrochronologia.* **67**, 125841. https://doi.org/10.1016/j.dendro.2021.125841.

Mihai, G., Curtu, A.-L., Alexandru, A.-M., *et al.* 2022 Growth and adaptive capacity of Douglas fir genetic resources from Western Romania under climate change. *Forests.* **13**, 805. https://doi.org/10.3390/f13050805.

Miller, T.W., Stangler, D.F., Larysch, E., *et al.* 2022 Longer and faster: intra-annual growth dynamics of Douglas fir outperform Norway spruce and silver fir over wide climatic gradients. *Agric For Meteorol* **321**, 108970. https://doi.org/10.1016/j.agrformet.2022.108970.

Nicolescu, V.-N. 2019 Natural range, site requirements and shade tolerance. In *Douglas-Fir – An Option for Europe*. H., Spiecker, M., Lindner, J., Schuler (eds). European Forest Institute, Joensuu, Finland, pp. 33–39.

Nicolescu, V.-N., Mason, W.L., Bastien, J.-C., *et al.* 2023 Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) in Europe: an overview of management practices. *J For Res* **34**, 871–888. https://doi.org/10.1007/s11676-023-01607-4.

Noordermeer, D., Velasco, V.M.E. and Ensminger, I. 2021 Autumn warming delays the downregulation of photosynthesis and does not increase the risk of freezing damage in interior and coastal Douglas-fir. *Front For Glob Change* **4**, 688534. https://doi.org/10.3389/ffgc.2021.688534.

Perin J, Hebert J, Lejeune P. *et al.* 2016 Nouvelles normes sylvicoles pour les peuplements purs équiennes d'épicéa et de Douglas, Gembloux Agro-Bio Tech, Université de Liège, Gembloux, Belgium, p. 26.

Piao, S., Ciais, P., Friedlingstein, P., *et al.* 2008 Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature.* **451**, 49–52. https://doi.org/10.1038/nature06444.

R Core Team 2022 *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org.

Raspe, S., Fleck, S., Beuker, E., *et al.* 2020 Meteorological measurements. Version 2020-1. In *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests*. Programme Co-ordinating Centre of ICP Forests, Thünen Institute of Forest Ecosystems, Eberswalde, Germany.

C. Renard 2023 *Caractérisation du Risque de Stress Hydrique édaphique Dans Des Peuplements de Douglas en Région Wallonne - Approche de Terrain et modélisation* (Master thesis). Université Catholique de Louvain - UCLouvain, Faculté des Bioingénieurs, Louvain-la-Neuve, Belgium. Prom : Vincke, Caroline; Guisset Camille. https://dial.uclouvain.be/memoire/ucl/object/thesis:40951.

Restaino, C.M., Peterson, D.L. and Littell, J. 2016 Increased water deficit decreases Douglas fir growth throughout western US forests. *Proc Natl Acad Sci U S A* **113**, 9557–9562. https://doi.org/10.1073/pnas.1602384113.

Rossi, S., Anfodillo, T., Čufar, K., *et al.* 2016 Pattern of xylem phenology in conifers of cold ecosystems at the northern hemisphere. *Glob Change Biol* **22**, 3804–3813. https://doi.org/10.1111/gcb.13317.

Saintonge, F.-X., Nageleisen, L.-M., Boutte, B., *et al.* 2023 *La santé Des forêts, 2e édition: Diagnostic, prévention et Gestion*. CNPF-IDF, Orléans, France, p. 644.

Sergent, A.-S., Rozenberg, P. and Bréda, N. 2012 Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. *Ann For Sci* **71**, 697–708. https://doi.org/10.1007/s13595-012-0220-5.

Thomas, F., Eichstaedt, R. and Werner, W. 2015 Interaction between Douglas fir and European beech - investigations in pure and mixed stands. *Forstarchiv* **86**, 83–91. https://doi.org/10.4432/0300-4112-86-83.

Thomas, F.M., Rzepecki, A. and Werner, W. 2022 Non-native Douglas fir (Pseudotsuga menziesii) in Central Europe: ecology, performance and nature conservation. *For Ecol Manage* **506**, 119956. https://doi.org/10.1016/j.foreco.2021.119956.

Trouvé, R., Bontemps, J.-D., Collet, C., *et al.* 2014 Growth partitioning in forest stands is affected by stand density and summer drought in sessile oak and Douglas-fir. *For Ecol Manage* **334**, 358–368. https://doi.org/10.1016/j.foreco.2014.09.020.

Vacek, Z., Vacek, S. and Cukor, J. 2023 European forests under global climate change: review of tree growth processes, crises and management strategies. *J Environ Manage* **332**, 117353. https://doi.org/10.1016/j.jenvman.2023.117353.

Vejpustková, M. and Čihák, T. 2019 Climate response of Douglas fir reveals recently increased sensitivity to drought stress in Central Europe. *Forests.* **10**, 97. https://doi.org/10.3390/f10020097.

Vitali, V., Büntgen, U. and Bauhus, J. 2018 Seasonality matters—the effects of past and projected seasonal climate change on the growth of native and exotic conifer species in Central Europe. *Dendrochronologia.* **48**, 1–9. https://doi.org/10.1016/j.dendro.2018.01.001.

Vitali, V., Büntgen, U. and Bauhus, J. 2017 Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in South-Western Germany. *Glob Change Biol* **23**, 5108–5119. https://doi.org/10.1111/gcb.13774.

Weber, P., Bugmann, H., Pluess, A.R., *et al.* 2013 Drought response and changing mean sensitivity of European beech close to the dry distribution limit. *Trees.* **27**, 171–181. https://doi.org/10.1007/s00468-012-0786-4.

Wigley, T.M.L., Briffa, K.R. and Jones, P.D. 1984 On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J Clim Appl Meteorol* **23**, 201–213. https://doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2.

Zang, C. and Biondi, F. 2015 Treeclim: an R package for the numerical calibration of proxy-climate relationships. *Ecography.* **38**, 431–436. https://doi.org/10.1111/ecog.01335.

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https://doi.org/10.1093/forestry/cpag027
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