



Contents lists available at ScienceDirect

Dendrochronologia

journal homepage: www.elsevier.com/locate/dendro

Drought resilience of three coniferous species from Belgian arboreta highlights them as promising alternatives for future forests in Western Europe

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ARTICLE INFO

Keywords:

Dendroecology
Arboreta
Abies nordmanniana
Chamaecyparis lawsoniana
Thuja plicata
Western Europe
Drought response
Radial growth

ABSTRACT

Searching for drought tolerant species is one of the adaptative management measures that could be implemented to improve forest resilience in the context of more intense and frequent droughts brought by climate change. Western European forests are already suffering from drought-induced tree mortality, in native as well as in well-established non-native species. Novel non-native species (i.e., non-native species that have not yet undergone thorough operational testing or previously been grown at forestry scale) with high drought resistance in their original geographic range could be an alternative. To this end, the ecology and drought response of these species need to be investigated in their area of introduction. We applied a dendroecological approach on trees of *Abies nordmanniana* (Steven) Spach (AN), *Chamaecyparis lawsoniana* (A.Murray bis) (CL), and *Thuja plicata* Donn ex. D. Don. (TP) from Belgian arboreta (Western Europe). First, we identified the main climatic drivers of species radial growth, using Bootstrapped Correlation Coefficients between tree ring indices and climate indicators related to drought, heat, and cold stresses. Second, we assessed the species growth response to exceptional drought events, using resistance, recovery and resilience indices and an integrated index comparing the actual resilience to a theoretical full resilience. We investigated the effects of species and drought timing on these indices using linear mixed models. The radial growth of the three species was negatively influenced by the water deficit during the previous growing season (especially in fall and summer), lower precipitation in the previous October, colder temperatures in late winter-early spring, and lower minimal temperatures in May. TP is the most sensitive species to previous summer conditions as it was negatively affected by the number of days with a mean temperature above 30°C, while AN was the least sensitive species with no significant Bootstrapped Correlation Coefficients for previous summer precipitation and temperatures. AN and TP differed from CL in being negatively affected in spring by higher maximal temperatures versus lower precipitation respectively. The effects of species and drought timing on resistance and recovery were significant. Overall, early and whole growing season droughts had a stronger negative effect than late droughts. AN and CL were more resistant to early and late droughts than TP, while the opposite was observed for recovery. The species showed less pronounced differences in resilience. CL was the species the closest to the theoretical full resilience, followed by AN: these two species appear to be good candidates for improving drought resistance of Western European forests. However, one must not forget that introducing novel species is associated with ecological risks and a thorough assessment of these risks must be carried out before promoting these species in forestry. Future research could focus on a comparison of novel non-native species with already well-established species in Western Europe such as Norway spruce and Douglas fir and explore how AN, CL and TP interact with native species in mixed stands.

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<https://doi.org/10.1016/j.dendro.2024.126282>

Received 4 July 2024; Received in revised form 5 November 2024; Accepted 28 November 2024

Available online 6 December 2024

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1. Introduction

Increasing disturbances and uncertainties brought by global change is threatening the resilience of forests worldwide (Anderegg et al., 2022). In particular, tree drought-induced mortality events have already been reported in numerous forest ecosystems around the world (Hartmann et al., 2022). Hotter droughts (i.e. droughts coupled with higher temperatures) are indeed more likely to induce mortality and these events will become more frequent in the future, pointing toward a greater vulnerability of forests to these drought events (Allen et al., 2015; Brodribb et al., 2020). European forests are not spared: summer precipitation is decreasing, heat extremes and droughts are becoming more frequent and intense (IPCC, 2021; Spinoni et al., 2018). They are also facing large-scale forest disturbances and tree species migration (Vacek et al., 2023). Several of the most abundant forest species in Europe are currently suffering from decline, significant growth reduction or even drought-induced mortality (Hanewinkel et al., 2013; Schuldt et al., 2020; Thom et al., 2023).

To maintain forest resilience to global changes and mitigate its negative impacts, a series of adaptive management measures need to be implemented (Spittlehouse and Stewart, 2003; Thomas et al., 2022). Searching for more drought resistant species, among native minor species (Kunz et al., 2018; Schmucker et al., 2023), non-native species, or other provenances is one of them (Vacek et al., 2023). Non-native species have been introduced in Europe over centuries to increase forest cover and meet society's demand for wood. They cover about 3 % of the European forest area (9 % in Western Europe) and this percentage is expected to increase (Forest Europe, 2020). Yet, some of them, such as the well-established non-native Norway spruce (*Picea abies* (L.) H. Karst.), are currently suffering from growth reductions and drought-induced mortality, following the recent drought of 2018–2020 (Schuldt et al., 2020; Thom et al., 2023).

In view of this massive decline of abundant species (native and well-established non-native), novel non-native species (i.e. non-native species that have not yet undergone thorough operational testing or previously been grown at forestry scale) that show a high resistance to disturbances in their original geographic range, including drought (Bolte et al., 2009) could be promoted. In the context of climate change, these species would indeed (i) maintain a certain forest growth level, (ii) increase forest resilience, and (iii) support biodiversity related to the threatened indigenous species (Ennos et al., 2019).

However, we are lacking information on the ecology of novel non-native species (Ennos et al., 2019). Their ecological requirements and climate sensitivity would need to be determined in their areas of introduction to assess their silvicultural and ecological potential. In this context, multi-species comparisons under similar site conditions could be a useful tool to determine which species would be the most suitable in a given introduction area (e.g., Hoffmann et al., 2018; Klisz et al., 2023). In Europe, several studies have compared native and non-native species, though they mainly focused on already well-established non-native species, such as Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (e.g. Feliksik and Wilczyński, 2009; Lévesque et al., 2014; Vitali et al., 2018; Wrzesiński et al., 2024a). To our knowledge, only a few studies have compared novel exotic species, most of them were based on a limited number of sites and trees (e.g., Cedro and Nowak, 2024; Hoffmann et al., 2020; Hoffmann et al., 2018; Medina-Villar et al., 2024; Song et al., 2022).

As novel non-native species are still rare in forest stands in Europe, ecological studies must rely on dedicated plantations. Commons gardens and arboreta have a long history of being used for scientific research such as species conservation and selection. More recently, the scientific community has been interested in their potential for ecological restoration or studying the effects of environmental conditions and climate change on tree growth and adaptation (Ducattillon et al., 2022; Fady and Rihm, 2022; Hirons et al., 2021; Primack and Miller-Rushing, 2009; Song et al., 2022). In Belgium, a network of about 25 arboreta

containing more than 200 species originating mainly from Europe, western North America, and eastern Asia was established by the Belgian Forest Department in the early 1900s (Galoux, 1951). The original goal was to assess the adaptive and silvicultural potential of these species to diversify and restore the cover of the degraded Belgian forests at that time. Today, 14 public arboreta remain in Wallonia (Southern Belgium), covering a diversity of ecological regions (Scholzen et al., 2016) and representing a unique opportunity to investigate the ecology of novel non-native species in their area of introduction.

In this research, we assessed the autecology of three novel non-native conifer species that present a high drought resistance in their original geographic range: *Abies nordmanniana* (Steven) Spach, *Chamaecyparis lawsoniana* (A.Murray bis) Parl. and *Thuja plicata* Donn ex D.Don. We applied a dendroecological approach on tree populations located in 11 arboreta of Wallonia (Belgium). Our first objective was to characterize the radial growth response of these species to climate between 1954 and 2014. We computed correlation functions between tree ring indices and climate indices related to drought, heat and cold stresses. Our second objective was to assess radial growth response of these species to exceptional climatic drought events. Here, we defined climatic drought as sustained periods of anomalously low water availability (i.e., at levels rarely experienced based on historical records; Phillips et al., 2016). We applied the resilience approach of Lloret et al. (2011) and a complementary and more integrative approach of full resilience (Schwarz et al., 2020) to compare species resistance, recovery and resilience to drought events occurring at different timing in the growing season.

2. Material and methods

2.1. Selected species, study sites and sampling

The three studied species, *Abies nordmanniana* (Nordmann fir), *Chamaecyparis lawsoniana* (Lawson cypress) and *Thuja plicata* (Western Red Cedar) were selected based on three aspects: (1) their resistance in their original geographic range to drought, extreme temperatures (both positive and negative), wind, late frost, pathogens; (2) their silvicultural potential (wood quality and growth rate); and (3) their presence and abundance in Walloon arboreta.

Abies nordmanniana originates from temperate regions of the western Caucasus located between 400 and 1400 m of elevation. The mean annual temperatures vary between 10°C and 14°C and annual precipitation varies between 600 and 1500 mm, mainly occurring in the winter period (Arbez, 1969; Caudullo et al., 2016). In its native range, this species grows on a wide variety of soils, from deep acidic schists to shallower calcareous soils. The late bud burst of Nordmann fir contributes to its tolerance to late frosts. This species is also quite resistant to summer droughts due to its avoidance strategy, which includes a highly sensitive stomatal regulation in response to water stress, a deep taproot and the completion of annual growth in height before summer (Aussenac, 2002).

Chamaecyparis lawsoniana is native to Oregon and California, near the Pacific coast of the USA, where it grows at elevations ranging from sea level to 1500 m (Zobel, 1990). The climate is characterized by cool and wet winters followed by warm and dry summers. Precipitation varies between 1000 and 1500 mm per year (mainly concentrated in winter), and average annual temperatures vary between 5.5°C and 11°C depending on the elevation (Zobel, 1990). In its native range, it reaches its optimum growth on deep soils with good water supply, though it can also grow on relatively dry and shallow soils (Zobel, 1990). Lawson cypress leaf traits values allow to delay water loss, which helps it to cope with dry conditions. Its root system is mainly horizontal, with some vertical sinkers to get water from deeper soil layers (Zobel et al., 1985). Finally, the species exhibits a relatively slow and constant radial growth throughout its ontogenetic stages (Zobel et al., 1985).

Thuja plicata's native range extends from northern California to southern Alaska, from sea level to elevations of more than 2000 m

(Minore, 1990). It grows under a wide range of climatic conditions: annual precipitation from 700 mm to 6600 mm, a mean annual temperature of 10–11°C and extreme minimal temperatures as low as –47°C (Galoux, 1951; Wilson et al., 2016). In its area of origin, the species is most productive on deep, acidic, and moist though well-drained soils but can tolerate very poor drainage. Western red cedar is described as tolerant to biotic and abiotic stress, with an ability to survive and grow, albeit slowly, under long-lasting adverse conditions (Antos et al. (2016). The species has no taproot, but a dense network of fine roots (Minore, 1990).

We selected 11 arboreta from different biogeographical zones of Wallonia (Fig. 1; Van der Perre et al., 2015). The mean annual precipitation of our study sites ranges from 840 mm (Seraing) to 1299 mm (Bouillon), and the mean annual temperatures range from 7.6°C (Saint-Hubert) to 10°C (Seraing). All sites are located on loamy soils (Cambisol and one Luvisol in the WRB classification) with small variations at the local scale (see Table S1 for the exact soil code of the Walloon soil map; Legrain and Engels, 2007). In each arboretum, we selected 4–15 trees per species and sampled two wood cores at a height of 1.3 m and in perpendicular directions during summer 2016. Trees were selected from the greatest circumference, in even-aged monospecific groups of a minimum of five trees. Damaged or badly shaped trees were avoided, as well as trees near stand borders. In total, 70 *A. nordmanniana* (AN, hereafter), 99 *C. lawsoniana* (CL), 76 *T. plicata* (TP) trees were sampled, ranging from 60 to 106 years at sampling height (Table 1).

2.2. Climatic data and indicators

Daily series for temperature (minimum, maximum and mean) and precipitation were available from the RMI (Royal Meteorological Institute of Belgium) from 1954 to 2015. These data are the result of an interpolation of daily measurements on a grid of 5 km x 5 km cells. Monthly precipitation (sum of daily precipitation) and monthly temperatures (absolute minimum and maximum) were derived from the daily series. Six indicators, related to drought, cold and heat stress, were calculated at the site scale and at the scale of Wallonia by averaging the indicators of all the study sites. The potential evapotranspiration was estimated according to Hargreaves (1994). We computed the Standardized Precipitation-Evapotranspiration Index (SPEI), at a timescale of 4 months (Vicente-Serrano et al., 2010). The Water deficit index was estimated for four seasons (whole growing season from March to October, spring from March to May, summer from June to August, and fall from September to October) using the difference between potential evapotranspiration and precipitation during the season. We calculated the number of days with a minimum temperature below zero between April and June (*Late frost days*) and the sum of the minimum temperatures below freezing between April and June (*Late frost temperatures*; in cumulated degrees). Finally, we counted the number of days with a mean temperature below –5°C (*Cold days*) and the number of days with a maximum temperature above 30°C (*Hot days*).

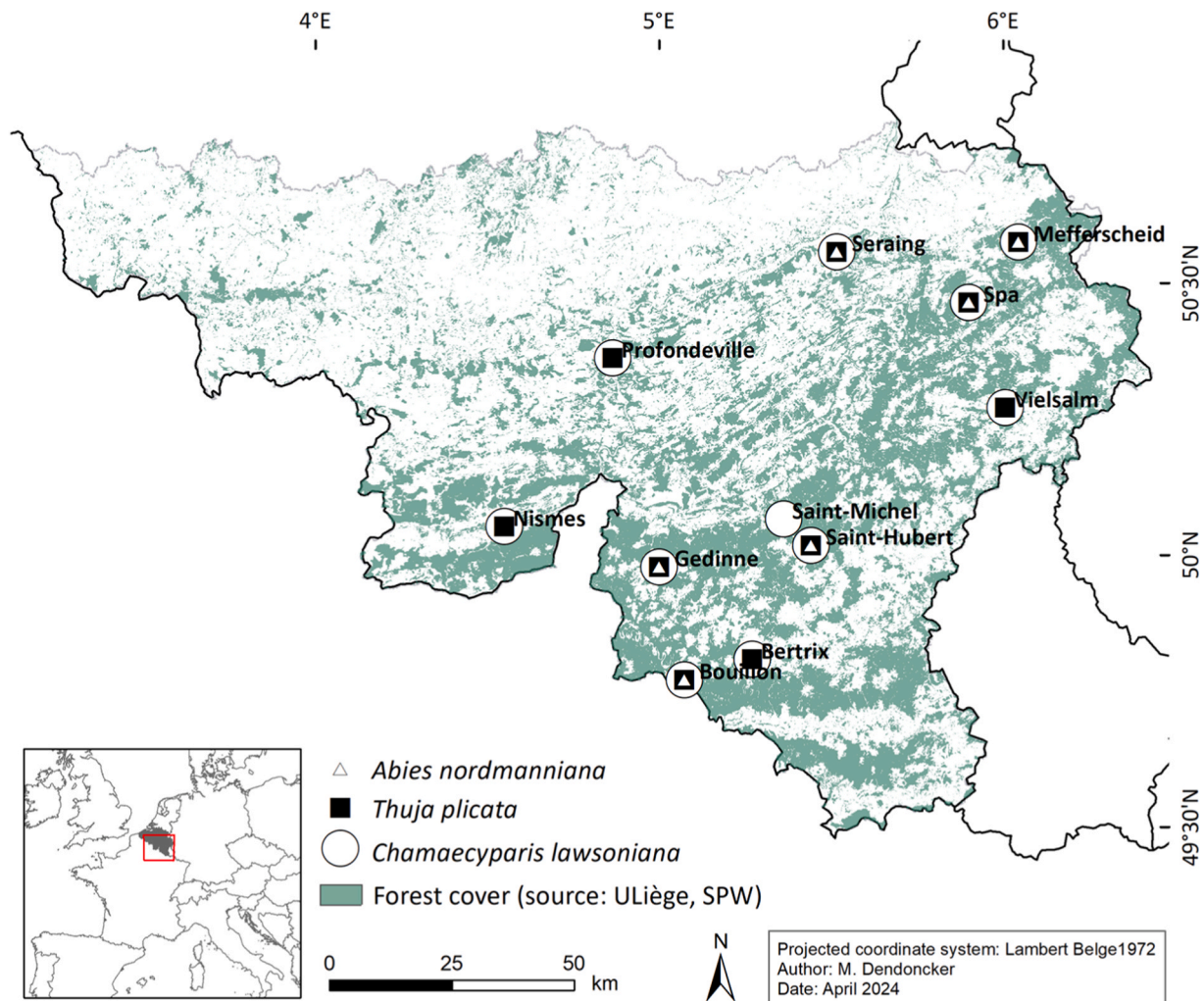


Fig. 1. – Location of the 11 arboreta in Wallonia (Belgium) and the species sampled at each site. The green background represents the Walloon forest cover in 2018 (geoportail.wallonie.be).

Table 1 –

Chronology statistics for the period 1954–2014: number of trees (N), average ring width (RW_{av}) and its standard deviation (sd), coefficient of variation (CV), mean sensitivity of site (MS), first order auto-correlation (AC1), interseries correlation (ICor), Expressed Population Signal (EPS) and Signal-to-Noise Ratio (SNR). RW_{av} , CV, MS, and AC1 were computed on the raw tree-ring series and ICor, EPS and SNR on the standardized master series. In grey, the sites that were not included in site-scale analyses due to their small sample size ($N < 8$).

Arboretum	N	Plantation date	Estimated age	RW_{av} (\pm sd)	CV	MS	AC1	ICor	EPS	SNR
<i>Abies nordmanniana</i>										
Bouillon	14	1906	103	2.21 (\pm 0.54)	0.25	0.24	0.76	0.44	0.80	3.92
Gedinne	13	1940	60	2.93 (\pm 0.62)	0.21	0.19	0.69	0.61	0.93	12.72
Mefferscheid	4	Unknown	85	4.03 (\pm 1.49)	0.37	0.20	0.80	0.46	0.67	1.99
Saint-Hubert	15	1911	92	4.14 (\pm 1.12)	0.27	0.20	0.72	0.64	0.92	11.17
Seraing	13	Unknown	89	2.73 (\pm 1.16)	0.42	0.23	0.78	0.56	0.86	6.07
Spa	11	1920-1922	87	3.35 (\pm 1.13)	0.34	0.20	0.73	0.52	0.84	5.4
TOTAL	70			3.1 (\pm 0.74)	0.24	0.22	0.74	0.49	0.94	17.55
<i>Chamaecyparis lawsoniana</i>										
Bertrix	6	1928-1933	82	2.24 (\pm 0.74)	0.33	0.25	0.74	0.59	0.83	4.93
Bouillon	9	1906	106	2.03 (\pm 0.57)	0.28	0.30	0.62	0.65	0.91	9.93
Gedinne	9	1911-unknown	85	2.81 (\pm 0.71)	0.25	0.22	0.60	0.64	0.93	12.58
Mefferscheid	10	Unknown	97	3.18 (\pm 0.65)	0.20	0.25	0.61	0.61	0.92	11.20
Nismes	15	1906-1928	107	1.23 (\pm 0.43)	0.35	0.27	0.70	0.69	0.95	17.51
Profondeville	5	1918	87	1.92 (\pm 0.59)	0.30	0.25	0.65	0.69	0.86	6.35
Saint-Hubert	8	1911	100	3.30 (\pm 1.07)	0.32	0.28	0.62	0.58	0.91	9.54
Saint-Michel	15	1924-1928	91	2.21 (\pm 0.63)	0.28	0.27	0.63	0.70	0.95	20.84
Seraing	10	1916-1936	92	2.26 (\pm 0.66)	0.29	0.29	0.57	0.69	0.94	15.38
Spa	5	1916	86	2.74 (\pm 1.66)	0.60	0.27	0.74	0.65	0.90	8.65
Vielsalm	7	1905-1910	100	2.70 (\pm 0.64)	0.24	0.24	0.62	0.69	0.90	8.63
TOTAL	99			2.3 (\pm 0.46)	0.20	0.28	0.50	0.59	0.98	66.09
<i>Thuja plicata</i>										
Bertrix	11	1910-1934	85	3.89 (\pm 1.03)	0.27	0.25	0.67	0.59	0.88	7.43
Bouillon	6	Unknown	104	3.57 (\pm 0.95)	0.27	0.30	0.69	0.56	0.79	3.71
Gedinne	6	1914-1923	91	3.57 (\pm 1.67)	0.47	0.22	0.77	0.61	0.82	4.42
Mefferscheid	8	1904-1916	95	4.71 (\pm .79)	0.17	0.25	0.60	0.43	0.74	2.85
Nismes	8	1904	95	1.75 (\pm 0.88)	0.50	0.27	0.75	0.50	0.82	4.66
Profondeville	5	1917	80	3.79 (\pm 1.42)	0.37	0.25	0.48	0.67	0.85	5.75
Saint-Hubert	10	1911	102	3.32 (\pm 0.86)	0.26	0.28	0.66	0.55	0.86	5.95
Seraing	10	1916-1926	90	3.33 (\pm 1.19)	0.36	0.29	0.69	0.42	0.85	5.78
Spa	7	1916	92	4.25 (\pm 1.13)	0.26	0.27	0.63	0.55	0.83	4.95
Vielsalm	5	1917-1930	96	4.01 (\pm 1.0)	0.25	0.24	0.55	0.56	0.83	5.03
TOTAL	76			3.59 (\pm 0.77)	0.21	0.27	0.61	0.51	0.97	31.61

2.3. Dendroecological approach

The increment cores were prepared using a core microtome and scanned at a resolution of 1200 dpi. Tree rings were measured with WinDendro software (version 2009b, Regent Instruments, Canada) and then crossdated using COFECHA software (Grissino-Mayer, 2001; Holmes, 1983). Individual cross-dated tree-ring series were obtained by averaging the ring width of the two cores. They were then detrended

using a negative exponential combined with a 20-year cubic smoothing spline with a 50 % frequency response cut-off using the dplR package in R software (Bunn, 2008). Master series were built for each site, from the individual tree-ring series and the individual standardized series, using a biweight robust mean (with autocorrelation retained).

The following statistics were calculated on the raw tree-ring series of each site from 1954 to 2014: (i) the average ring width (RW_{av}) and its standard deviation (sd); (ii) the coefficient of variation (CV) calculated

as the ratio between sd and RW_{av} ; (iii) the first order serial autocorrelation (AC1) which describes the influence of the previous year on the ring formation; and (iv) the mean sensitivity (MS) which expresses the interannual variability between tree rings of two successive years (Biondi and Qeadan, 2008). A null value indicates that rings of two successive years have the same width and a value of two indicates a null width for one of the two years. Mean sensitivity for one site is the average of all individual MS of this site.

Three additional statistics were computed on the standardized master series to assess the strength of the signal in each series: the inter-series correlations (ICor) which is the mean of the correlation between each individual tree ring series and a master chronology calculated by averaging all individual series without the studied series; and the expressed population signal (EPS) and signal-to-noise ratio (SNR) to assess the strength of a shared signal compared to the total signal (shared signal + noise) (Buras, 2017; Cook and Pederson, 2011; Wigley et al., 1984). EPS values above 0.85 ensure that the master chronology is well representative of the studied population (Wigley et al., 1984).

The growth-climate relationship was assessed for the three species, first at the regional scale, pooling together all the series from all sites, and then at the site scale. Sites with fewer than eight sampled trees were removed from the site scale analysis but kept for the regional scale. We calculated Bootstrapped Correlation Coefficients (BCCs), between standardized master series and climate indices, using the dcc function of the Treeclim package in R (Zang and Biondi, 2015). Climate indices corresponding to the year of ring formation (hereafter “current year”) and the year prior to ring formation (hereafter “previous year”) were included in the correlation function.

2.4. Resilience approach

For each site drought events were identified based on the SPEI 4 months, using the threshold of -1.5 . We separated the (i) early droughts, identified by the SPEI of May (integrating the climatic conditions from February to May) and (ii) late droughts, identified by the SPEI of September (climatic conditions from June to September). The years that had both May and September SPEI values below -1.5 were qualified as “whole growing season drought”.

For each drought event, the individual tree response was evaluated using an adapted version of the three indices of Lloret et al. (2011): (i) the resistance, representing ability of tree to maintain its growth during a drought (Eq. 1); (ii) the recovery, ability of tree to restore growth after the drought (Eq. 2); and (iii) the resilience, capacity of the tree to recover its reference growth level (Eq. 3) (Lloret et al., 2011; Steckel et al., 2020).

These indices were adapted from Lloret et al. (2011), as followed:

$$Resistance = \frac{RWI_t}{RWI_{ref}} \quad (1)$$

$$Recovery = \frac{(RWI_{t+1} + RWI_{t+2}) \times 0.5}{RWI_t} \quad (2)$$

$$Resilience = \frac{(RWI_{t+1} + RWI_{t+2}) \times 0.5}{RWI_{ref}} \quad (3)$$

Where:

- RWI_t is the ring width index of the tree during the year identified as a drought;
- RWI_{ref} is the mean of all ring width indices except those corresponding to years identified as drought;
- RWI_{t+1} and RWI_{t+2} are the ring width indices of the two years following the drought.

Before calculating the indices, we removed the first 10 ring width

indexes of each individual chronology to avoid juvenile growth patterns. To prevent the overlapping of drought recovery periods, we discarded drought years followed by another dry year within the next two years. To assess the influence of species and timing of drought (early drought, late drought, or whole growing-season drought) on the tree response, we performed linear mixed models for each index (resistance, recovery and resilience), with species and timing of drought as fixed factors and site as random factor.

For one index (Resistance, Recovery or Resilience) I_{ijt} of a tree i , in arboretum (site) j and year t :

$$I_{ijt} = \alpha + \alpha_j(0, \sigma_{site}^2) + S_i + D_{early} + D_{late} + D_{early_i} + D_{late_i} + \varepsilon_{ijt}(0, \sigma^2) \quad (4)$$

Where:

- α is the overall intercept, corresponding to the index value for the AN species and the “whole season” timing (reference);
- α_j is the value of the random factor for each site;
- S_i is the effect of species i , with i being either CL or TP for the reference timing (whole season);
- D_{early} is the effect of early drought for the reference species (AN);
- D_{late} is the effect of a late drought for the reference species (AN);
- D_{early_i} is the effect of early drought for the species i , with i being either CL or TP;
- D_{late_i} is the effect of late drought for the species i , with i being either CL or TP;
- $\varepsilon_{ijt}(0, \sigma^2)$ is the independent and identically distributed error term.

We performed post hoc Tukey tests to check the significance of differences between estimated marginal means of each species and timing of drought, using the R package emmeans (Lenth, 2023).

To complement this approach, we implemented the “full resilience” approach (Schwarz et al., 2020) to compare all three species resilience to a theoretical full resilience level based on the relationship between the three indices of Lloret et al. (2011). Assuming a full resilience (i.e. resilience set to 1), the Eq. 5 can therefore be used to describe the relationship between recovery and resilience.

$$Recovery = Resilience / Resistance = 1 / Resistance = Resistance^{-1} \quad (5)$$

For each tree and each drought event, we calculated the vertical distance between the actual recovery and the full resilience curve and expressed it as the missing recovery percentage to reach full resilience. We selected the observations corresponding to a resistance level below 1, to focus only on the trees whose growth was reduced during drought events. We then performed linear mixed models on these distances to full resilience, to assess whether the species exhibited similar behavior regarding their ability to recover from drought. The model follows the same structure as Eq. 4, with I_{ijt} being the distance to theoretical full resilience.

3. Results

3.1. Mean growth chronology and statistics

All trees were between 80 and 110 years old at the time of sampling, except for a relatively younger stand of AN (Gedinne) which was 60 years old (Table 1). The average ring width (RW_{av}) varied between 2.2 and 4.1 mm for AN, 1.2 and 3.3 mm for CL, and 1.7 and 4.7 mm for TP, depending on the study site. The coefficient of variation (CV) varied with similar amplitude for the three species, between 0.2 and 0.6. The mean sensitivity (MS) ranged from 0.2 to 0.3, and the first order correlation (AC1) between 0.5 and 0.8 for all three species. The quality of the crossdating was confirmed by the values of the interseries correlation (ICor), which were all above 0.4. All chronologies had EPS values of at least 0.67, with most values above 0.85, indicating a strong common

signal (Wigley et al., 1984). The two lowest values, 0.67 and 0.74 for AN and TP, respectively, were found on the same site (Meffersheid). The mean annual ring width, calculated over the period 1954–2014 on the chronologies at the regional scale (Table 1, Fig. 2 A), was significantly higher for TP (3.6 ± 0.8 mm) than for AN (3.1 ± 0.7 mm), and significantly higher for TP and AN than for CL (2.3 ± 0.5 mm), according to the ANOVA and post-hoc Tukey test ($p < 0.01$, Fig. 2 A). The three mean chronologies (ring width and ring width indices, Fig. 2B) showed a similar behavior during the years 1956, 1976, 2006 and 2011, when the growth of the three species decreased strongly.

3.2. Influence of climate on growth

At the regional scale, three parameters significantly influenced the radial growth of the three species, as showed by the Bootstrapped Correlation Coefficients (BCCs, Fig. 3). The precipitation in the previous October had a positive influence on growth, as did the minimal temperatures in May of the current year. The water deficit of the previous growing season (from March to October) had a negative influence, especially the summer (June to August) and fall (September–October) components.

There were several differences at the species level (Fig. 3). First, regarding the response to precipitations, AN growth was positively

affected by a greater amount of rainfall during April of the current year; CL and TP growth was positively affected by a greater amount of rain during the previous summer (June and July for TP, July for CL); and CL growth was negatively impacted by high precipitation during August of the current year. Second, regarding the response to the maximum temperatures, higher maximum temperatures during December, January and February positively influenced AN and CL growth. AN growth was also positively correlated to the maximum temperature of August of the current year. CL and TP growth was negatively correlated with high maximum temperatures during the previous July, and TP growth was negatively correlated with high maximum temperatures during May of the current year. Third, regarding the minimum temperatures, CL and TP growth were positively correlated with minimum temperatures in June and December of the previous year and positively correlated with minimum temperatures during March and May of the current year. CL growth was also positively correlated with minimum temperatures in February of the current year. AN growth was also positively correlated with minimum temperatures in May and August of the current year. Finally, for the stress indices, CL growth was negatively correlated with the number of cold days in February of the current year and TP was sensitive to the number of tropical days in the previous year (negative effect).

At the site scale, BCCs showed that CL and TP had a more

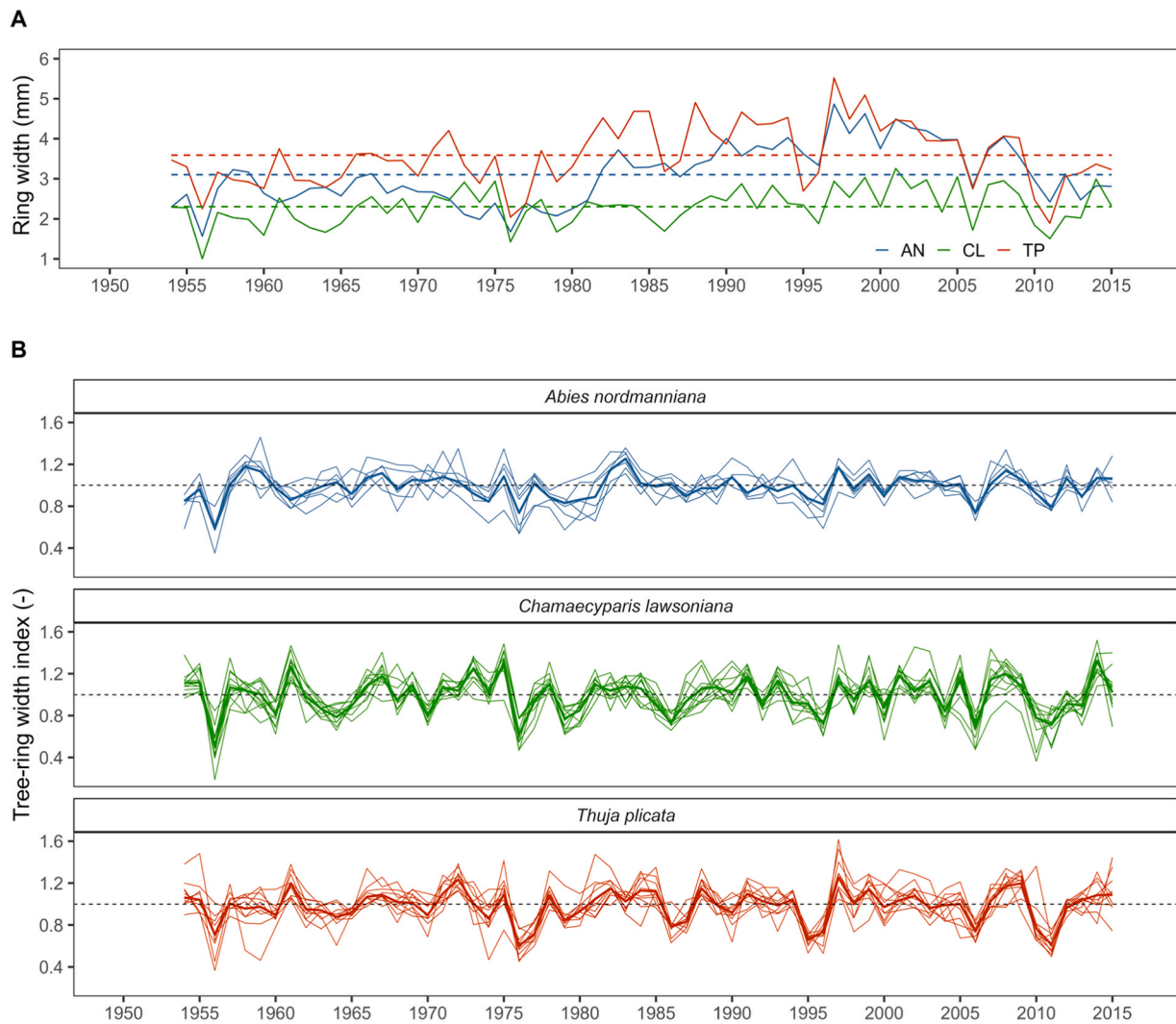


Fig. 2. - A. Mean growth chronology of ring width for the three species at the scale of Wallonia. Dotted lines represent the averaged ring width for the period 1954–2014. The colors indicate the species (AN: *Abies nordmanniana*, CL: *Chamaecyparis lawsoniana*; TP: *Thuja plicata*); B. Mean standardized chronology per site, the mean for Wallonia is in bold.

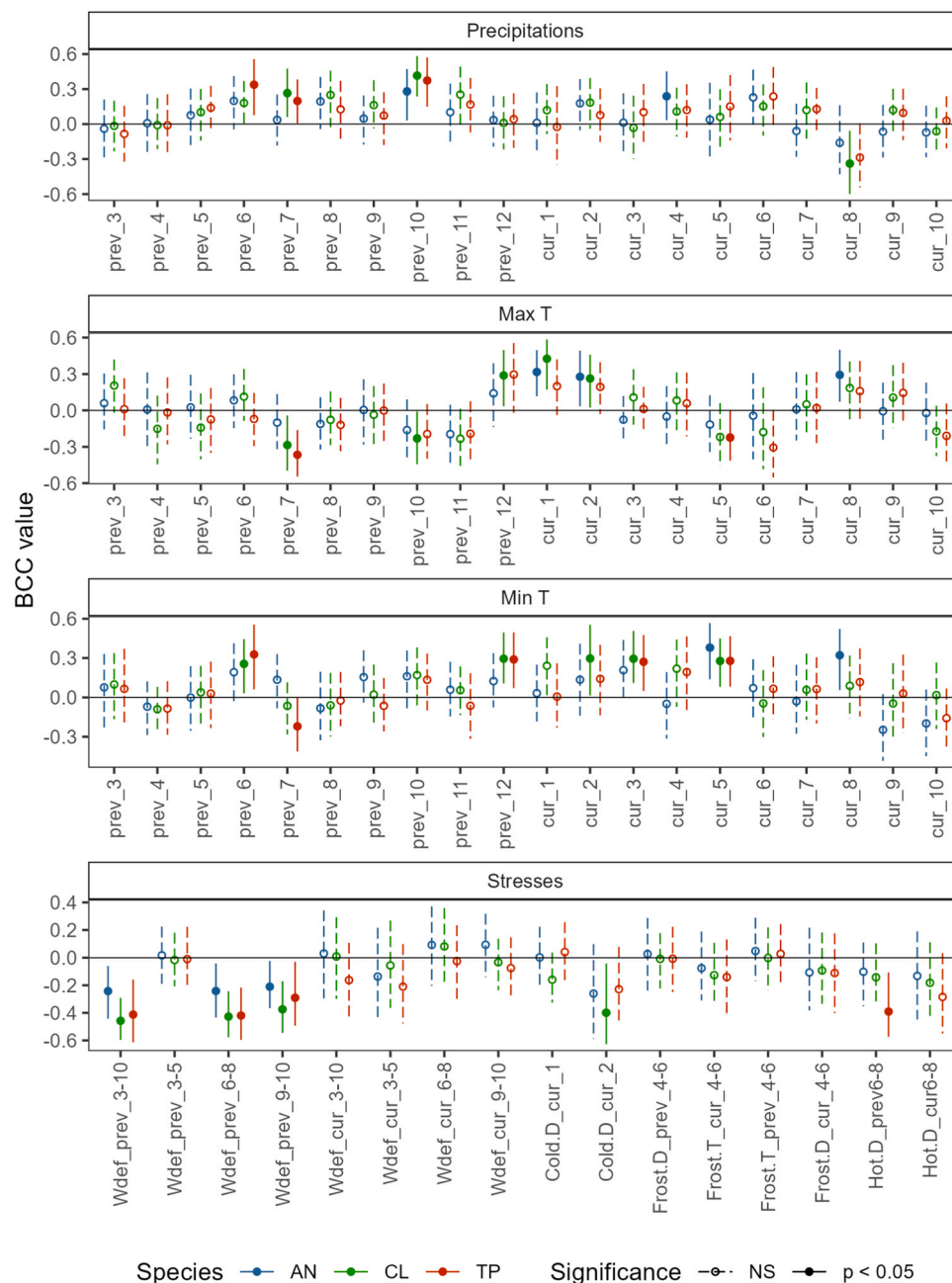


Fig. 3. – Bootstrapped correlation coefficients for the three species at the regional scale (Wallonia). prev = previous year. cur = current year. Numbers refer to months. The colors indicate the species (AN: *Abies nordmanniana*, CL: *Chamaecyparis lawsoniana*; TP: *Thuja plicata*). Solid lines indicate significant coefficients at $p < 0.05$.

homogeneous response across sites than AN (Figure S1). For example, the positive BCC with the rainfall of the previous October was marked for CL and TP on every site whereas no parameter was significant for AN on all sites. The total water deficit of the previous year (March to October) was the indicator that presented significant negative BCC for the greatest number of sites, for the three species together.

3.3. Growth response to drought

We identified four to seven drought events (early, late and/or whole growing season) for each site (Figure S2, Table S2). All sites were impacted by a late drought in 1959, by a whole growing season drought in 1976, and by an early drought in 2011. The year 2003 was identified as a late drought for all but one of the study sites (Gedinne). The number

of late droughts was generally higher than the number of early droughts. Gedinne was the arboretum that presented the fewest drought events, while Nismes, Seraing, Spa and Vielsalm presented the highest number of drought events (7). To avoid the overlapping of drought recovery periods for consecutive dry years, we had to discard the years 2009 and 2011 for the Saint-Michel site and 1973, 1974 and 1976 for Seraing.

3.3.1. Resistance, recovery, and resilience

Linear mixed models showed that overall, species had a significant effect ($p < 0.001$) on tree resistance and recovery, but not on tree resilience (Table S3). The timing of drought (early vs late vs whole season drought) had a significant effect ($p < 0.001$) on the three indicators, including in interaction with the species ($p < 0.001$). Model coefficient estimates and their significance are presented in Figure S3

and Table S4.

We calculated estimated marginal means for each species, drought timing, and their interactions (Table S5). Overall, and regardless of the drought timing, both AN and CL had a significantly higher mean resistance (95.1 % and 91 %) than TP (82.2 %) as confirmed by the Tukey post-hoc test on estimated marginal means. The opposite was observed for the recovery, with significantly lower values for AN and CL (114.9 % and 122.2 %) than for TP (134.9 %). The three species did not show significant differences in resilience when all drought timings were considered.

Regardless of the species, tree resistance was highest for late drought (105.7 %), followed by early drought (83.8 %), and by whole growing season drought (78.8 %). Mean recovery was also significantly different for each drought timing, following the opposite order as for resistance: the lowest recovery for late drought (104.4 %), followed by early drought (129.9 %), and whole season drought (138.5 %). Finally, tree resilience to late drought (103.0 %) was higher than resilience to early drought (96.6 %) and to whole season drought (96.3 %).

The estimated marginal means of the interaction between drought timing and species are presented in Fig. 4. For early droughts, TP presented the lowest mean resistance (73.3 %) while AN and CL presented higher similar mean resistances (89.6 % and 88.3 %). On the contrary, TP recovery (149.2 %) was higher than both AN (120.9 %) and CL recovery (117.0 %), which were not significantly different. AN was more resilient to early droughts (99.8 %) than CL (91.8 %) but was not significantly more resilient than TP (97.3 %). For late droughts, the species effect was significant only for resistance, as the three species did not show differences in their mean recovery and resilience. TP showed the lowest mean resistance to late drought (98.4 %), compared to AN and CL (109.8 % and 108.9 %). For whole season droughts, the three species did not present any significant difference in resistance (85.8 % for AN, 75.8 % CL and 74.8 % TP). AN showed a lower mean recovery (122.8 %) than both CL (149.7 %) and TP (142.9 %). AN also showed a lower mean resilience (91.8 %) than CL (102.1 %), but not significantly different from TP (95.9 %).

3.3.2. Full resilience approach

The fitted curves (i.e., the relationship between recovery and resistance) of the three species bring another perspective on the species drought response when compared to the theoretical full resilience (Fig. 5 A). According to the F test, the curve of each species was significantly different from the full resilience ($p < 0.001$). AN, CL and TP crossed the theoretical full resilience at a resistance of 0.99, 0.83, and 0.79, respectively. The percentage of points (i.e., couples one tree – one drought-event) that present a resistance below 1 equals 52.5 % for AN, 55.6 % for CL and 67.1 % for TP.

The species alone did not have a significant effect on the mean distance between each point and the theoretical curve, i.e., the lack of recovery to reach the theoretical full resilience (see Table S4 for detailed results of the mixed models). However, the effect of drought timing was significant ($p < 0.001$): late droughts showed a mean positive distance to the theoretical curve (2.3 %) compared to early and whole season droughts (mean distance of -6.6 % and -6.4 %), meaning that trees, whatever the species, overall were “full resilient” facing late droughts.

The effect of the interaction between species and the timing of drought was however significant (p-value of Anova < 0.001 ; Fig. 5B). For whole season droughts, CL was significantly closer to the full resilience (distance of 2.3 %) than TP (-8.2 %) and AN (-13.2 %). For early droughts, AN mean distance to full resilience was the smallest (-1.0 %) but was not significantly different from CL (-11.7 %) and TP (-7.1 %). For late droughts, the mean distances to full resilience were positive and similar for the three species (0.5 % for AN, 2.6 % for CL and 3.8 % for TP). Finally, AN presented a similar distance to full resilience for early droughts and late droughts, while CL and TP showed a distance to full resilience to late droughts significantly higher than the distance for early droughts.

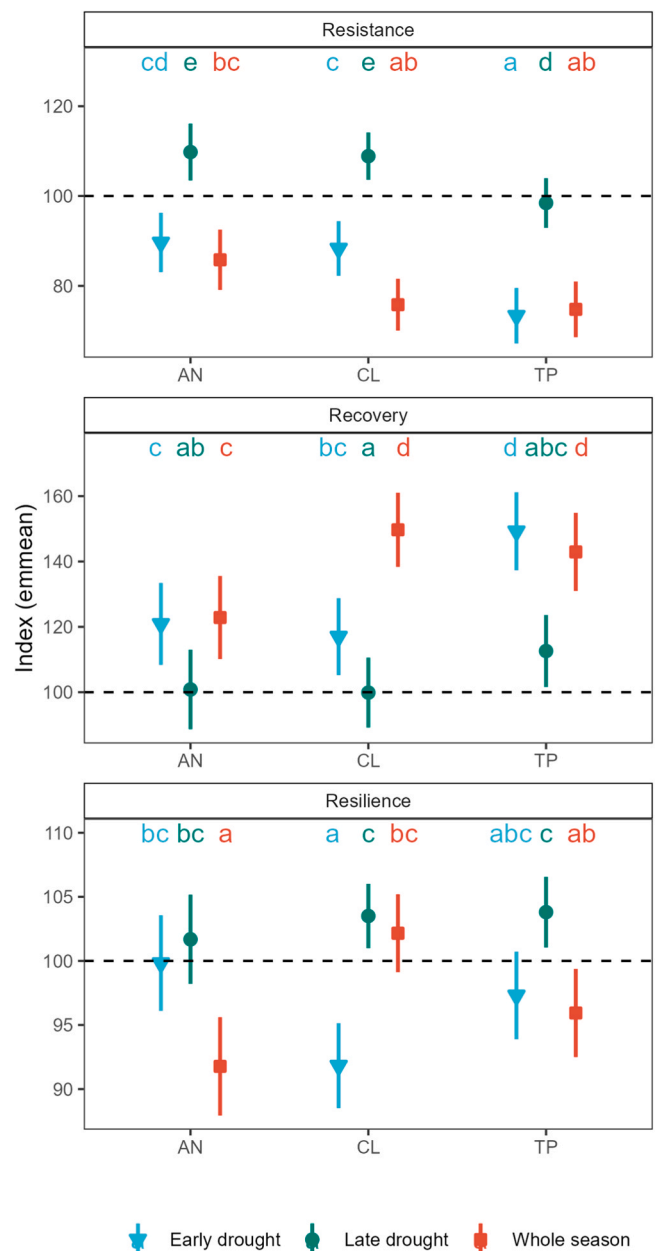


Fig. 4. – Mean resistance, recovery, and resilience as predicted by the model (emmeans, with 95 % confidence intervals), according to species and drought timing. Means with no letter in common are significantly different (Tukey HSD-test; $\alpha = 0.05$). Complete results are presented in Table S5.

4. Discussion

The autecology of three non-native species, *Abies nordmanniana* (AN), *Chamaecyparis lawsoniana* (CL), and *Thuja plicata* (TP) was investigated in their area of introduction in Western Europe on trees located in 11 arboreta of Wallonia (Belgium). First, the main climatic drivers of the radial growth of these species were identified using correlation functions between tree ring indices and climatic indices. We showed that the three species radial growth presented three common climatic drivers at the regional scale: the water deficit of the previous season, the precipitation of the previous October, and the minimal temperatures of May of the current year. Overall, the three species also presented positive BCC for values of climatic parameters indicative of a mild winter and an early spring. The three species did, however, show some species-specific differences in the BCCs of climatic parameters

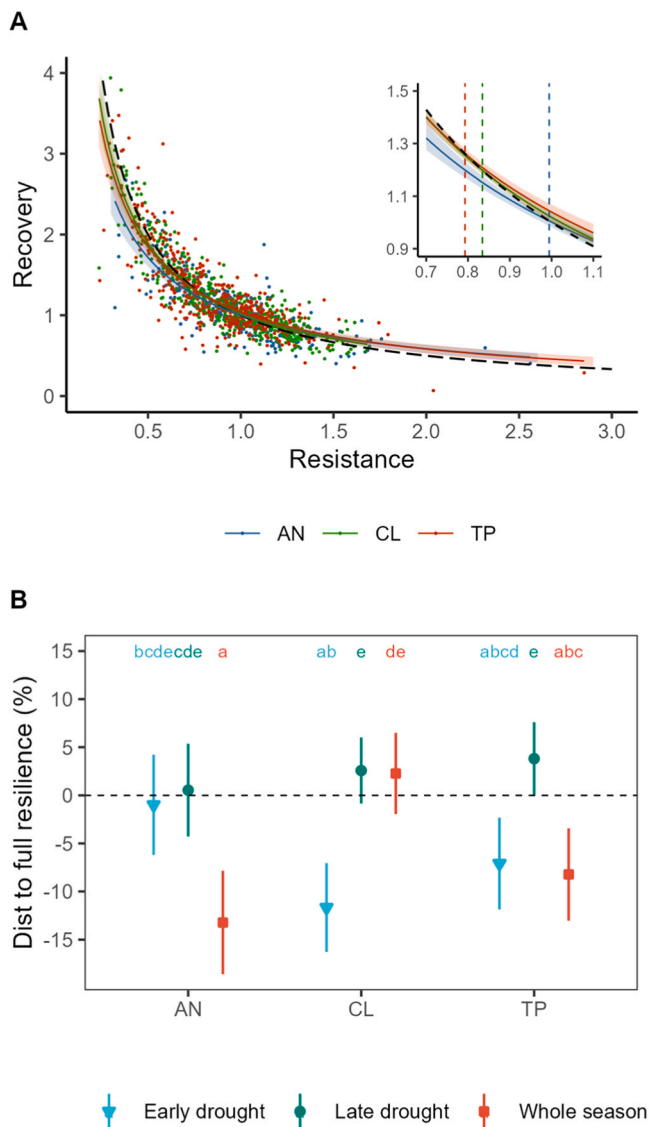


Fig. 5. – A. Comparison of the relation between the actual recovery and resistance of the three species with the theoretical full resilience line (dashed). The zoom on the top-right highlights the intersection of the species fitted curves with the theoretical full resilience curve; B. Mean distance to the theoretical full resilience for the three species (emmeans, with 95 % confidence intervals). Means with no letter in common are significantly different (Tukey HSD-test; $\alpha = 0.05$). Detailed results in [Table S5](#).

linked to the previous summer precipitation and temperatures. Second, species response to past exceptional drought events was assessed by computing the resistance, recovery and resilience indices (Lloret et al., 2011) and the distance to a theoretical full resilience curve (Schwarz et al., 2020). The effect of species and drought timing (early, late, whole growing season) both had a significant influence on the tree growth response. In particular, the resistance to early droughts was always lower than for late droughts for the three species, while the recovery showed the opposite trend. The distance to full resilience approach highlighted a similar behavior of the three species to early and late droughts (negative distance for early and positive for late), while CL was the species that was the closest to the full resilience for whole growing season droughts.

4.1. Climatic drivers for AN, CL and TP radial growth

AN, CL and TP all had a negative radial growth response to water

deficit (PET-P) in the previous growing season, in particular during summer and fall. For CL and TP, this was consistent with the negative impact of drier and warmer previous summer conditions. In addition, TP was the only species being negatively affected by the number of tropical days during the previous summer. TP has recently been shown to be sensitive to hot and dry summers in its native range (Andrus et al., 2024; Klinka and Brisco, 2009), as is CL, especially during June of the previous year (Carroll and Jules, 2005). This seems to be confirmed in their area of introduction in Belgium. AN, on the other hand, showed no significant sensitivity to summer temperatures and precipitation. This could be related to its taproot system which allows it to reach deep soil layers (Aussenac, 2002), a morphological feature not shared by CL and TP that instead have mostly horizontal root systems (Minore, 1990; Zobel et al., 1985). The lower radial growth associated with dry conditions during the previous growing season could be linked to the reduced carbon storage subsequent to the stomatal closure and/or hydraulic failure of the xylem conduits (Choat et al., 2018; McDowell et al., 2008).

In line with the negative impact of water deficit of the previous fall, the radial growth of the three species is higher when it is wetter at the end of the previous growing season (October). Similar results were observed for TP in Poland (Cedro and Nowak, 2024). This could indicate the importance of soil water refill during fall. It could also mean that trees accumulate non-structural carbohydrates during this period, that could be mobilized the next spring to better cope with unfavorable conditions (McDowell et al., 2008).

Milder temperatures during late winter and early spring (December to May) favor radial growth of the three species. This result has been observed for several species in Central Europe (Feliksik and Wilczyński, 2009; Wrzesiński et al., 2024b) as well as for TP and CL in their native range (Carroll and Jules, 2005; Klinka and Brisco, 2009) and in Central Europe (Cedro and Nowak, 2024; Hoffmann et al., 2020). The ability of evergreen conifers to photosynthesize under mild winter conditions ($\sim 5^{\circ}\text{C}$) and thus improve carbon storage for the following growing season, is a possible explanation for these positive correlations (Guehl et al., 1985). Mediterranean firs such as AN have been shown to photosynthesize down to 0°C (Aussenac, 2002). Milder temperatures during winter and early spring could also have the effect of reducing the exposure to late frost and winter desiccation (Vejpustková and Cihák, 2019) caused by low night temperatures combined with high daytime irradiation (Malmqvist et al., 2018). Finally, higher temperatures in early spring can induce an early onset of cambial activity, thereby extending the growing season (Begum et al., 2013; Rossi et al., 2016).

The radial growth of AN, CL, and TP was favored by higher minimum spring temperatures (especially in May), which may indicate a sensitivity of the three species to late frosts. However, the two climatic indicators tested in this study for late frost sensitivity (cumulated temperatures and number of days) did not present significant BCC. Having a relatively low sensitivity to late frost in their area of origin was one criterion used to select our study species, and this last result seems to indicate a similar behavior in the Western European context. Late frost sensitivity could be a limiting factor for species' growth, particularly under climate change which could lead to a warmer spring and an extended growing season, subsequently increasing the risk of frost during this period (Liu et al., 2018). Late frost sensitivity is therefore important to take into consideration in the context of introducing novel non-native species.

The negative impact of reduced precipitation for AN in April and of higher maximum temperatures for TP in May suggest that these two species are negatively affected by heat waves and dry conditions during spring. George et al. (2015) showed a stronger influence of early droughts than late droughts for AN in its native range, and Andrus et al. (2024) a sensitivity of TP to warmer temperatures in May in its native range. Temperature and amount of precipitation in May are indeed important determinants for the water availability during the rest of the growing period (Andrus et al., 2023).

4.2. Significant effect of species on drought response

The three species showed contrasted radial growth drought response in terms of resistance and recovery. For resilience, the species effect was only significant in interaction with drought timing. AN and CL were more resistant to early and late droughts than TP. The reverse pattern was observed for the recovery, with overall higher values for TP than for the other two species. This trade-off between resistance and recovery is a generally observed trend (Gazol et al., 2017; Hoffmann et al., 2018), which can partly be explained by the higher recovery potential linked to lower resistance. The difference between species resilience was less pronounced, though we showed that AN was more resilient to early droughts than CL, while CL was more resilient to whole growing season droughts than AN.

Overall, for the three components of resilience, radial growth was more strongly affected by whole growing season and early droughts than late droughts. This higher sensitivity to early droughts of AN was reported by George et al. (2015) in its area of origin as most of its radial growth occurs in spring or early summer. TP was also identified as sensitive to May-June conditions of temperatures and precipitations (Andrus et al., 2024).

The integrated full resilience approach showed that the fitted curve for the three species crossed the theoretical full resilience line at different resistance thresholds: CL and TP had a better potential to fully recover from the lowest resistance level, taking into account all past drought events between 1954 and 2012. However, it is important to consider the interaction between species and drought timing. Linear mixed models on the distance to full resilience showed that whole growing season droughts are the ones that better distinguish the species: for these droughts CL is closer to a full resilience than AN and TP. The higher sensitivity of CL to early droughts is confirmed as this species did not have the ability to fully recover from early drought events. On the other hand, AN on average fully recovered from early droughts. For late droughts, all three species had the ability to fully recover.

Functional traits and plant strategies strongly influence species-specific behavior with respect to drought response (Hoffmann et al., 2018; McCulloh et al., 2014). Regarding morphological traits, the deep taproot system of AN (Aussenac, 2002), and the vertical sinkers of the CL root system (Zobel et al., 1985) could explain their higher resistance compared to TP, allowing them to get water from deeper soil layers inaccessible to TP with its dense but mainly horizontal root system (Minore, 1990). CL has another morphological adaptation to reduce water loss: the species has small leaves closely appended to the stem and narrow stomatal cleft (Zobel et al., 1985).

At the wood anatomy level, smaller xylem conduits, which correlate with smaller annual ring widths, may be another anatomical adaptation to improve resistance to cavitation (Gessler et al., 2020). Some studies have indeed shown that slow-growing trees are less susceptible to hydraulic failure than fast-growing trees (Büntgen et al., 2019; Jansen et al., 2013). This could be an explanation for the lowest resistance observed for TP, as it was also the species with the highest average ring width over the period studied. CL, on the other hand, had the lowest average ring width and the highest resistance together with AN.

Differences in the physiological strategies to cope with drought can be described by locating the species on the continuum of isohydry and anisohydry strategies (Fu and Meinzer, 2019). More isohydric species maintain a relatively stable leaf water potential by decreasing their stomatal conductance, while more anisohydric species allow gas exchange to continue as their leaf water potential decreases (McDowell et al., 2008). AN and TP are described as more isohydric species (Aussenac, 2002; McCulloh et al., 2014), while CL is described as more anisohydric (Rizzuto et al., 2023). The observed higher resistance and lower recovery of CL compared to TP could be explained by these different strategies. The early closure of the stomata under unfavorable conditions of isohydric species such as TP indeed limits photosynthetic activity, leading to low carbon availability and allocation for cell

division (Eilmann et al., 2011). As a consequence, isohydric species show lower radial growth during drought, but a higher ability to recover when conditions return to being favorable. However, in the case of repeated or prolonged droughts, this strategy can lead to carbon starvation and other subsequent effects such as reduced resistance to biotic agents (McDowell et al., 2008). This could explain the TP mortality observed in its native range following prolonged warm and dry conditions (Andrus et al., 2024).

4.3. An opportunity to establish new species in Western European forests

Of the three studied species CL seems to have the highest potential for introduction as a novel non-native species in the context of climate change as it presented a greater ability to fully recover (closer to the full resilience curve) when considering all drought events from 1954 to 2012. AN could also be an interesting alternative, as it showed resistance to early and late droughts as high as CL, and less sensitivity to summer temperatures and precipitation than the two other species. TP appeared more sensitive than CL and AN, with lower resistance and resilience to late and early droughts.

Our study was carried out on trees growing in arboreta, (i.e. non-natural forest stands), which implies different silvicultural management than in semi-natural forest stands. These historical arboreta still provide inestimable experimental set-ups to assess the adaptive potential of non-native species. To our knowledge, this is one of the first studies to apply the integrative full-resilience approach (e.g., Che et al., 2023; Móríciz et al., 2021; Wu et al., 2023) to compare different novel non-native species under similar sites conditions. Our research allowed us to identify three good candidates to functionally diversify Western European forests, particularly *Abies nordmanniana* and *Chamaecyparis lawsoniana*. Indeed, mixing species presenting contrasting drought response strategies can ensure stability and improve adaptive potential of forest ecosystems (Schnabel et al., 2021).

Nonetheless, one must not forget that introducing novel non-native species involves some ecological risks (e.g., invasive potential, introduction of associated pathogens) (Dimitrova et al., 2022; Felton et al., 2013). A thorough assessment of these risks, which are species-specific, must be carried out in the perspective of using them in forestry (Felton et al., 2013; Vacek et al., 2023). Introducing non-native species in indigenous species in forests stands should be accompanied by a close monitoring of the plantations to ensure the non-invasive characteristics of the introduced species (Brundu and Richardson, 2016). Implementing an uneven-aged silvicultural system could also be a way to reduce possible negative impact and benefit from their economic performance (Krumm and Vítková, 2016). Overall, promoting functional forest diversity at the stand and landscape scale, could be a key element to maintain productivity (Liang et al., 2016; Feng et al., 2022), increase stability (Schnabel et al., 2021), and mitigate or protect against the impacts of climate change and extreme events (Delalandre et al., 2022; Isbell et al., 2015).

5. Conclusion

We investigated the autecology of three non-native species, *Abies nordmanniana*, *Chamaecyparis lawsoniana*, and *Thuja plicata* in their area of introduction in Western Europe (Wallonia, Belgium), using a dendrochronological approach on trees located in 11 arboreta. We first identified the main climatic drivers of their radial growth, and then assessed their response to exceptional drought events. The radial growth of the three species was influenced by common climatic drivers, such as the positive influence of milder winter and early spring temperatures. Drought response analysis highlighted a significant species effect in interaction with drought timing (early, late, whole growing season). This study provides insights into the potential of introducing these novel non-native species in Western European forests, to increase forest resistance to drought. Future research could expand the drought

response comparison with other native and non-native species well-established in Western Europe, such as Norway spruce or Douglas fir and explore how the three novel non-native species (*Abies nordmanniana*, *Chamaecyparis lawsoniana*, and *Thuja plicata*) behave and interact with native species in mixed stands.

CRedit authorship contribution statement

Morgane Dendoncker: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Camille Guisset:** Writing – original draft, Visualization, Methodology, Investigation, Data curation, Conceptualization. **Mathieu Jonard:** Writing – review & editing, Methodology. **Alexandra Delente:** Investigation, Conceptualization. **Quentin Ponette:** Writing – review & editing, Supervision, Resources, Conceptualization. **Caroline Vincke:** Writing – review & editing, Supervision, Resources, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Acknowledgements

This research was supported by the Plan Quinquennal de Recherches et de Vulgarisation Forestières funded by the Walloon forest service (Département de la Nature et des Forêts – Service Public de Wallonie, Belgium). We thank Pierre Lhoir, Olivier Bouchez and François Plume for their help during field sampling and lab processing. We are grateful for the English editing made by Lana B. Ruddick.

Authors contributions

AD, MD, CG, QP and CV designed the study. AD and CG collected the wood samples. AD, MD and CG performed growth rings measurements. MD conducted the other analyses with the help of CG and MJ. MD and CG wrote the manuscript with the contribution of MJ, QP and CV.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dendro.2024.126282](https://doi.org/10.1016/j.dendro.2024.126282).

Data availability

Data will be made available on request.

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