

**Travail de fin d'études en gestion des forêts et des espaces naturels :  
Dendrochronological potential of secondary species: bases for the  
development of the study of sycamore maple (*Acer pseudoplatanus*), black  
alder (*Alnus glutinosa*) and common hornbeam (*Carpinus betulus*).**

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**DENDROCHRONOLOGICAL POTENTIAL OF SECONDARY SPECIES: BASES FOR THE DEVELOPMENT OF THE STUDY OF SYCAMORE MAPLE (*ACER PSEUDOPLATANUS*), BLACK ALDER (*ALNUS GLUTINOSA*) AND COMMON HORNBEAM (*CARPINUS BETULUS*)**

**SIMON MUSIN**

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**ANNEE ACADEMIQUE 2025-2026**

**(CO)-PROMOTEUR(S): TOM DE MIL, JAN VAN DEN BULCKE**



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## **Appreciations:**

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## **Stakeholders:**

- The Joint Wood Lab at Gembloux AgroBioTech, Forest and Natural Resources Management Section (GFEN), Forest is life, University of Liège.
- The Gent-Woodlab team, part of the Department of Environment, Faculty of Bioscience Engineering at Ghent University (Belgium).
- Georg Josef Wilhelm, German silviculture specialist and developer of the QD method.

## Résumé :

Le changement climatique affecte de manière croissante la stabilité, la productivité et la résilience des forêts européennes, notamment à travers la récurrence des épisodes de sécheresse et l'augmentation des températures. Bien que la recherche dendrochronologique se soit principalement concentrée sur les principales espèces feuillues commerciales, cette étude examine le potentiel de trois espèces feuillues jusqu'ici peu étudiées : l'érable sycomore (*Acer pseudoplatanus*), l'aulne glutineux (*Alnus glutinosa*) et le charme commun (*Carpinus betulus*). La recherche combine des méthodes dendrochronologiques classiques avec la tomographie par rayons X (XCT) afin d'analyser la largeur des cernes de croissance (TRW), la densité maximale du bois final (MXD) ainsi que les variations intra-annuelles de densité du bois. Les relations climat-croissance ont été étudiées à partir de séries de données de température et de précipitations. Les résultats montrent que les trois espèces étudiées produisent des cernes de croissance suffisamment distincts et synchrones pour permettre une analyse dendrochronologique fiable. Dans l'ensemble, cette étude confirme le potentiel de ces espèces feuillues secondaires pour de futures recherches dendro-écologiques.

**Mots-clés :** Dendrochronologie, Dendroclimatologie, Tomographie par rayons X (XCT), Largeur des cernes, Densité maximale du bois final, Changement climatique, *Acer pseudoplatanus*, Erable sycomore, *Alnus glutinosa*, Aulne glutineux, *Carpinus betulus*, Charme commun.

## Abstract:

Climate change is increasingly affecting the stability, productivity, and resilience of European forests, particularly through recurrent drought events and rising temperatures. While dendrochronological research has extensively focused on major commercial broadleaved species, this study investigates the potential of three underrepresented broadleaved species: sycamore maple (*Acer pseudoplatanus*), black alder (*Alnus glutinosa*), and common hornbeam (*Carpinus betulus*). The research combined classical dendrochronological methods with X-ray Computed Tomography (XCT) to analyse tree-ring width (TRW), maximum latewood density (MXD), and intra-annual wood density variations. Climate-growth relationships were further explored using temperature and precipitation datasets. The results demonstrate that the three studied species produce sufficiently distinct and synchronous growth rings to allow reliable dendrochronological analysis. Overall, this study confirms the potential of these secondary broadleaved species for future dendroecological research.

**Keywords:** Dendrochronology, Dendroclimatology, X-ray Computed Tomography (XCT), Tree-ring width, Maximum latewood density, Climate change, *Acer pseudoplatanus*, Sycamore maple, *Alnus glutinosa*, Black alder, *Carpinus betulus*, Common hornbeam.

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## Abbreviations

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- **DBH** – Diameter at Breast Height
- **EPS** – Expressed Population Signal
- **GLK** – Gleichläufigkeit (Coefficient of Agreement)
- **MXD** – Maximum Latewood Density
- **MXDi** – Maximum Latewood Density Index
- **Q1–Q4** – Radial Quartiles of the Annual Ring
- **QD** – Qualification–Dimensioning (Silvicultural Method)
- **QWA** – Quantitative Wood Anatomy
- **RBAR** – Mean Inter-series Correlation
- **RWI** – Ring-Width Index
- **SNR** – Signal-to-Noise Ratio
- **TRW** – Tree-Ring Width
- **XCT** – X-ray Computed Tomography

# 1. Introduction: state of the art

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## 1.1 Context

### 1.1.1 Climate change

Climate change refers to a long-term alteration of the Earth's climate system, primarily associated with the human-induced increase in the concentration of greenhouse gases in the atmosphere. These gases trap a greater portion of the infrared radiation emitted by the Earth's surface, thereby leading to a rise in the global average temperature (*IPCC, 2021*).

This accumulation in the atmosphere has already resulted in a warming of approximately 1 °C compared to the pre-industrial period, and the global mean temperature is expected to reach an increase of about 1.5 °C in the coming decades, likely between 2030 and 2052 (*IPCC, 2018*).

The increase in global temperature does not occur uniformly across the planet. Continents generally warm more rapidly than oceans. This rise in temperature also leads to changes in the climate system, including an increase in the frequency and intensity of certain extreme events such as heatwaves.

Due to the inertia of the climate system and the long atmospheric lifetime of CO<sub>2</sub>, warming persists over long periods, even in the case of emission reductions. Therefore, limiting the increase in global temperature strongly depends on the speed and magnitude of reductions in greenhouse gas emissions (*Lescarmontier & al., 2019*).

### 1.1.2 The state of European forests

Forest dieback refers to the progressive decline in tree vitality, often linked to increasing environmental stresses. Over the past decades, European forests have experienced a rise in dieback episodes, mainly due to more frequent and intense droughts associated with climate change. The combination of hotter summers and prolonged water deficits weaken trees, which can lead to increased mortality and promote the emergence of opportunistic biotic agents (*Bouget & al., 2023*).

Among European forests, those in Central Europe have shown the highest vulnerability. In these temperate regions, coniferous species such as Norway spruce (*Picea abies*) have experienced increased mortality due to persistent water deficits and high temperatures. This primary stress has facilitated outbreaks of bark beetles (*Ips typographus*), pests that exploit weakened trees, resulting in losses of harvestable timber volumes measurable in millions of cubic meters of damaged or lost wood.

In broadleaved production species such as European beech (*Fagus sylvatica*) and certain oak species (*Quercus* spp.), drought has caused significant defoliation, reducing the trees photosynthetic capacity and their carbon reserves.

Over the period 2018–2022, these combined abiotic stresses have led to a significant increase in tree mortality, net losses in harvestable volume, reduced annual growth, and increased susceptibility to infestations by xylophagous insects in both coniferous and commercially important broadleaved stands. Altogether, these factors threaten the sustainability of European productive forest systems by reducing available timber stocks, degrading resource quality, and compromising natural regeneration in certain key species (Seidl & al., 2025).

In conclusion, these trends highlight an urgent need to adapt forest management practices and production models to the increasing frequency of extreme conditions driven by ongoing climate change.

### **1.1.3 Forest management facing dieback**

In response to the decline of major commercial tree species, forest managers should prioritize adaptive management strategies aimed at strengthening stand resilience. This involves placing each species within its ecological optimum, considering climate, soil conditions, and water availability, and, where necessary, complementing them with secondary species suited to future climatic stresses.

Genetic and species diversity is essential to limit the spread of pests, dilute health risks, and promote protective interactions between species. Dynamic silviculture, through earlier and more intensive thinning operations, reduces competition among trees, improves their physiological balance, and limits their vulnerability to storms, diseases, and drought, while also accelerating the production of high-quality timber.

Furthermore, the protection of water resources, through the preservation of soil water storage capacity and the selection of deep-rooting species, is crucial in the face of increasing water stress.

Finally, the observation and maintenance of semi-natural forests provide models of resilience and guide management practices toward more irregular, mixed, and environmentally adapted forest structures. These measures help prepare major commercial tree species to withstand climatic and sanitary crises while ensuring the long-term sustainability of forest ecosystems (Claessens, 2016).

## 1.2 Essential theoretical concepts

### 1.2.1 Dendrochronology

Dendrochronology is the scientific discipline that studies and dates the annual growth layers of trees (growth rings; *Smith, 2007*). Each ring corresponds to one year and consists of earlywood, formed in spring, and latewood, produced at the end of the growing season. These structures, influenced by environmental conditions, constitute natural archives with annual resolution, useful for dating events and reconstructing past environmental conditions.

In the 1960s, Hal Fritts formalized the relationships between radial growth and climate, while Polge introduced X-ray densitometry, enabling the analysis of wood density and improving the accuracy of climate reconstructions.

Ring formation results from the activity of the vascular cambium, a layer of actively dividing cells that functions only during the growing season. Earlywood cells, which are larger and have thinner walls, contrast with the denser latewood cells.

Anomalies such as missing rings or false rings may occur depending on climatic conditions, but they can be detected by comparing multiple trees from the same site using cross-dating techniques (*Smith, 2007*).

Seven principles govern this discipline (*Smith, 2007*):

1. Principle of uniformitarianism: the relationships between growth and environment observed today also existed in the past.
2. Principle of the limiting factor: growth is controlled by the most restrictive environmental variable (often water or temperature).
3. Principle of aggregate growth: each growth ring reflects multiple factors (age, climate, local disturbances, random effects).
4. Principle of ecological amplitude: trees respond more strongly to environmental variations when they grow at the limits of their distribution range (altitude, latitude, aridity).
5. Principle of site selection: choosing locations where a single factor limits growth optimizes the environmental signal.
6. Principle of cross-dating ensures the absolute dating of each growth ring.
7. Principle of replication: increasing the number of samples (multiple trees, multiple radii per tree) helps reduce biological noise and enhances the common signal.

The construction of a master chronology involves three steps:

1. Cross-dating of series to identify missing or false rings.
2. Standardization to remove effects related to tree age or size, producing ring-width indices.
3. Compilation into a regional chronology representative of the dominant environmental constraints (Smith, 2007).

Since the 1980s, wood microanalysis has profoundly renewed the discipline. These techniques make it possible to study tree responses to seasonal variations in temperature, moisture, and radiation (Coulthard, 2013).

In conclusion, dendrochronology also aims to interpret the physical and chemical information contained within these growth rings. Annual tree growth varies according to numerous environmental and biological factors, and this variability can be conceptualized by the following equation:

Equation 1: Conceptual formulation of the dendrochronological signal (Cook, 1987).

$$TR_t = A_t + C_t + D_{1t} + D_{2t}$$

Where  $TR_t$  represents the measured ring parameter for year  $t$ .  $A_t$  represents the trend related to the biological age of the tree;  $C_t$  denotes the influence of climatic conditions on growth;  $D_{1t}$  corresponds to ecological factors specific to the individual tree; and  $D_{2t}$  represents factors affecting the entire stand, such as diseases or regional disturbances.

### 1.2.2 Dendroclimatology

According to Bradley (2015), dendroclimatology is the scientific study of past and present climate variations using tree growth rings. Growth-ring series constitute a continuous, annual natural archive that is widely distributed across the globe. The width, density, and chemical composition of the rings reflect the environmental conditions that influenced tree growth.

Furthermore, variations in wood density (measured via radiography) provide a highly sensitive climate indicator, particularly the maximum density of latewood, which is strongly correlated with summer temperatures. These data, combined with isotopic measurements of the wood, allow for more precise reconstructions of past climate variations (Bradley, 2015).

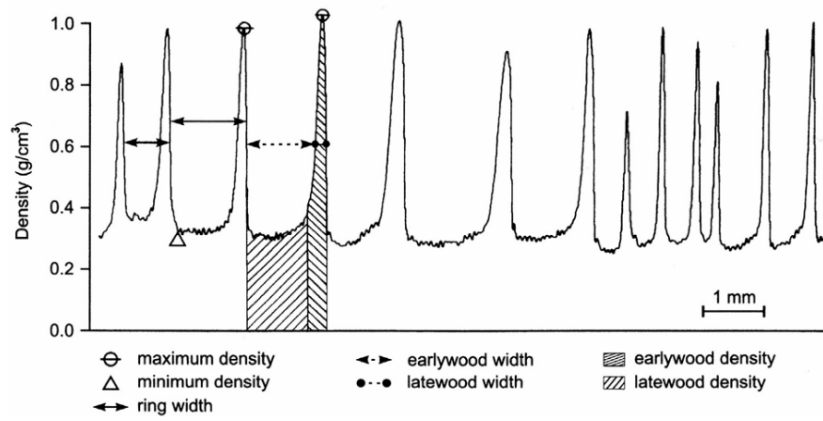


Figure 1- Theoretical graph of the density profile to serve as an input for dendroclimatological analysis, featuring the ring width (earlywood and latewood) as well as the density variables (Bradley, 2015)

### 1.2.3 Cross-dating

The foundation of dendrochronology relies on the cross-dating of growth-ring series, which allows for the precise dating of each ring. The success of this method depends on the coherence of the common climatic signal among trees from the same site. Studies focus on areas where a single climatic factor limits growth (temperature, precipitation, etc.).

Trees located at the edges of their distribution range (high altitude or latitude) are particularly sensitive to climatic variations. Analyses often focus on ring width, latewood density (MXD), or the distinction between earlywood and latewood, which serve as indicators of different seasons.

Chronologies are established from multiple trees at a given site. Each series is standardized to remove age-related effects and highlight the common climatic signal. The statistical reliability of a chronology is measured by the expressed population signal (EPS).

Statistical relationships (transfer functions) between climatic variables and growth parameters enable the reconstruction of past conditions, sometimes spanning several millennia (Luckman, 2013).

This method also corrects for common growth anomalies:

- False or intra-annual rings, produced by temporary stress,
- Missing or partial rings, when annual growth is interrupted.

Cross-dating multiple series makes these errors detectable and allows the construction of robust chronologies.

#### 1.2.4 Comparative Advantages of Dendrochronology

Dendroecology and Anatomy are closely related disciplines within tree ring science.

Dendroecology studies the relationships between tree growth and ecological factors such as competition, disturbances, soil conditions, and environmental change, using tree-ring patterns to reconstruct past ecosystem dynamics and assess tree responses to biotic and abiotic stresses. Dendro-anatomy focuses on the microscopic structure of wood tissues and cells formed during annual growth, providing detailed information on physiological processes and environmental conditions influencing xylem formation. Together, these disciplines complement dendrochronology and dendroclimatology by linking tree-ring variability to ecological functioning and wood anatomical responses at multiple spatial and temporal scales (*Fritts, 1976; Cook, 1990*).

While approaches such as remote sensing (LiDAR) allow for rapid, large-scale assessment of stand structure (height, density, or tree distribution, etc.), dendrochronology retains a unique role by providing a precise temporal record of tree growth and responses to climatic stress and disturbances. This historical and physiological dimension cannot be captured by remote sensing methods, which offer spatial snapshots but do not track the annual or decadal evolution of tree vitality. Thus, even though alternative techniques facilitate forest analysis over vast areas, dendrochronology remains essential for understanding growth mechanisms and species responses to environmental variations, complementing and enriching the structural data provided by other methods (*Leduc, 2025*).

The formation of growth rings results from the seasonal activity of the cambium, which produces new xylem cells. These cells undergo several successive differentiation phases before forming functional wood. The final anatomical characteristics of the cells depend on the physiological and environmental conditions encountered during these developmental stages.

Consequently, the structure of an annual ring records the combined influence of climatic and biological factors acting during the growing season. Measurable parameters, such as ring width, cell anatomy, wood density, or isotopic composition, contain information about the environmental conditions prevailing during wood formation. Although dendrochronological series are generally interpreted at annual resolution, the properties of cells within a single ring can also reflect seasonal variations during growth, which justifies dividing each ring into equal quarters (cf. 2.7.2).

This sectoral approach offers an important methodological advantage: whereas MXD provides a synthetic indicator of the late-season thermal signal, dividing the ring into four quantiles allows reconstruction of the intra-annual dynamics of wood formation and highlights a progressive shift in climatic control, from water availability in spring to temperature in summer. It thus refines the

interpretation of climate–growth relationships and enhances understanding of the underlying ecophysiological mechanisms (Bytebier & al., 2022).

However, the interpretation of these intra-annual signals remains complex, as the different phases of cell differentiation do not occur simultaneously and may overlap in time. This dynamic results in a non-linear relationship between the radial position of cells within the ring and the exact timing of their formation.

Despite these limitations, detailed analysis of intra-annual ring properties allows for improved temporal resolution in environmental reconstructions and a better understanding of the physiological mechanisms controlling tree growth (Rathgeber, 2016; Pérez-de-Lis & al., 2022). Two recent publications have indeed provided new insights into the growth and dynamics of silver birch (*Betula pendula*, Zeoli, 2025) and small-leaved lime (*Tilia cordata*, Latte, 2020).

### **1.2.5 X-ray Computed Micro Tomography ( $\mu$ XCT) in Dendrochronological Research**

X-ray Computed Tomography (XCT tomography) is a non-destructive imaging technique based on X-ray attenuation, allowing the reconstruction of high-resolution three-dimensional images of wood structure and density.

In dendrochronological studies, XCT enables the analysis of increment cores without extensive sample preparation, while simultaneously providing measurements of tree-ring width (TRW), maximum latewood density (MXD), and quantitative wood anatomy (QWA) data. One of the major advantages of this method is its ability to acquire anatomical and densitometric information at multiple spatial scales, ranging from inter-ring variability to cellular structure, while preserving the integrity of the samples.

XCT tomography also allows high-throughput processing and reproducible measurements, making it particularly suitable for large dendroecological and dendroclimatological datasets. The integration of three-dimensional density and anatomical data improves the characterization of tree growth responses to environmental and climatic variability, thereby extending the analytical potential of traditional dendrochronological approaches (De Mil, 2023).

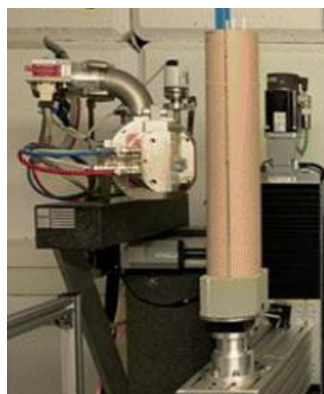


Figure 2-Image of the XCT scanner (Verschuren, 2023)

### 1.3 Research Gap

The scientific literature already provides a substantial body of dendrochronological studies on high-yield broadleaved tree species, such as European beech (*Fagus sylvatica*, *Drobyshev & al., 2010*), oaks (*Quercus* spp., *Haneca & al., 2009*), and other major species (e.g., ash, *Fraxinus excelsior*, *Bochenek, 2010*).

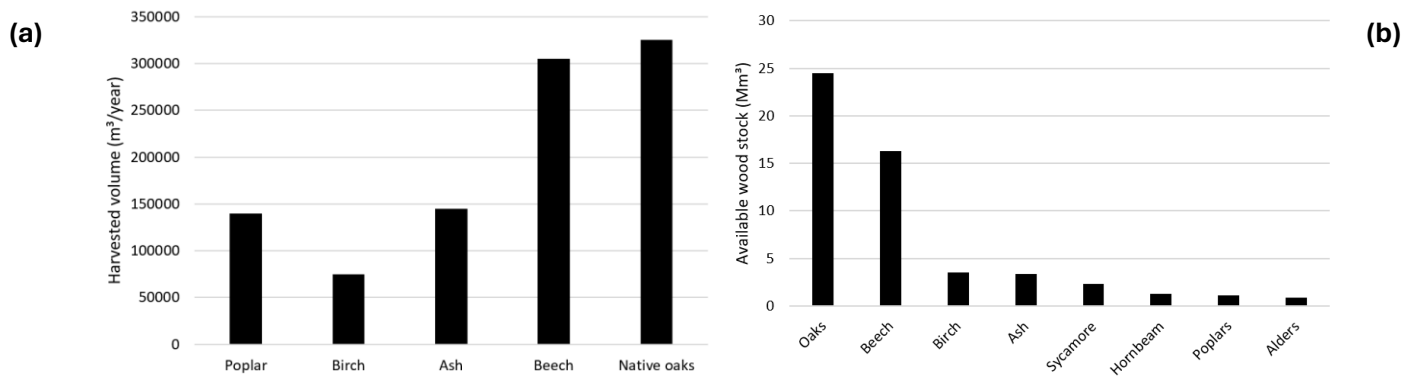


Figure 3-Harvested volume in Wallonia of the main broadleaf species (a, *Panorabois 2024*) and Available wood stock (b, in million m³) in the Greater region (Greater region's statistic portal, 2025)

In Wallonia, for example, the broadleaved forest composition is largely dominated by these two species (*Latte & al., 2022*). Furthermore, they account for the largest share of regional timber production (Figure 3). This predominance reflects their economic and ecological importance in the Walloon forest landscape (*Panorabois, 2024*) and, consequently, justifies the priority of studying these species within the forest environment. But what about the other species?

Beyond oak and beech, the Great Region hosts substantial hardwood resources of secondary species. Although less dominant in forest composition and timber production, these species represent an important and locally abundant resource, offering significant potential for diversification and wood valorisation within regional forest ecosystems (*Greater region's statistic portal, 2025*).



Figure 4-Overall map of the Greater Region (*Interreg, 2026*)

The European Union Interreg projet Wood Added Value Enabler (W.A.V.E), aims to strengthen the local wood sector in the Great Region by improving sustainable forest management, promoting innovation in wood processing (*Interreg, 2024*).

However, despite these advances, several species remain underrepresented in in-depth dendroecological analyses. Species such as hornbeam (*Carpinus betulus*), sycamore maple (*Acer pseudoplatanus*), and black alder (*Alnus glutinosa*) still

raise questions regarding their responses to environmental factors. The present study fits within this perspective of expanding knowledge,

exploring the dendrochronological potential and specificities of these lesser-documented species.

## 1.4 Ecology, anatomy and wood of study species

### 1.4.1 *Acer pseudoplatanus* L. — Sycamore maple

Sycamore maple (*Acer pseudoplatanus*) is a large deciduous broadleaved tree that can reach 30 to 35 meters in height. It is characterized by a broad rounded crown, a strong root system, and large opposite, palmately lobed leaves with five lobes. A monoecious species, it produces paired samaras arranged in a “V” shape, enabling efficient wind dispersal.

Its natural range covers Central and Eastern Europe, the southern European mountain ranges, the Caucasus, and northern Asia Minor.



Figure 5-Image of the sycamore maple (Author)

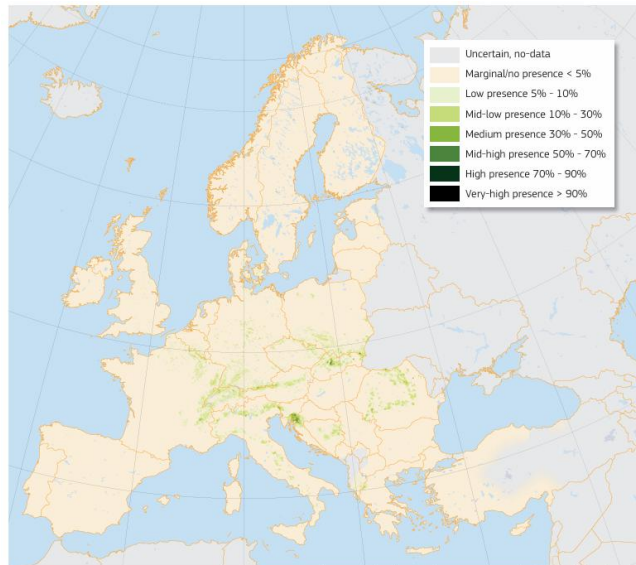


Figure 6- Map of natural distribution of *Acer pseudoplatanus* (Pasta, 2016)

The species prefers nutrient-rich, well-watered soils and thrives particularly in shaded microclimates, often at the base of slopes or in ravines. It tolerates a wide range of soil conditions, from calcareous substrates to more acidic soils, but does not withstand prolonged drought periods.

*A. pseudoplatanus* is a shade-tolerant, moisture-loving species capable of regenerating under closed-canopy stands. It often dominates mixed, cool, and humid broadleaved forests, particularly in Tilio-Acerion communities on slopes, screes, and ravines, priority forest habitats in Europe (Pasta, 2016). Additionally, it has a moderately deep, spreading root system, approximately one meter in depth.

Highly tolerant to air pollution, salt spray, and low summer temperatures, *A. pseudoplatanus* adventitious roots contribute to soil stabilization and erosion control, particularly in mountainous regions (Durrant, 2016).

As shown in Figure 7, *A. pseudoplatanus* accounts for approximately 10% of the Walloon forest, representing a significant portion of its area. It is also important to note that the species reaches

its ecological optimum across most of the territory, except in the eastern region, where its tolerance range is broader (*Fichier écologique des essences*).

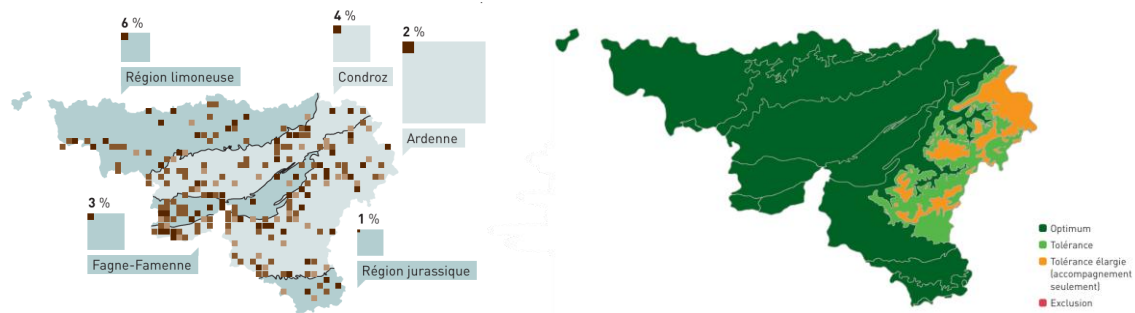


Figure 7-Proportion of *A. pseudoplatanus* across the Walloon forests and its ecological suitability (FEE)

Maple wood is homogeneous and diffuse-porous, characterized by small vessels evenly distributed throughout the xylem tissue (Figure 8). The rays are multiseriate, ranging from 1 to 8 cells in width. It does not exhibit scalariform perforations, but the vessels show spiral thickenings. The parenchyma is primarily paratracheal or apotracheal and dispersed, contributing to the wood's homogeneous and finely textured structure (Jourez, 2024).

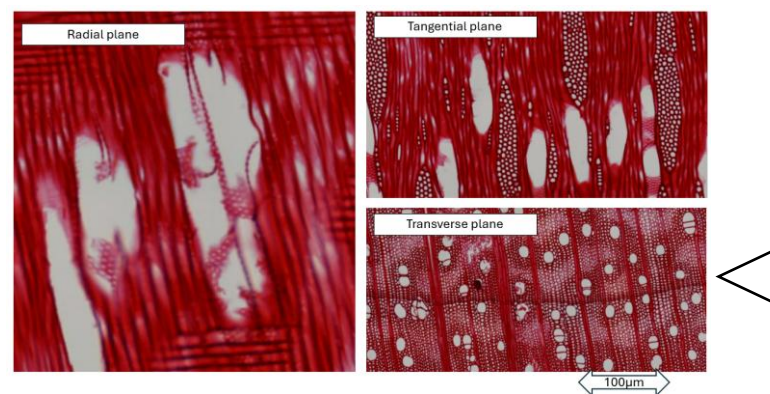


Figure 8-Anatomical demonstration of the sycamore maple (*Xylogis*)

#### 1.4.2 *Alnus glutinosa* (L.) Gaertn. — Black alder

Black alder (*Alnus glutinosa*) is a medium-sized broadleaved species, typically reaching 10 to 25 meters in height. It is fast-growing but has a relatively short lifespan, averaging around 120 years. Additionally, it possesses a deep and strong root system, extending several meters.

The natural range of *A. glutinosa* covers most of Europe, from Scandinavia to the Mediterranean regions, and includes parts of North Africa. The species primarily grows below 1,000 meters in altitude (Durrant, 2016).



Figure 9-Image of black alder leafs (Author)

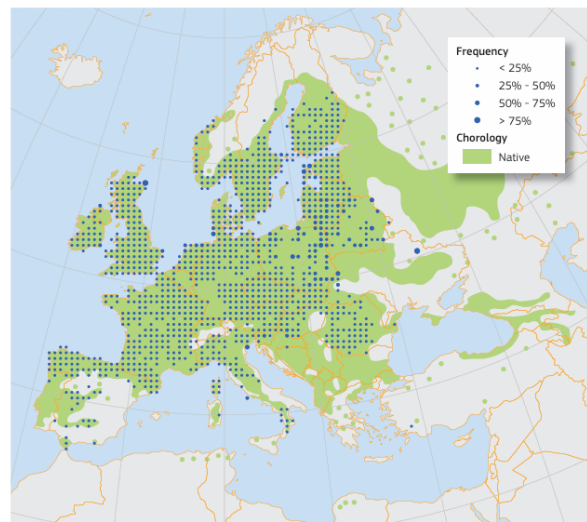


Figure 10-Map of natural distribution and frequency of *Alnus glutinosa* (Durrant, 2016)

As shown in Figure 11, black alder accounts for approximately 3% of the Walloon forest area. It is also important to note that alder reaches its ecological optimum across nearly the entire region, except in the eastern part, where its tolerance range is broader (*Fichier écologique des essences*).

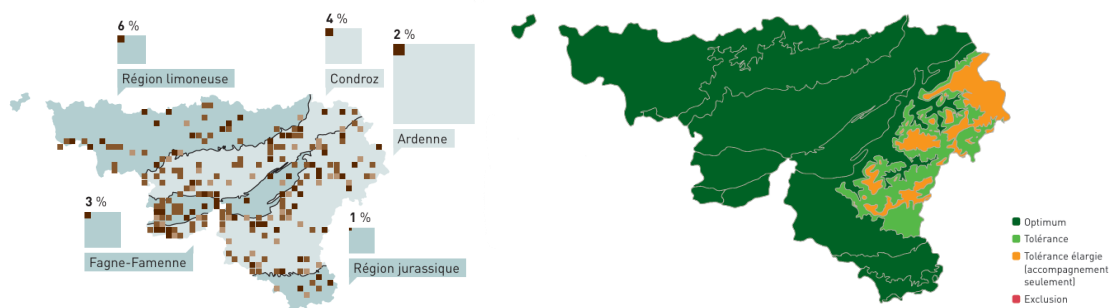


Figure 11- Proportion of *A. glutinosa* across the Walloon forests and its ecological suitability (FEE)

Highly dependent on water, black alder is commonly found along riverbanks, in wetlands, marshes, and floodplains. It tolerates a wide range of soil types, if moisture is sufficient, but performs poorly on calcareous soils.

*A. glutinosa* fixes atmospheric nitrogen through a symbiosis with the bacterium *Frankia alni* in its root nodules. This ability, combined with its nitrogen-rich litter, makes it an important pioneer species, capable of improving soil fertility and facilitating the establishment of other tree species. It also plays a crucial ecological role in bank stabilization and hydrological regulation (Durrant, 2016).

Finally, alder wood is homogeneous and diffuse-porous, with small vessels evenly distributed (Figure 12). The rays are primarily uniseriate, though rarely biseriate. Perforation plates are

scalariform, and the parenchyma is apotracheal and dispersed. False rays are frequently observed, sometimes giving the wood a slightly irregular appearance (Jourez, 2024).

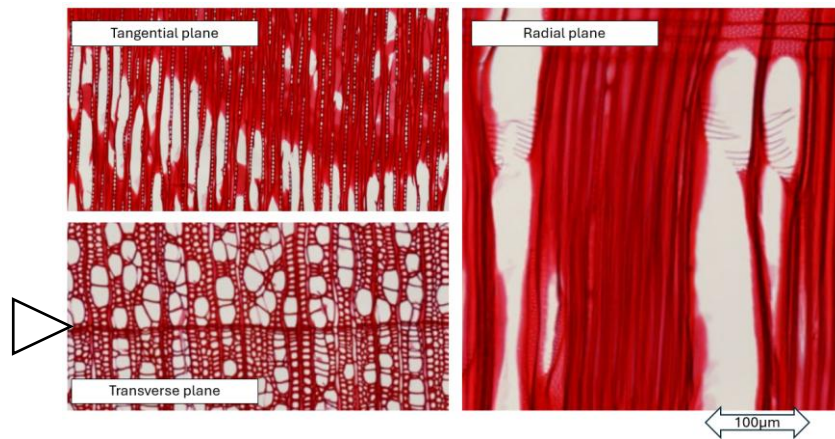


Figure 5-Anatomical demonstration of the black alder (*Xylogis*)

### 1.4.3 *Carpinus betulus* L. — Common hornbeam

Common hornbeam (*Carpinus betulus* L.) is a broadleaved tree typically reaching 20 to 25 meters in height. It is characterized by its marcescent foliage, with leaves that only fall in spring during bud burst (Sikkema & al., 2016).

Its natural range extends from the northern Iberian Peninsula and the Pyrenees to southern Sweden, and eastward to Iran. It is primarily found in temperate zones of Central and Western Europe, from sea level up to approximately 1,000 meters in altitude.



Figure 13-Image of Hornbeam leafs (Author)

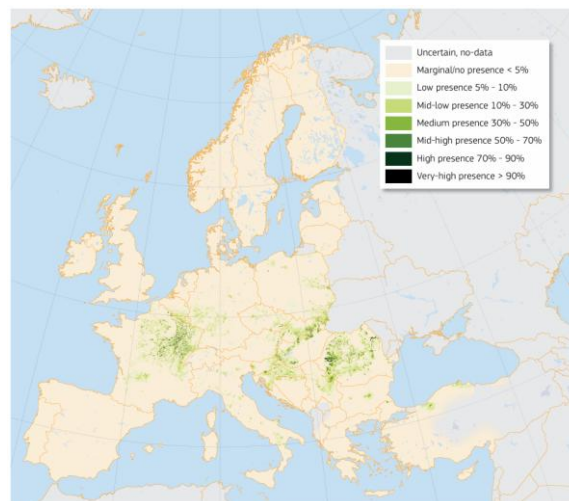


Figure 14-Map of natural distribution of *Carpinus betulus* (Sikkema & al, 2016)

A mesophilic species, it tolerates a wide range of soil conditions. It grows well in shade and under competition, allowing it to function as a secondary or understory species in mixed forests, notably in oak–hornbeam and beech stands (Sikkema & al., 2016). Additionally, it has a moderately deep root system, reaching approximately one meter in depth.

As illustrated in Figure 15, hornbeam accounts for about 13% of Walloon forests, with only 6% of this area in pure stands. Considered a moderately fast-growing species, hornbeam shows real silvicultural potential in the region, which remains underexploited. It should also be noted that the species reaches its ecological optimum over most of the territory, except in the eastern part, where its tolerance range is broader (*Fichier écologique des essences*).

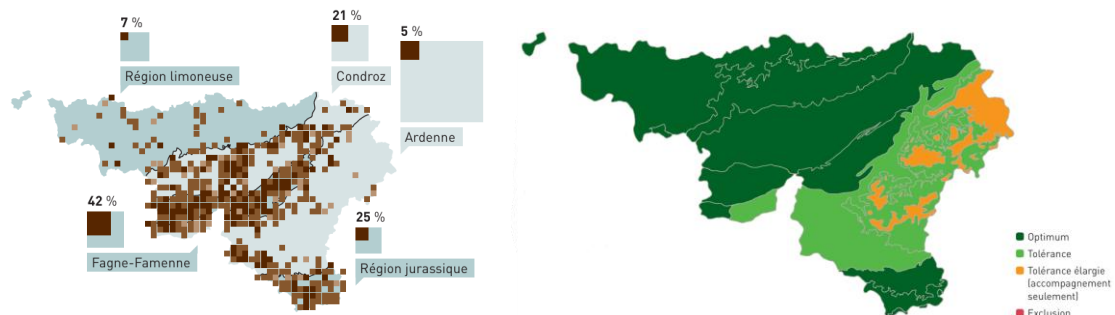


Figure 15- Proportion of *C. betulus* across the Walloon forests and its ecological suitability (FEE)

Hornbeam wood is a homogeneous, diffuse-porous material, with small vessels evenly distributed throughout the structure (Figure 16). The wood rays are multiseriate, generally 1 to 3 cells wide. It does not exhibit scalariform perforations, but the vessels show spiral thickenings. Parenchyma is abundant, often clearly visible around the vessels. Growth-ring boundaries are wavy, and false rings are frequently observed, reflecting seasonal variations in growth (*Jourez, 2024*).

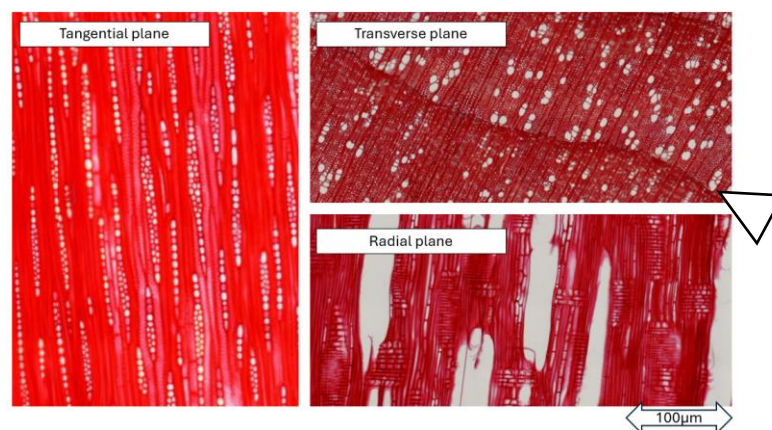


Figure 16-Anatomical demonstration of the hornbeam (*Xylogis*)

## 1.5 Alder, maple and hornbeam woods: an opportunity for the industry

### 1.5.1 *A. pseudoplatanus*

For the wood sector, sycamore maple represents a high value-added resource: its light-coloured, homogeneous, regular, and fine-textured wood is highly sought after for veneer, cabinetmaking, fine joinery, musical instruments, flooring, decorative uses, and energy production (*Ollivier, 2010; Appendix 1*). It offers good mechanical properties, excellent machinability and finishing qualities, and strong aesthetic value (*Pasta, 2016*).

Producing sycamore maple therefore represents a significant industrial opportunity, as it supplies high-quality markets with high unit prices, while also contributing to the resilience of mixed forest stands (*Hein & al., 2025*).

### 1.5.2 *A. glutinosa*

For the wood industry, alder represents a valuable opportunity: its wood is homogeneous, soft, and lightweight, making it easy to work with. It is stable after drying and performs well in moist environments when submerged or protected from air.

It is used for piles, submerged structures (notably in Venice), light structural frameworks, veneer, rotary cutting, plywood, interior joinery, furniture, panels (*Durrant, 2016*), and as fuelwood (*Ollivier, 2010; Appendix 1*). Its valorisation is particularly attractive because it can be grown on sites where high-value species perform poorly, making it an economic opportunity on constrained sites (*Claessens & al., 2010*).

### 1.5.3 *C. betulus*

Although sometimes underestimated in production, hornbeam represents a valuable resource for the wood industry due to its very dense, hard, and wear-resistant wood. However, it is difficult to work with because of its irregular grain and significant shrinkage during drying.

Its high mechanical properties make it a sought-after material for technical components, flooring, tools, handles, and parts subjected to impact and friction (*Sikkema & al., 2016*), as well as for high-calorific-value fuelwood (*Ollivier, 2010; Appendix 1*).

Its ability to produce highly resistant technical wood within mixed forest contexts makes it an interesting opportunity for product diversification and market development, particularly for sectors promoting locally sourced hardwoods (*Sokolowski & al., 2024*).

## 1.6 Tree (wood) response to climate change

### 1.6.1 Global response

Wood anatomy varies with latitude, altitude, and temperature, as these factors influence characteristics such as vessel diameter and frequency. Wood from warmer regions generally exhibits wider and fewer vessels, with little or no scalariform perforations, whereas species from colder areas display a finer and denser anatomy. These relationships allow wood anatomical traits to be used as climatic indicators (*Baas, 2011*).

Wood density, linked to tissue proportions and cell wall thickness, is a good indicator of hydraulic safety and the ecological adaptation of species.

With climate warming, plant species tend to shift their distribution ranges, either altitudinally or latitudinally toward cooler areas. Species from cold or dry environments, adapted to extreme hydraulic conditions, are particularly vulnerable to rising temperatures and climatic irregularities.

Experimental studies show that increases in CO<sub>2</sub> and temperature influence growth, density, and vessel structure, although no universal trend is observed. Overall, warming may render certain xylem structures less efficient, increasing the risk of cavitation or hydraulic failure.

Wood anatomy thus emerges as a key indicator of the adaptation, evolution, and resilience of woody species in response to climate change (*Baas, 2011*).

Wood anatomical characteristics observed in growth rings are valuable indicators of environmental changes. Numerous studies have investigated continuous and discontinuous anatomical modifications (ring width, density, etc.) in relation to climatic factors (temperature, precipitation) and atmospheric pollution (*Wimmer, 2002*).

Results show that climatic parameters, particularly temperature and precipitation, strongly influence wood formation, the size of tracheid and vessels, and xylem density. These findings confirm that global warming affects both growth and wood structure, leaving a lasting imprint in tree rings. Xylem therefore appears to be a key indicator of tree sensitivity to climatic conditions (*Pandey, 2021*).

### 1.6.2 Climate response recorded in the Sycamore maple's wood

*A. pseudoplatanus* shows adaptive potential in response to climate change, supported by substantial genetic variation in key traits such as growth and frost resistance. This species is characterized by high phenotypic plasticity, allowing it to adjust its biological responses to local environmental variations and emerging climatic constraints (*Kunz, 2018*).

A major challenge for sycamore maple lies in its sensitivity to late spring frosts, often exacerbated by earlier budburst induced by global warming. However, research indicates a

positive correlation between growth vigour and resistance to climatic stress, suggesting that the most vigorous families are also better equipped to withstand winter and spring damage. This genetic heterogeneity, observed both at the family and population levels, is essential for maintaining forest resilience and supports the implementation of dynamic conservation programs for genetic resources.

Thus, *A. pseudoplatanus* appears to possess the biological capacity to gradually adapt, provided that the genetic diversity of its populations is preserved to cope with future climatic instability (Pliūra, 2007).

### **1.6.3 Climate response recorded in the Black alder's wood**

*A. glutinosa* demonstrates a remarkable capacity to adapt to the challenges posed by global climate warming, largely due to its high phenotypic plasticity, which enables it to respond rapidly to changes in its immediate environment. This plasticity is reflected in direct physiological responses to variations in local soil and climatic conditions, providing short-term protection against environmental disturbances.

However, climate warming also exacerbates certain vulnerabilities, particularly by inducing earlier budburst, which increases the exposure of young shoots to late spring frosts, a major stress factor affecting growth and survival.

Research shows a positive correlation between growth rate and frost resistance, suggesting that the most vigorous individuals are better equipped to rapidly pass through developmental stages that are most sensitive to climatic hazards. This genetic diversity, especially pronounced in phenological traits among different populations, constitutes an essential basis for developing conservation and selection strategies aimed at maintaining the stability of forest ecosystems in the face of rising temperatures and the expected increase in extreme weather events (Pliūra, 2004).

### **1.6.4 Climate response recorded in the Common hornbeam's wood**

*C. betulus* exhibits a contrasting response to climate change depending on the regions studied. In the Arasbaran forests of northwestern Iran, hornbeam radial growth is primarily limited by water availability, with a positive correlation between ring width and precipitation, and a negative correlation with temperature.

The species therefore shows high sensitivity to drought, while still retaining potential for dendroecological studies and regional climate reconstruction (Emaminasab & al., 2023).

In Central Europe, *C. betulus* also demonstrates moderate drought tolerance and relatively stable growth characteristics on moist sites. Although its annual growth is generally lower than that of European beech (*Fagus sylvatica*) or oak (*Quercus* spp.), it can withstand short periods

of drought due to a relatively stable sap flow and a capacity for post-stress recovery. It is well suited to moist environments and can be associated with beech to help maintain forest stability under climate warming (*Schmucker & al., 2023*).

Thus, *C. betulus* combines sensitivity to drought periods (particularly in young trees) with resilience in mature individuals. This duality suggests that, although vulnerable to increasing temperatures and reduced precipitation, the species can contribute to the stability of temperate forests when established on moist sites or in mixture with drought-tolerant species.

## 1.7 Research questions

Based on these elements, it is appropriate to formulate the research questions underlying this study:

1. Do hornbeam, sycamore maple, and black alder exhibit sufficiently distinct, synchronous, growth rings to allow for dendrochronological analysis?
2. Is there a common growth signal, strong and consistent enough among individuals, to enable robust cross-dating and the construction of master chronologies for these species?
3. To what extent are these species capable of recording and reflecting environmental variations, and therefore providing a solid basis for future dendroecological studies?
4. How can X-ray Computed Tomography (XCT) based wood density analyses improve the detection of common growth and environmental signals in hornbeam, sycamore maple, and black alder for chronology building and dendroecological applications?

## 2. Materials and Methods

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### 2.1 Materials

- QGIS geographic information system (GIS) software
- Pressler increment borer (5 mm diameter)
- Garmin GPSMAP 65s GPS device
- Measuring tape (for circumference measurements)
- White paper straws (6 mm diameter)
- Cylindrical storage holder
- Paper adhesive tape
- X-ray tomography system (including drying oven and silica gel, UGent)
- Computer running Microsoft Windows (Word and Excel)
- MATLAB Runtime and XCT Toolchain software suite (developed in MATLAB)
- Software: RingIndicator and CoreComparison
- R software (v4.5.2) and RStudio development environment
- Meteorological data (daily temperature and precipitation).

### 2.2 Foreword

A preliminary study was first conducted in Gembloux (Belgium) on a limited number of samples to assess the feasibility of dendrochronological analysis for the species under investigation. This initial step aimed to determine whether these woods were suitable for analysis and whether the proposed methods were applicable.

As the results confirmed this feasibility (see Results and Discussion), a second sampling campaign was subsequently carried out in South-Germany, this time with enough samples to enable a comprehensive (and representative of the Greater region) dendrochronological analysis.

The present section therefore describes in detail the methodological approach implemented in Gembloux. As the same procedure was applied in the study conducted in Germany, it is not repeated here to avoid redundancy, since the overall approach and steps remain identical, albeit at a larger sampling scale.

### 2.3 Identification of the study areas

#### 2.3.1 Preliminary study in Gembloux (Belgium)

The Jacques Rondeux Forest, owned by the faculty, constitutes a particularly suitable study site due to the availability of trees of sufficient size and age for dendrochronological analysis (see Sampling). Its immediate proximity to the faculty facilitates field access and allows analyses to

be conducted without logistical constraints. Moreover, this forest is specifically dedicated to educational purposes, making it an appropriate setting for scientific research and teaching activities.

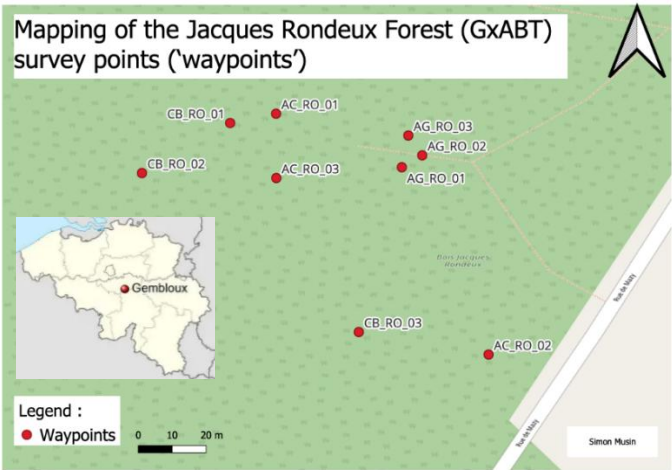


Figure 17-Mapping of the survey points in Gembloux (Belgium)

The study area is located within the Atlantic biogeographical region, more specifically in the Hesbino-Brabançon climatic zone. This territory consists of a plateau characterized by a basal area of 24.8 m<sup>2</sup> per hectare, with a total stem density of 284 stems per hectare. The species under study, such as hornbeam and alder, are relatively underrepresented, each accounting for only 1 to 5% of the total number of stems. In contrast, maple constitutes approximately one third of the stand (Figure 18). All three species are within their ecological optimum in the study area.

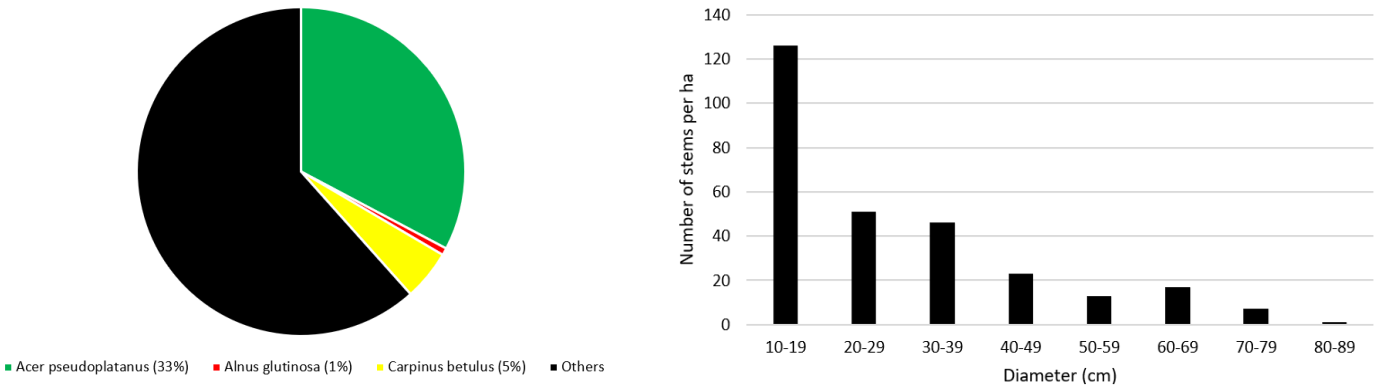


Figure 18-Distribution of stem density (N/ha) by diameter class and relative proportion (%) of the studied species within the total stand

### 2.3.2 Large-scale study in Blieskastel (Germany)

The Qualification–Dimensioning (QD) method, developed by Georg Josef Wilhelm, has been integrated into regional silvicultural strategies for several decades. This near-natural silvicultural approach aims to produce high-quality timber by guiding stand dynamics through the management of tree competition, particularly interactions related to height growth, shade tolerance, and crown expansion.

The method distinguishes two successive phases: a qualification phase, during which natural selection favours the most vigorous individuals with minimal intervention, and a dimensioning phase, where selected future crop trees are released from competition to promote crown and diameter growth. By focusing growth on a limited number of high-potential trees, the QD method supports the production of valuable timber while maintaining structurally diverse and multifunctional forest stands (Wilhelm, 2025).

Given the advanced age of the sampled trees, earlier management mainly consisted of conventional stand-scale thinning, whereas the QD method has been applied in the sampled plots since 1998.

The first stand type is dominated by alder (85% of stems per hectare), which was the target species for sampling, accompanied by hornbeam (10%) and sycamore maple (5%). The second type is primarily composed of maple (70%), which explains its selection for sampling, associated with beech (25%) and ash (5%). The third type presents a more diverse composition, with beech dominance (50%), followed by sessile oak (30%) and hornbeam (20%). A sub-selection of the latter hornbeams was sampled in this stand.

Available dendrometric parameters correspond to average estimates per hectare. For the first stand type, the basal area is estimated at approximately 28 m<sup>2</sup>/ha for a density of 180 stems/ha. The second type has a basal area of about 34 m<sup>2</sup>/ha for 120 stems/ha, while the third type is characterized by a lower basal area of around 21 m<sup>2</sup>/ha with a density of approximately 90 stems/ha. These values should be considered as approximate, as the QD method relies more on field observations and the manager's judgment.

For this study, these stand-level details were the only data provided.



Figure 19-Sampling map of the studied tree species in Blieskastel (Germany, Author)

## 2.4 Sampling

### 2.4.1 Core collection

In Belgium, three black alders, three sycamore maples, and three hornbeams, dominant or co-dominant, each with at least thirty growth rings, were selected. For each tree, two cores were extracted (Figure 20) using a 5 mm diameter Pressler increment borer (*Bradley, 2015*).



Figure 20-Tree sampling using a Pressler increment borer (Author)

In Germany, ten black alders, eleven sycamore maples, and ten hornbeams, either dominant or co-dominant, each with a minimum of thirty years, to avoid juvenile effects, were selected (Figure 19). For each tree, two cores were extracted and analysed following the method described above (Table 1).

Table 1-Study sites characteristics (altitude, coordinates, sample size, DBH and tree mean age).

| Sites             | Tree species             | Alt. (m) | Coordinates       | Trees (Cores) | DBH Range (cm) | Mean age (years, with MIN/MAX) |
|-------------------|--------------------------|----------|-------------------|---------------|----------------|--------------------------------|
| Gembloux (BEL)    | <i>A. pseudoplatanus</i> | 140      | (50.542N;4.693E)  | 3(6)          | (39;42.7)      | 51 (42; 53)                    |
|                   | <i>A. glutinosa</i>      | 140      | (50.542N;4.693E)  | 3(6)          | (36.6;38.5)    | 52 (37; 55)                    |
|                   | <i>C. betulus</i>        | 140      | (50.542N;4.693E)  | 3(6)          | (40.4;44.9)    | 64 (44; 73)                    |
| Blieskastel (GER) | <i>A. pseudoplatanus</i> | 218      | (49.267N ;7.250E) | 11(22)        | (57 ;75.3)     | 65 (47; 136)                   |
|                   | <i>A. glutinosa</i>      | 218      | (49.271N ;7.262E) | 10(20)        | (33 ;60)       | 83 (60; 193)                   |
|                   | <i>C. betulus</i>        | 218      | (48.168N ;7.335E) | 10(20)        | (37.9 ;70.7)   | 92 (85; 160)                   |

### 2.4.2 Establishment of the number of cores

Although standard recommendations in dendrochronology generally suggest a minimum of 15 to 20 cores per species and per site to ensure optimal statistical robustness, several studies have shown that reliable chronologies can be established from smaller sample sizes (*Bradley, 2015*).

Studies conducted in specific forest contexts have produced usable sequences from fewer than ten cores (*Jin & al., 2022*). These findings indicate that the quality of the dendrochronological signal depends more on the inter-individual coherence of the series, the sensitivity of trees to environmental factors, and the accuracy of measurements than on the absolute number of samples alone. When the climatic or environmental signal is strong and shared among the sampled individuals, a small sample size may be sufficient to reveal synchronous and statistically significant trends (*Wigley, 1984*).

In an exploratory phase or potential assessment study, the primary objective is to identify the presence of a common signal and the feasibility of chronological alignment. At this stage, a limited number of cores may therefore be sufficient to evaluate the relevance of a larger sampling effort. Preliminary analysis helps determine whether the wood exhibits exploitable interannual variability and a level of synchronization compatible with a more in-depth dendrochronological approach.

### 2.4.3 Storage and transport of cores

The increment cores were stored in white paper straws with a diameter of 6 mm, whose ends were carefully sealed and adjusted to allow their insertion into a cylindrical storage holder (*De Mil, 2023*).



Figure 21-Standard sample storage (Author)

Each straw was labelled with the sample code, the identification of its owner, and a clear indication of the side corresponding to the cambium (bark side, Figure 21). Fragmented cores were reassembled using paper adhesive tape, ensuring that the orientation of the fibers was preserved (*De Mil, 2023*).

Finally, each sampled tree was georeferenced using a GPS device (Garmin 65s), and its diameter (DBH [cm]) was measured using a measuring tape.

Prior to scanning, all samples were oven-dried for 24 hours at 103 °C, then cooled in an airtight container containing enough silica gel to prevent any moisture reabsorption (*Verschuren, 2025; De Mil, 2023*).

## 2.5 Sample analysis

An X-ray computed tomography (CT) analysis pipeline (Figure 22) was used to scan the cores at a resolution of 30  $\mu\text{m}$  (average resolution) to measure tree-ring width (TRW), maximum latewood density (MXD), as well as other parameters, without the need for sample sanding (*De Mil, 2023*).

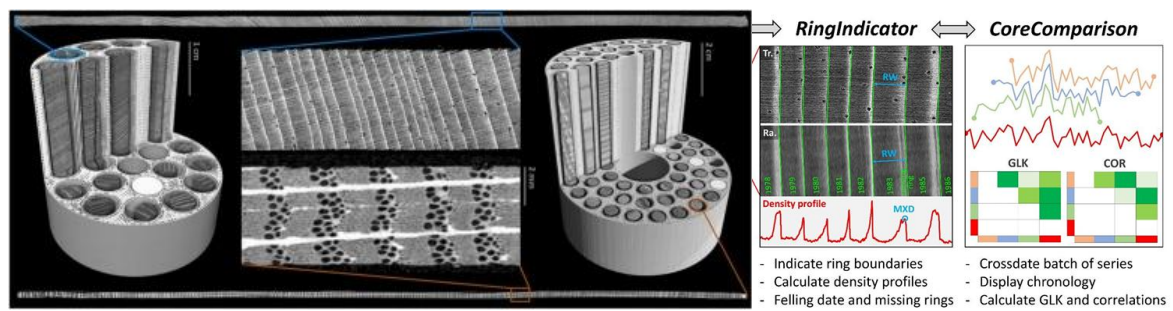


Figure 22-XCT (Scan, Softwares) toolchain presentation (Verschuren, 2025)

The acquired images were processed using specialized software: RingIndicator and CoreComparison (Verschuren & al., 2025; De Mil, 2023).

Analyses were carried out using the XCT Toolchain software suite, developed in-house and based on MATLAB. This suite includes RingIndicator, used for semi-automatic ring detection and density profile calculation, as well as CoreComparison, dedicated to cross-dating. The software, compiled for the Microsoft Windows environment, requires prior installation of MATLAB Runtime (Figure 22).

Ring widths and their density were measured directly from the images, after which the growth series were dated through cross-dating between trees to ensure temporal consistency and accuracy of the established chronologies (Vannoppen & al., 2017). This methodological approach enables reliable interpretation of the results and supports the derivation of robust conclusions.

### 2.5.1 The RingIndicator software

The process begins by opening the RingIndicator application, followed by manually placing markers (green bars) on the image, starting from the pith or the oldest available ring and ending with the most recent one, to correct structural deviations along the transverse and radial planes of the core (De Mil, 2023). This step is performed carefully to precisely align with the angle of each ring and to slightly extend beyond its visible boundary, thereby capturing the full extent of the available anatomical information (Figure 23).

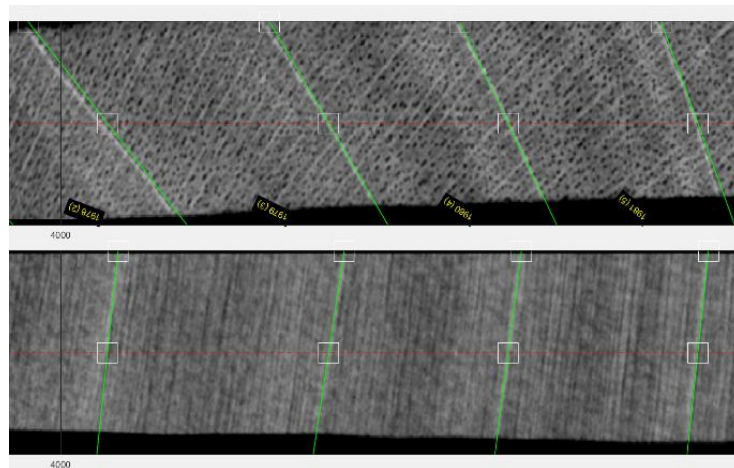


Figure 23-RingIndicator software used to analyse an *Acer sp.* sample during the study (30µm resolution)

Once all rings have been correctly marked, the analysis can be initiated in the application after entering the reference year for the analysis (here, 2025, corresponding to the last year of growth before sampling) and specifying that the program should focus its analysis on the core of the sample. The software then generates .txt files containing quantitative data, including ring density and width (Verschuren & al., 2025).

### 2.5.2 Wood Anatomical Features and Implications for Dendrochronological Readability

The comparative analysis of the wood anatomy of *A. pseudoplatanus*, *A. glutinosa*, and *C. betulus* highlights clear differences that directly influence the readability of growth-ring boundaries in scanned samples (Jourez, 2024).

In *A. pseudoplatanus*, the homogeneous diffuse-porous structure, with evenly distributed vessels and relatively well-defined ring boundaries, results in high legibility, facilitating accurate ring identification and measurement.

In contrast, *A. glutinosa* presents moderate difficulties due to the frequent presence of medullary spots and anatomical irregularities, which can locally obscure ring limits and introduce ambiguity during measurement. These features, although inherent to the species' wood structure, complicate the visual continuity of annual growth patterns.

The most challenging species is *C. betulus*, whose wood is characterized by aggregated rays and markedly wavy growth-ring boundaries. These anatomical traits, combined with the frequent occurrence of false rings, reduce the clarity of ring delimitation and increase the risk of misinterpretation.

Overall, these observations demonstrate that, beyond ecological and climatic responses, intrinsic wood anatomical characteristics play a decisive role in the reliability and precision of dendrochronological analyses (Figure 24).

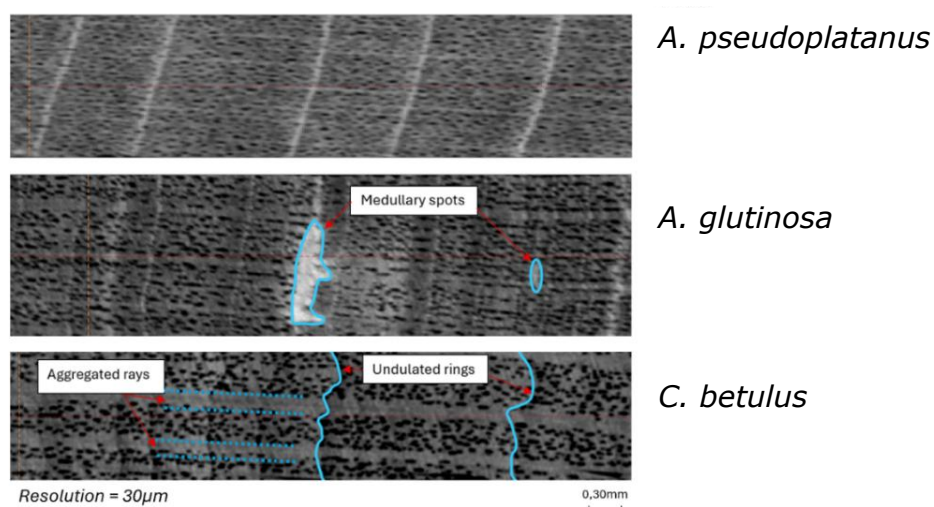


Figure 24- Representative scanned images illustrating growth-ring readability in the three studied species

### 2.5.3 The CoreComparison software

The obtained series must then be validated through a cross-dating step to verify the correct alignment of growth years between the different samples from the same tree (Figure 25). This verification is carried out using the CoreComparison tool, which allows for the detection of false rings or missing years (Verschuren & al., 2025; De Mil, 2023).

The main objective of this method is to obtain ring-width curves (in mm) over time that follow similar trends, to validate the information contained across all trees of a species, and more specifically within a given study area (Figure 26).

The secondary objective of this procedure is to achieve the highest possible GLK (Gleichläufigkeit) value. GLK is a widely used indicator for quantifying the percentage of agreement in the sign of interannual growth variations between samples, originally developed in 1969 and revised in 2015 (Equation 2). Consequently, a high GLK value indicates strong coherence in growth trends and, therefore, reliable crossdating (Buras, 2015).

Equation 2: adjusted determination of the glk (Buras, 2015)

$$glk(x, y) = 1 - \frac{1}{n-1} \sum_{i=1}^{n-1} |G_{ix} - G_{iy}|$$

Here,  $\Delta_{ix} = x_{i+1} - x_i$  and  $\Delta_{iy} = y_{i+1} - y_i$  for two series  $x$  and  $y$  being compared. The possible values of both  $G$  terms are therefore  $+\frac{1}{2}$  (if  $\Delta i > 0$ ),  $0$  (if  $\Delta i = 0$ ), and  $-\frac{1}{2}$  (if  $\Delta i < 0$ ).

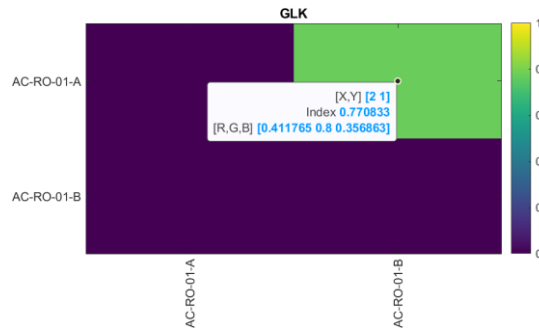


Figure 25-CoreComparison cross-dating example showcasing a high GLK value between two Acer sp. samples

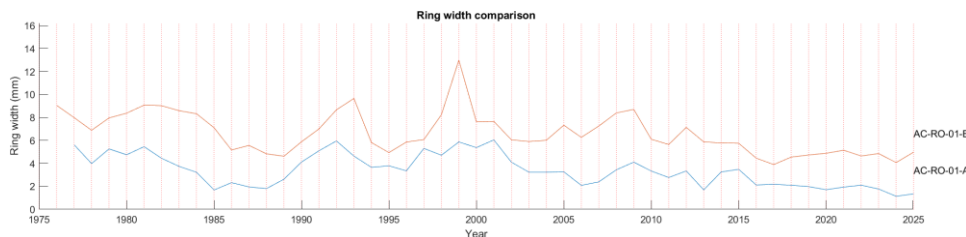


Figure 26-CoreComparison cross-dating example showcasing a high agreement between the two Acer sp. samples ring width graphs

Once the samples are validated, the Excel files exported by CoreComparison can be used to analyse ring density and width, and to compare these parameters with climatic data for the

study area. The CoreComparison tool also allows for corrections to cuts made in RingIndicator and to update the analysis accordingly, enabling real-time observation of improvements made to the study (De Mil, 2023).

## 2.6 Data processing

The analyses were performed using R software (version 4.5.2, R CORE Team, 2025) within the integrated development environment RStudio (version 2026.01.1+398, Posit., 2026). Data processing, structuring, and manipulation were carried out using the packages readxl (version 1.4.5, Wickham, 2023), dplyr (version 1.2.0, Wickham & al., 2023), and tidyr (version 1.3.1, Wickham & al., 2023). Dendroclimatological analyses were conducted with the dplR package (version 1.7.4, Bunn, 2008, 2010, 2020) and treeclim (version 2.0.7.1, Zang, 2015).

### 2.6.1 Building chronologies: analyses on R software

A chronology corresponds to a reference time series constructed from multiple trees of the same species at a given site, with the aim of extracting a common growth signal (Schweingruber, 1988). It is obtained by aligning and averaging individual ring-width or density series after cross-dating and, most often, statistical standardization to remove trends related to tree age and size. This procedure reduces individual noise (local, biological, or accidental effects specific to each tree) and enhances the shared environmental component.

Thus, a chronology represents an average curve that reflects the collective response of a stand to variations in external factors, particularly climatic ones. It constitutes the central object of dendroclimatological analyses: by correlating it with meteorological series (temperature and precipitation), the sensitivity of radial growth to climatic conditions can be quantified, and response functions can be established (Schweingruber, 1988).

A chronology is therefore a synthetic curve, specific to a species and site, serving as a robust basis for studying growth–climate relationships and environmental reconstructions (Carrer & al., 2017; Cook, 1987).

The dplR package allows the import of ring-width series in standard formats (notably Tucson), the structuring of datasets, and the generation of descriptive graphs and statistics (Briffa, 1990).

First, descriptive statistics of the ring-width series were calculated using the rwi.stats() function to assess series quality and inter-individual consistency.

The package includes detrending methods, an essential step that removes the age-related biological trend of a tree to isolate the environmental signal. Detrending produces ring-width indices (RWI), obtained by dividing observed growth by expected growth according to the fitted

curve. The series were therefore standardized by fitting a modified negative exponential curve via `detrend(method = "ModNegExp")` (Briffa, 1990).

From these indices, `dplR` allows the construction of chronologies using the `chron()` function, average series representative of a site, calculated with a robust mean to obtain a standardized series reflecting the common signal and limiting the influence of outliers.

`dplR` also provides advanced quality control tools for cross-dating, a process aimed at verifying the calendar accuracy of each ring. These tools include segment correlations between each series and a reference chronology, moving correlations to assess temporal stability, and cross-correlation functions to identify potential dating offsets (missing or false rings).

Additionally, the package generates automated skeleton plots highlighting years of exceptionally low or high growth, facilitating visual comparison among series.

Furthermore, `dplR` calculates inter-series coherence statistics via the `rwi.stats()` function, including intra- and inter-tree correlations and the expressed population signal (EPS), indicating the extent to which the mean chronology represents the common signal of the stand. Since all processing is performed in R, analyses are fully scriptable and reproducible (Bunn, 2008, 2010 & 2020).

In addition to ring width (TRW, mm), maximum density (MXD, kg/m<sup>3</sup>) can be measured in the latewood portion of the annual ring, i.e., in the final wood formed at the end of the growing season (Bradley, 2015).

MXD represents the peak density reached in the latewood, just before the transition to the next ring. In this study, this variable was obtained by X-ray tomography (X $\mu$ CT) and then analysed using the `RingIndicator` tool, allowing high-resolution density profiles to be extracted without altering the samples (De Mil, 2023).

The main interest of MXD lies in its high sensitivity to summer temperature conditions, which, unlike ring width (primarily influenced by water availability), is significantly correlated with temperature, particularly from May to July (Bytebier & al., 2022).

In this report, wood density analyses were performed using the `XCT.read` function (V2, Verschuren, 2025). This function extracts and processes data from X-ray microtomography images (XCT).

The `path` parameter specifies the data location. The `output` argument defines the output type (here, density), while `densityType` specifies the calculation mode (e.g., fraction). The argument `area = c()` defines the radial portion of the ring considered for value extraction (typically latewood). The `fun` parameter controls the summary method applied to density values (e.g.,

mean), and  $x$  indicates the proportion of highest values to retain when applying a maxima-based calculation.

Additionally, `removeNarrowRings` and `minRingWidth` exclude rings that are too narrow according to a defined threshold. Finally, `overrideResolution` and `resolution` adjust or force the spatial resolution used during processing.

The remainder of the script extracts maximum density (MXD) values and associates them with samples and corresponding years in a single output file (.txt). This step relies on two internal functions: `mean_top_x`, which calculates the mean of the top  $x$  values in a vector, and `calculate_density`, which adapts density calculations based on the `fun` parameter (*Verschuren, 2025*).

Furthermore, the MXD series were detrended, following the same approach as for Ring Width Indices (RWI). This step removes age-related growth trends to isolate the environmental signal and produces Maximum Density Indices (MXDi). The function `detrend()` was applied using a 30-year spline to preserve interannual variability. The standardized series were then averaged with `chron()`, using a robust biweight mean and no prewhitening. Therefore, the resulting chronology represents the common environmental signal across the samples.

Finally, the data were analysed using the `dplR` function `corr.rwl.seg()` to assess the quality of the ring-width index (RWI) series for each species. To evaluate the stability of the RWI and MXDi variables, the `treeclim` moving-window function was applied.

In dendrochronology, autocorrelation quantifies the relationship between ring width or density in a given year and in previous years, reflecting the persistence of the growth signal. It is typically assessed using autocorrelation coefficients, particularly lag-1 autocorrelation. The function `rwl.stats` is commonly used to compute this statistic from ring-width series, often after standardization, by correlating each series with its time-shifted version (Cook, 1990). In this study, autocorrelation was calculated for both tree-ring width (TRW) and maximum latewood density (MXD) chronologies across the full sampling period to evaluate the temporal persistence of growth signals (*Robert & al, 2001; Brien et al, 2006*).

### **2.6.2 Statistical analyses based on chronologies**

#### EPS

The EPS (Expressed Population Signal) is a statistical indicator used in dendrochronology to assess the reliability and representativeness of a ring-width chronology. It quantifies the strength of the common growth signal shared by all trees in a sample, a signal generally attributed to large-scale environmental factors, particularly climatic ones. It thus allows evaluating the extent to which a chronology constructed from a finite number of trees accurately

reflects the theoretical signal of the studied forest population and serves as a measure of data quality (Equation 3).

Its value depends directly on the correlation strength between individual series and the sample size: as the number of analysed trees increases, the noise specific to each individual tends to cancel out, while the common signal dominates, thereby increasing the EPS. A threshold of 0.85 is commonly adopted in the literature as a robustness criterion: above this value, the chronology is considered sufficiently representative to reliably analyse radial growth–climate relationships.

The number of trees required to reach this threshold, however, varies by species: light-demanding species, often more sensitive to climatic variations, typically achieve a high EPS with a smaller sample size, whereas shade-tolerant species, characterized by greater individual growth variability, require larger samples.

In this context, EPS constitutes a central tool for validating the statistical robustness of chronologies before any dendroclimatic interpretation (Lebourgeois, 2012; Mérian, 2013).

Equation 3: determination of the EPS (Lebourgeois, 2012, Mérian, 2013).

$$EPS = \frac{t * Ceff * rbar.bt}{(t - 1) * rbar.bt + Ceff}$$

*The indicator is calculated based on the number of trees present at the site (t), the mean correlation among the individual series (rbar.bt), and the effective number of cores sampled (Ceff). Its value ranges between rbar.bt and 1. When it reaches 1, it indicates that individual tree-specific variations are eliminated, thus providing a perfect reproduction of the common growth signal for the entire studied population.*

### RBAR

In dendrochronology, RBAR (Mean Interseries Correlation, often denoted as rbar or rbt) is a central statistical indicator used to assess the internal coherence of a set of ring-width series. It corresponds to the mean correlation among all individual growth index series from the same sample or plot. This statistic quantifies the strength of the common signal shared by the trees: when individuals respond synchronously to environmental variations, particularly climatic factors, inter-series correlations increase and RBAR values are high.

Unlike EPS, which explicitly depends on sample size, RBAR primarily reflects the intrinsic quality of the common signal and is relatively insensitive to the number of trees analyzed. It provides information on the degree of growth response homogeneity and on the ratio between the shared environmental signal and individual noise (tree-specific effects, micro-site conditions, local disturbances).

RBAR (Equation 4) is also a key component in calculating EPS, which combines the mean inter-series correlation and sample size to estimate the representativeness of the chronology. In

practice, a high RBAR indicates that trees exhibit convergent growth dynamics and that it is appropriate to aggregate their series to construct a reliable chronology (Lebourgeois, 2012).

Equation 4: determination of RBAR (Lebourgeois, 2012).

$$rbar.bt = \frac{1}{2t(t-1)} \left( \sum_{j=1}^{t-1} \sum_{j'=1}^t r_{jj'} \right)$$

With  $t$  representing the number of trees at site  $i$  and  $j$ , and the tree under consideration, RBAR ranges from 0 to 1. It approaches 0 when individual series are independent of each other and approaches 1 when trees exhibit strong similarities in their growth responses.

### SNR

The signal-to-noise ratio (SNR) quantifies the strength of the common signal shared among the individual series of a chronology (Wigley & al., 1984). It measures the proportion of variability that is coherent between trees relative to non-shared variability, which is considered noise. The SNR is directly related to the Expressed Population Signal (EPS) according to the following relationship (Equation 5).

Equation 5: calculation of the SNR (Wigley & al, 1984)

$$EPS \approx \frac{SNR}{SNR + 1}$$

When the SNR is less than 1, the common signal is considered difficult to distinguish from noise, which may arise from various sources such as measurement errors, individual tree effects, or local environmental disturbances. Conversely, an SNR greater than 1 indicates that the common signal dominates the background noise. The higher the SNR, the stronger the inter-series coherence, and the more robust the statistical quality of the dendrochronological chronology is.

## 2.7 Climate data

Climate data used for the analyses were obtained from the Uccle Meteorological Station, operated by the Royal Meteorological Institute of Belgium and located approximately 35 km from Gembloux, and from the Saarbrücken-Ensheim Station, operated by the Climate Data Center and located approximately 26 km from Blieskastel.

Air temperature (°C) and precipitation (mm) series were used to construct ombrothermic diagrams based on monthly averages for the periods 1890–2025 and 1951–2025, respectively (Figures 27).

Finally, the approach of Buras & al. (2020) identifies pointer years, in which trees show synchronous and unusually strong growth deviations, reflecting a common response to extreme climatic conditions. Applied to RWI and MXD chronologies, pointer years complement climate–

growth analyses by highlighting periods of exceptionally favourable or unfavourable climatic conditions.

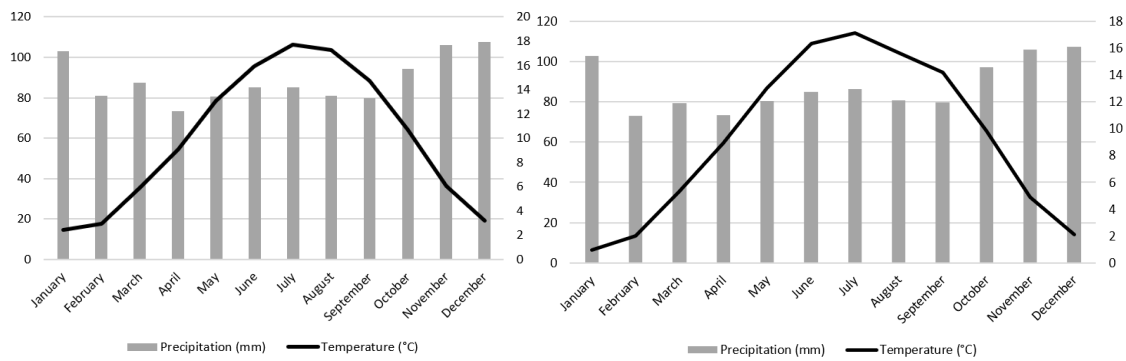


Figure 27-Ombrothermic diagram showing the average monthly temperatures (°C) and the average monthly precipitation (mm) for the station of Uccle from 1890 to 2025 (IRM, 2026) on the left and for the station of Saarbrücken-Ensheim from 1951 to 2025 (CDC, 2026) on the right

## 2.8 Growth-climate link

The R package Treeclim is an integrated tool designed for the numerical calibration of relationships between tree-ring chronologies and climatic variables. It consolidates and extends classical dendroclimatic methods by providing calculations of static and moving correlation and response functions, seasonal analyses, and procedures for evaluating the temporal stability of climate–growth relationships (Zang, 2015).

Among its functionalities, the package includes tools to generate monthly correlation plots between climatic variables and total ring width (TRW), showing for each month the strength and direction of the statistical relationship between a climatic parameter (here temperature or precipitation) and radial tree growth. These analyses rely on calculating correlation coefficients between the tree-ring chronology and monthly climate series to identify the periods of the year with the strongest influence on wood formation.

Specifically, the `dcc()` function was used to calculate static correlations between the standardized chronology and monthly precipitation over the covered temporal period. The analysis was conducted in a 25-year moving window with a one-year step, and the significance of the coefficients was estimated using stationary bootstrap ( $\alpha = 0.05$ ) to assess the temporal stability of climate–growth relationships.

A high positive correlation for a given month indicates that high climatic values during that month are associated with increased ring width, suggesting that the corresponding conditions favour growth. Conversely, a negative correlation indicates a limiting effect: high climatic values are associated with reduced radial growth. These plots thus allow the identification of critical temporal windows of climatic control overgrowth and provide insight into the monthly dendroclimatic sensitivity of trees.

The same analytical approach can be applied to maximum density (MXD, Figure 21). Literature shows that temperature is often the only climatic variable significantly correlated with MXD. This sensitivity is explained by the fact that latewood formation occurs at the end of the growing season, when cambial activity slows and cell wall thickening is strongly dependent on thermal conditions (*Bytebier & al., 2022*).

MXD therefore serves as an indicator more directly related to summer temperatures, with lower autocorrelation than ring width, meaning it primarily reflects current-year conditions rather than residual effects from previous years. As such, MXD constitutes a particularly relevant thermal proxy for dendroclimatic analyses (Bradley, 2015).

Additionally, a seasonal correlation analysis was performed using the *seascorr* function from the *Treeclim* package, applied to the output .txt file and climatic series (temperature and precipitation) over the period covered by the samples, with different season lengths (1 to 4 months).

A significance threshold of  $\alpha = 0.05$  and a minimum of eight complete years were required for the calculation. This approach allows the identification of seasonal windows during which climate–growth relationships are statistically significant (*Verschuren, 2025*).

### **2.8.1 Inter-annual density analysis and quantile approach**

Beyond analysing MXD alone, a more detailed approach can be implemented by subdividing each annual ring into four radial sectors of equal width, denoted Q1 to Q4. This subdivision allows examination of the intra-annual variability in wood density and the identification of climatic factors influencing successive phases of the growing season.

For each sector, the mean density is calculated, while the maximum density of the last sector (maxQ4) corresponds to the high-resolution MXD measurement. Results may reveal a progressive shift in the dominant climatic factors throughout the season.

The first two sectors (Q1 and Q2), corresponding to early spring growth, are primarily influenced by water availability, including late-winter and early-spring precipitation and temperatures (*Bradley, 2015*). Greater water availability during spring typically results in higher mean density in these early sectors.

In contrast, the later sectors (Q3 and especially Q4), formed later in the season, are increasingly dominated by temperature, while the influence of precipitation and humidity decreases. The mean density of the last sector (Q4), as well as the maximum density (MXD), may show correlations with May–July temperatures, confirming the key role of summer thermal conditions in latewood formation (*Bradley, 2015*).

To implement this method, each growth ring is subdivided into four equal portions, and the same data processing, analysis, and climatic correlation methodology applied for MXD is followed (see Section 2.7.1).

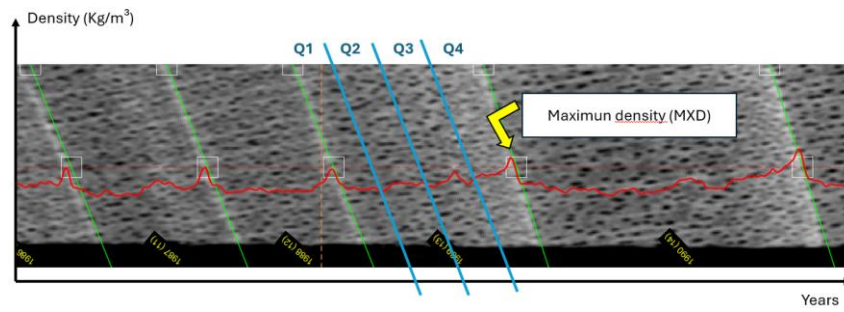


Figure 28-Transversal CT image with an overlay of the density profiles of the 1987–1990 tree-rings of an *Acer sp.* sample. Maximum Latewood Density (MXD) is shown, the quartile sector is indicated with Q1-Q4. In every sector, the mean density is determined (RingIndicator)

Quantitative analysis of wood anatomy is essential for developing proxies for climate reconstruction. However, the reliability of such analyses depends on the imaging methods used to identify and measure anatomical elements such as vessels, fibers, and tracheids within annual rings. In angiosperms, several approaches exist, including X-ray microtomography, which was employed in this study.

In this context, analysing wood density according to radial quadrants (Q1–Q4) constitutes a particularly relevant approach. By subdividing the annual ring into successive sectors, it becomes possible to capture intra-annual density variations and relate them to seasonal changes in anatomical structure. These sectoral wood densities ( $\rho Q1$ – $\rho Q4$ ) can thus serve as synthetic variables to approximate hydraulic parameters of the wood, such as  $K_s$  (theoretical specific hydraulic conductivity) or  $D_h$  (mean hydraulic diameter), when detailed anatomical measurements are not available. This approach has the advantage of being simpler and potentially applicable to large datasets while retaining functional information on the hydraulic properties of the wood (Peters & al., 2025).

# 3. Results

## 3.1 Blieskastel study (Germany)

### 3.1.1 RWI, MXDi and Quantiles statistical review

Table 2-Complete statistical review of the large-scale study (Ring width index, Maximum density index and Quantiles EPS, Rbar and SNR, with the Autocorrelation for the TRW and MXD)

| Species                  | Timespan  | Trees(cores) | Variables | EPS   | Rbar.bt | SNR   | AC_01 |
|--------------------------|-----------|--------------|-----------|-------|---------|-------|-------|
| <i>A. pseudoplatanus</i> | 1889-2025 | 11(22)       | RWi       | 0,895 | 0,301   | 8,612 | 0,625 |
|                          |           |              | MXDi      | 0,857 | 0,231   | 6,000 | 0,195 |
|                          |           |              | Q1        | 0,848 | 0,219   | 5,608 |       |
|                          |           |              | Q2        | 0,847 | 0,218   | 5,575 |       |
|                          |           |              | Q3        | 0,847 | 0,218   | 5,575 |       |
|                          |           |              | Q4        | 0,853 | 0,225   | 5,806 |       |
| <i>A. glutinosa</i>      | 1832-2025 | 10(20)       | RWi       | 0,881 | 0,271   | 7,434 | 0,702 |
|                          |           |              | MXDi      | 0,884 | 0,287   | 7,643 | 0,623 |
|                          |           |              | Q1        | 0,847 | 0,217   | 5,542 |       |
|                          |           |              | Q2        | 0,847 | 0,217   | 5,542 |       |
|                          |           |              | Q3        | 0,846 | 0,216   | 5,510 |       |
|                          |           |              | Q4        | 0,850 | 0,222   | 5,706 |       |
| <i>C. betulus</i>        | 1844-2025 | 10(20)       | RWi       | 0,877 | 0,263   | 7,137 | 0,829 |
|                          |           |              | MXDi      | 0,854 | 0,227   | 5,873 | 0,781 |
|                          |           |              | Q1        | 0,842 | 0,211   | 5,348 |       |
|                          |           |              | Q2        | 0,843 | 0,212   | 5,380 |       |
|                          |           |              | Q3        | 0,840 | 0,209   | 5,284 |       |
|                          |           |              | Q4        | 0,849 | 0,220   | 5,641 |       |

A statistical analysis of the chronologies was carried out, and the EPS, Rbar, and SNR values were determined. These calculations were based on the appropriate number of trees (n = 10 or 11), rather than on the number of individual samples, which could otherwise have biased the obtained values.

To perform the dendroclimatic analysis, a focus on the 1951–2025 period was done, applying an EPS threshold of 0.85 (using the *rwi.stats.running()* function in the *dpLR* package). Older trees are less numerous, leading to a decline in EPS outside this interval; consequently, EPS values are highest within the selected time window, which corresponds to the period used for climatic analysis. All metrics were computed using RW and MXD index values as the basis for analysis.

The SNR values are well above 1, indicating a low level of biological noise and a strong common signal among the sampled trees. Finally, Segment-wise correlations of RWI series of each species were additionally computed to further demonstrate the robustness of the signal (Appendix 2).

Afterwards, a statistical analysis of the chronologies was also carried out during the quantiles analysis. These calculations were based on the appropriate number of trees as well to not biased the obtained values.

As shown in Table 2, the SNR values are well above 1, indicating a low level of biological noise and a strong common signal among the sampled trees. Similarly, the EPS values are slightly under the commonly accepted threshold of 0.85, suggesting that the chronologies nearly reliably capture the population-level signal.

Therefore, as with the RWI/MXDi analysis, the dendroclimatic analysis considered the full 1951–2025 period, for which the mean EPS is below 0.85 (Table 2). However, analyses were restricted to the sub-periods where EPS exceeds the 0.85 threshold, ensuring that only statistically robust segments were used for climatic interpretation.

Finally, Autocorrelation (AC\_01), including lag-1, was computed for both TRW and MXD index chronologies using standardized series to assess the temporal persistence of the growth signal (Table 2; Cook, 1990).

### 3.1.2 Applied framework to the species investigated

Section 1.2.2 presents the theoretical framework of dendroclimatology, including the conceptual representation of ring width and wood density responses to climatic variability (Bradley, 2015). In this context, the following results provide an opportunity to apply this general framework to the species investigated in this study.

By comparing ring width and maximum density responses to climatic variables in *Acer pseudoplatanus*, *Alnus glutinosa*, and *Carpinus betulus*, the aim is to assess how these theoretical relationships translate into empirical patterns and to highlight differences in climatic sensitivity among species. This comparative approach allows a better understanding of how general dendroclimatic principles are expressed under different ecological strategies and wood functional traits (Figure 29).

Based on mean ring-width data from the large-scale study, species growth curves were constructed following the approach of Schmucker & al (2023) and are presented in Figure 30.

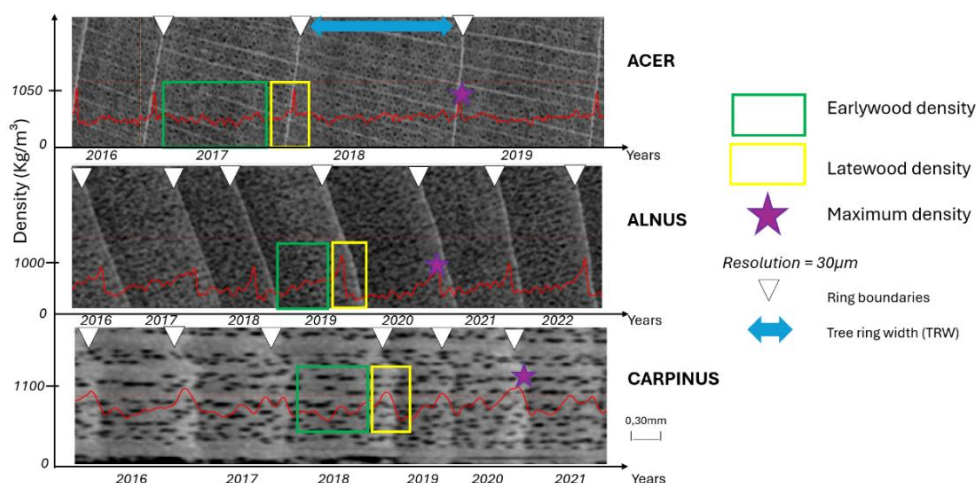


Figure 29-Illustration of ring width, density profile and wood density variables for the three study species

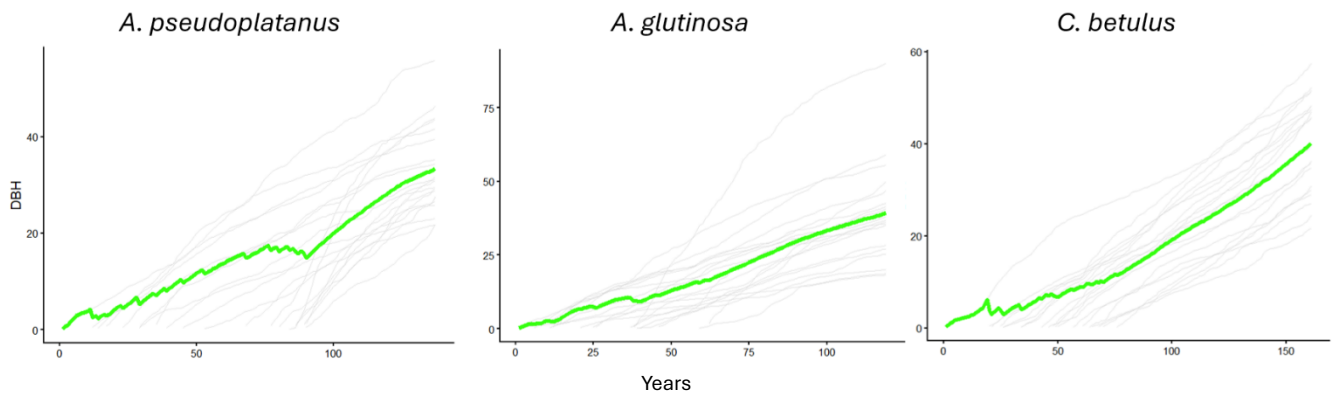


Figure 30- Species-specific mean growth curves (in green) and data range (in grey) over age for the studied species based on mean ring-width data

### 3.1.3 Chronology building and assessment of trees response

Figures 31 to 34 present the analysis of tree-ring width based on the Ring Width Index (RWI), following the methodology described in Section 2.6.2. This approach notably allows for the estimation of the age of the trees included in the study.

Two cores were extracted from each of the ten/eleven sampled trees. Consequently, the sampling depth should not be interpreted as 20 independent samples, as shown in Figure 31, but rather as ten paired measurements that reinforce the robustness of the analysis and complement each other.

As shown in Figure 32, *A. pseudoplatanus* does not exhibit any significant correlation between ring width and either temperature or precipitation. In Figure 33, *A. glutinosa* shows no significant correlation with temperature; however, a significant negative correlation with precipitation is observed in the months of June and August. This indicates that higher precipitation during summer is associated with reduced ring width.

Finally, Figure 34 shows that *C. betulus* does not present a significant correlation between ring width and temperature overall, although a significant positive correlation is observed with temperature during the months of April, May, and June. This suggests that ring width increases during the growing season when temperatures are higher.

Correlations observed from October to December should generally be disregarded, as they are likely false positives due to the cessation of tree growth during winter.

The results of the moving function from the dplR package in R that was applied to the RWI confirm the previously described patterns for the months identified above, while also highlighting that these relationships are not entirely stationary through time. Noticeable shifts in the correlation patterns emerge from around 1976 onward. In addition, this approach provides a useful means of assessing the temporal stability of the signal, demonstrating that the climatic response recorded by the RWI remains overall robust despite these changes (Appendix 3).

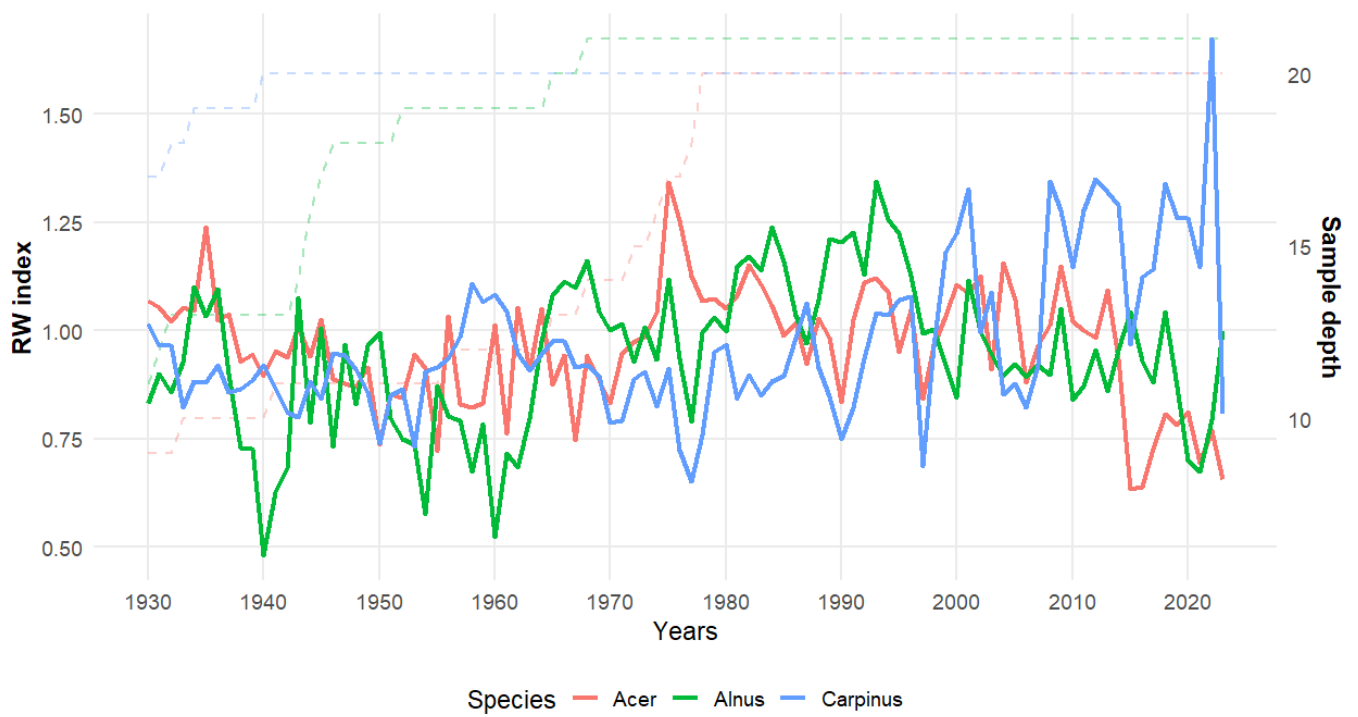


Figure 31-Species of study Ring Width Index (detrended) analysis between 1930 and 2025

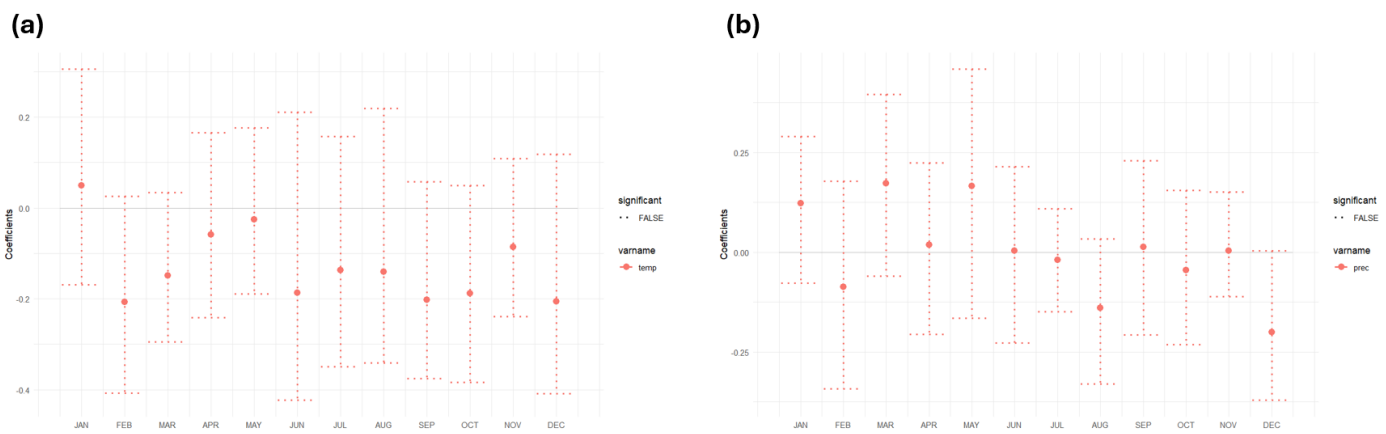


Figure 32-Acer sp. Ring Width analysis (detrended) monthly correlation with temperatures (a) and precipitations (b) for the 1951-2025 period

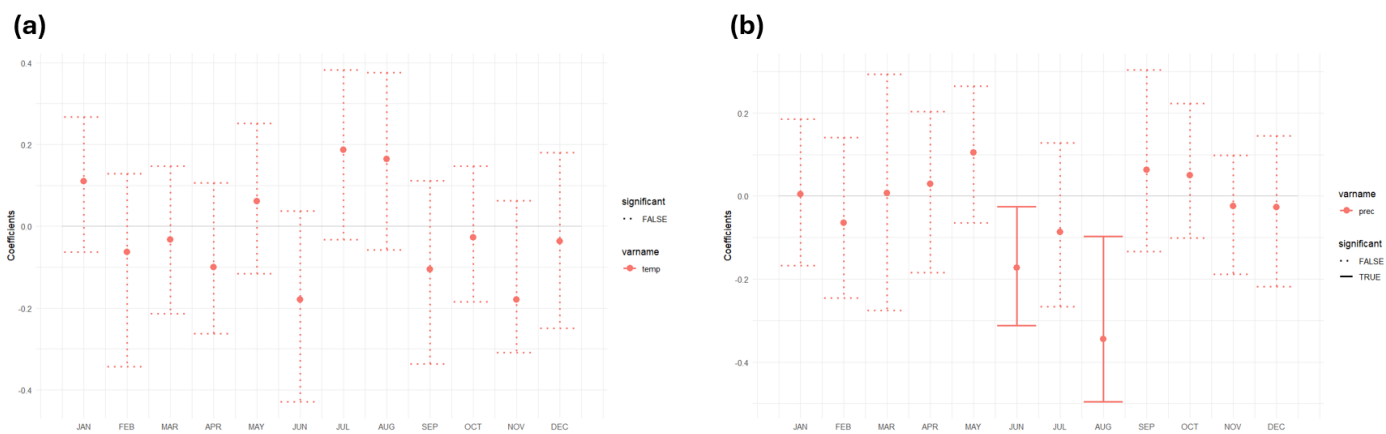


Figure 33-Alnus sp. Ring Width analysis (detrended) monthly correlation with temperatures (a) and precipitations (b) for the 1951-2025 period

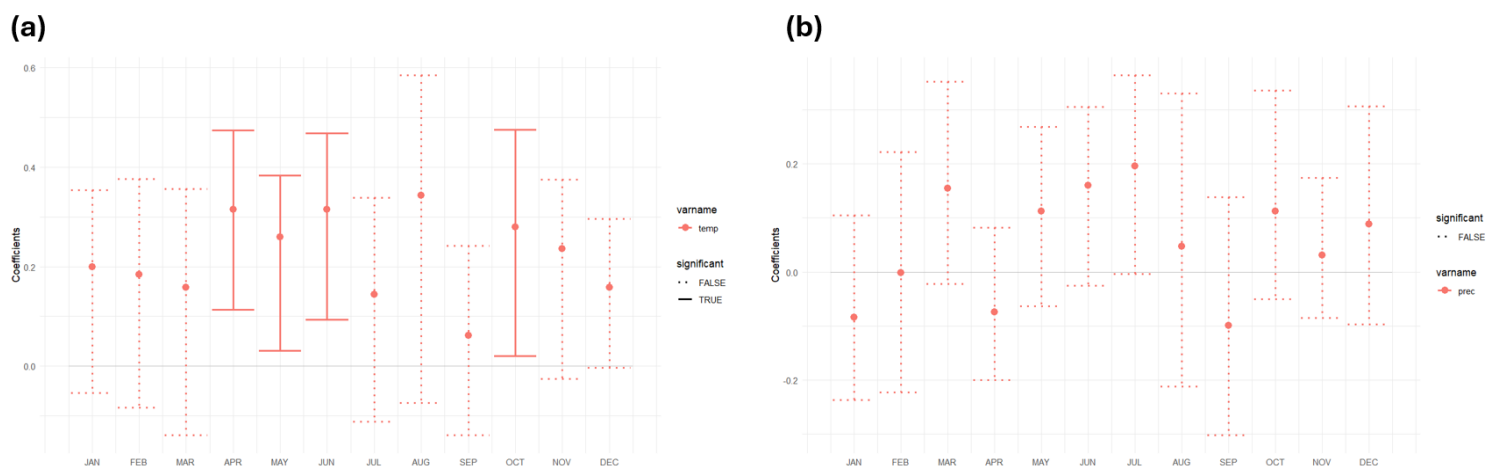


Figure 34-*Carpinus sp.* Ring Width analysis (detrended) monthly correlation with temperatures (a) and precipitations (b) for the 1951-2025 period

### 3.1.4 Maximum density (MXD) analysis

Figure 35 illustrates the detrended evolution of the Maximum Density Index ( $MXD_i$ ) over the period 1930–2025. This time window was selected because, as explained previously, the limited number of older samples makes the detrending procedure less reliable and the resulting graph difficult to interpret. This figure provides a clear visualization of temporal variations in maximum density and allows the identification of years that were favourable for tree growth.

Figures 36, 37, and 38 present the correlation analysis between MXD and climatic variables (temperature and precipitation), as well as a seasonal analysis based on grouped periods four months (Figure 39).

In Figure 36, *A. pseudoplatanus* shows a significant positive correlation with temperature in April, with no other significant relationships observed, including in the seasonal analysis (Figure 38). This indicates that maximum density increases when temperatures are higher in April. Figure 37 shows that *A. glutinosa* exhibits a significant negative response to temperature around April, a result that is confirmed by the seasonal analysis (Figure 39).

Finally, Figure 38 indicates that *C. betulus* responds positively and significantly to temperature over the period from April to June, which is also supported by the seasonal analysis (Figure 39). Additionally, a significant negative correlation with precipitation is observed in March. These results suggest that *Carpinus* benefits from mild temperatures during late spring and early summer, leading to increased wood density.

The results of the moving function also applied to the MXDI confirm the previously described patterns for the months identified above as well (Appendix 3).

A correlation matrix was constructed between the tree-ring width index ( $TRW_i$ ), the maximum latewood density index ( $MXD_i$ ) and the Quantiles index ( $Q_i$ ) to assess the strength of their

relationship. The Pearson correlation coefficients ( $r$ ) range from 0.15 to 0.40 ( $p$ -value  $> 0.05$ ). These results indicate weak and statistically non-significant associations, suggesting that no clear or consistent relationship exists between each variable in this dataset (Appendix 4).

To further the analysis, a correlation study between the values of RWI, MXDI and Quantiles index was conducted between the data from the small-scale and from the large-scale study over their overlapping period. The table showing the correlation values, that range from 0.18 to 0.61 ( $p$ -value  $> 0.05$ ) is available in the Appendix (Appendix 5). The Quantiles correlations are similar to each other, suggesting that the year-to-year density variation would be similar between the four quartiles.

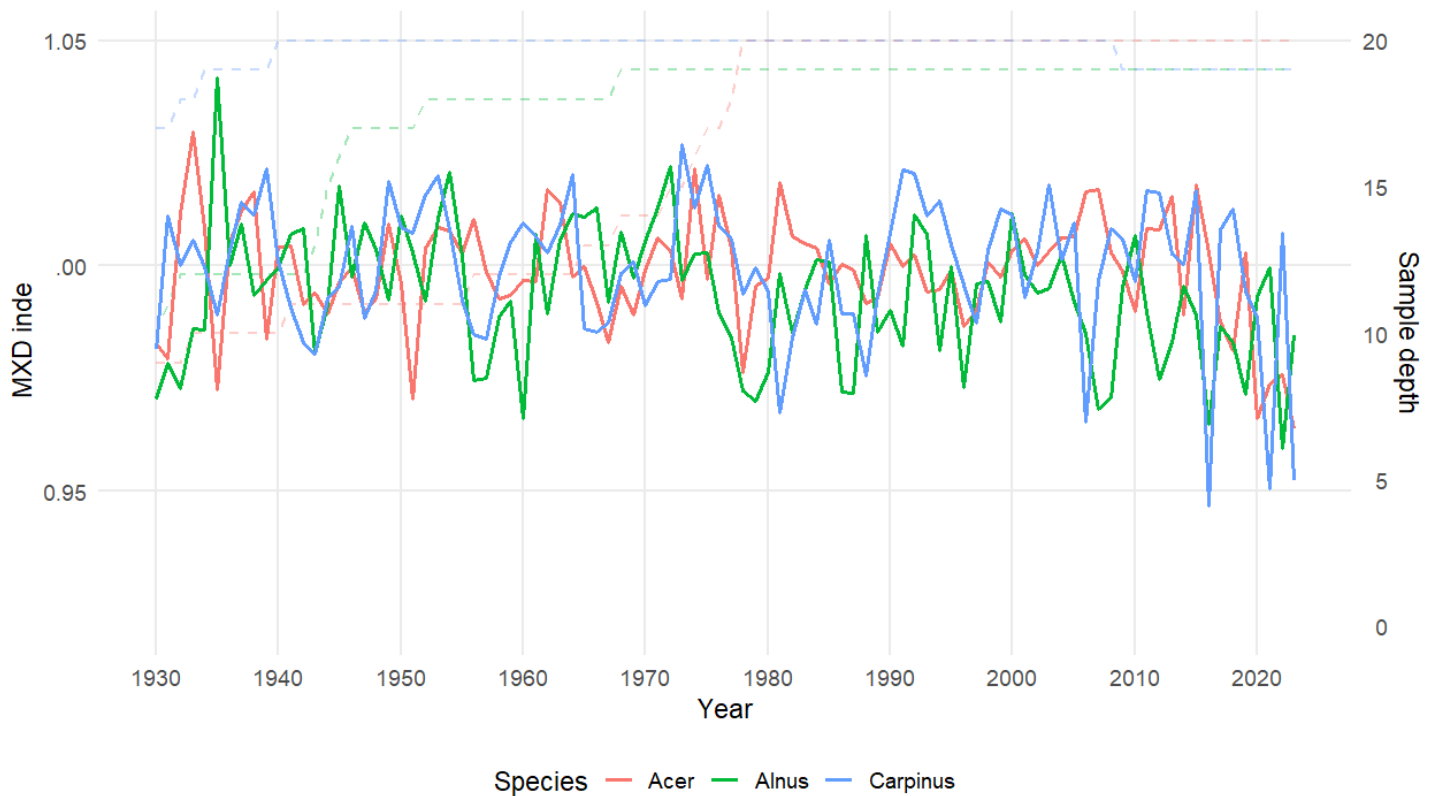


Figure 35-Species of study Maximum Density Index (detrended) analysis between 1930 and 2025

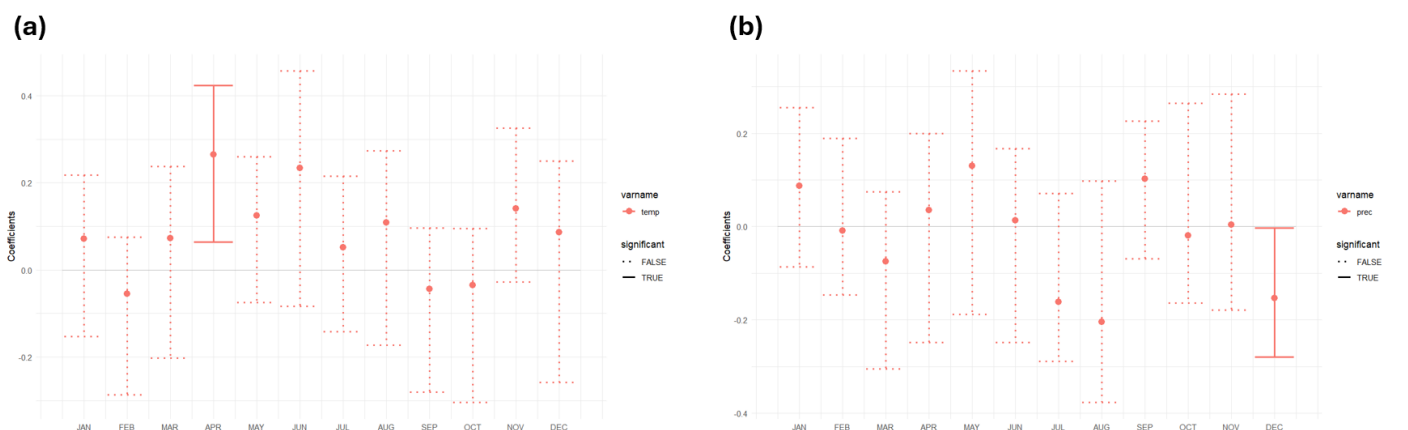


Figure 36-Acer sp. Maximum Density analysis and its monthly correlation with temperature (a) and precipitation (b) over the 1951–2025 period

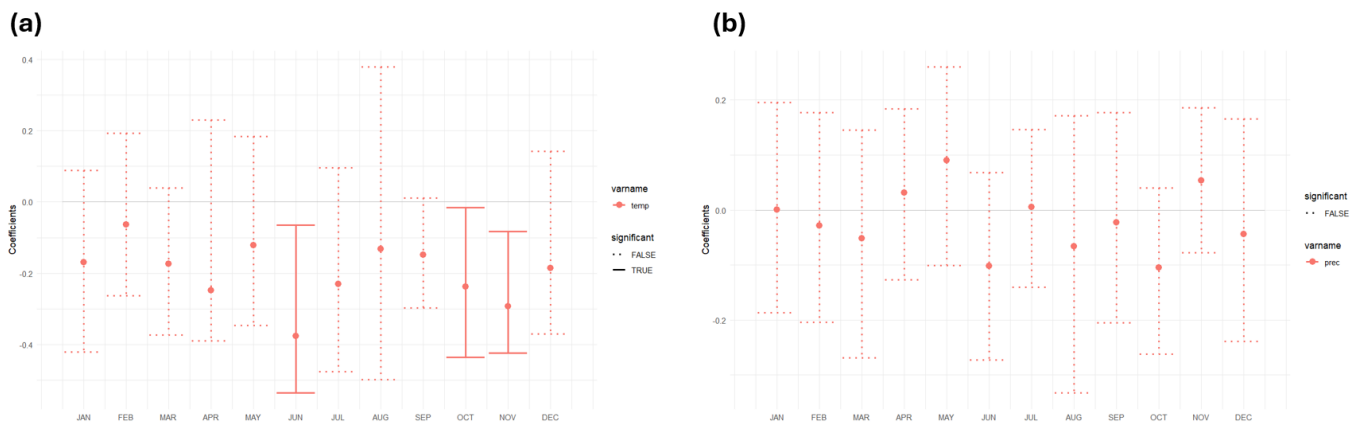


Figure 37-*Alnus sp.* Maximum Density analysis and its monthly correlation with temperature (a) and precipitation (b) over the 1951–2025 period

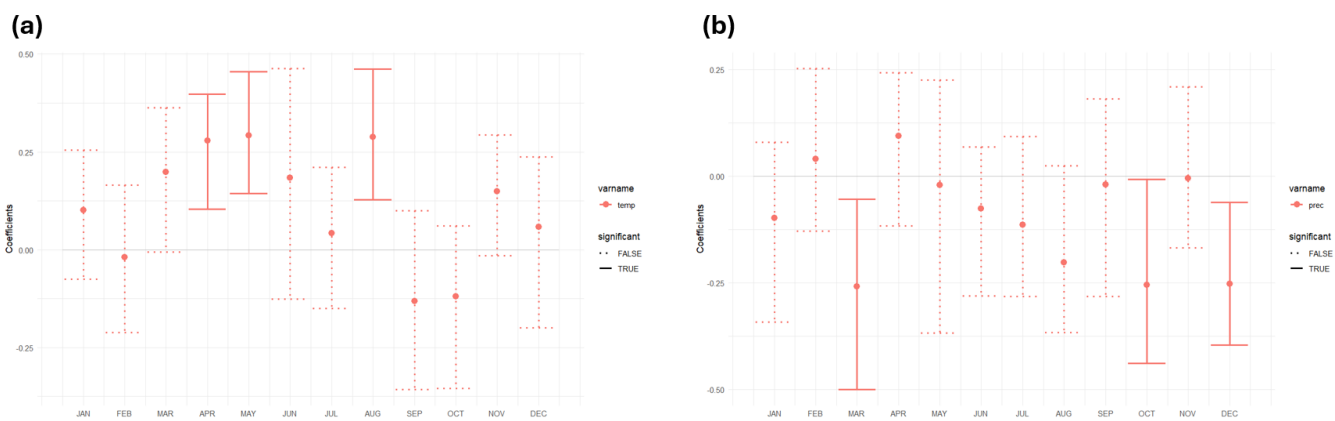


Figure 38-*Carpinus sp.* Maximum Density analysis and its monthly correlation with temperature (a) and precipitation (b) over the 1951–2025 period

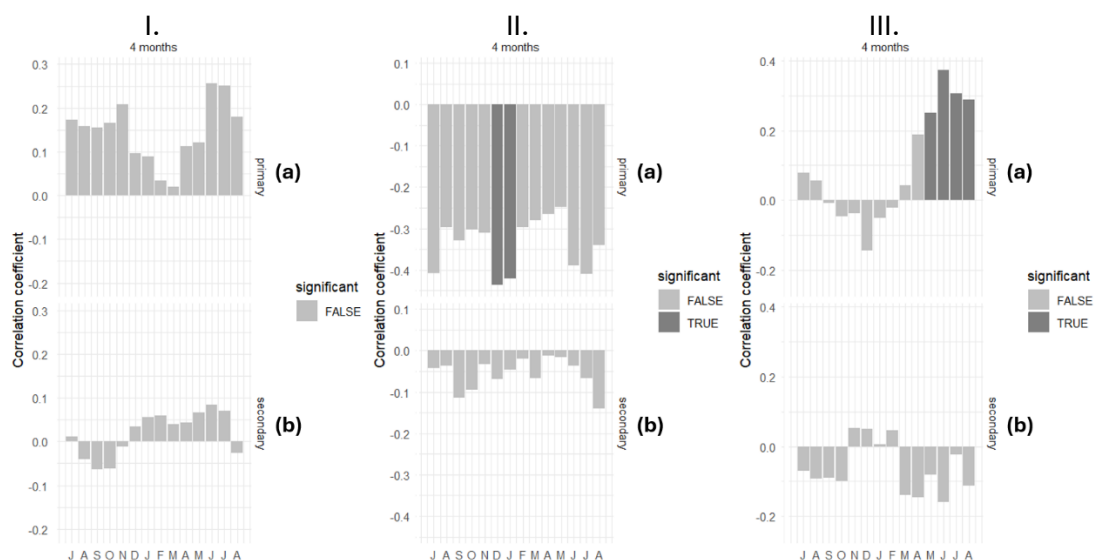


Figure 39-*A. pseudoplatanus* (I.), *A. glutinosa* (II.) and *C. betulus* (III.) seasonal MXDi correlations (4 months periods) with temperature (a) and precipitation (b) over the 1951–2025 period

### 3.1.5 Quantiles (Q1→Q4) analysis

According to Appendix 6, *A. pseudoplatanus* exhibits a significant positive correlation with temperature at its second quantile (Q2) between April and August. In contrast, no correlation at this level is observed for *A. glutinosa*. As shown in Appendix 6, *C. betulus* displays a significant positive correlation at the first quantile (Q1) from March to August.

Appendix 7 indicate no correlation between quantile densities and precipitation for either *Alnus* or *Acer sp.* However, for *C. betulus*, a significant negative correlation is observed at Q1 in August, at Q2 and Q3 in March, and at Q4 in both January and March.

At the level of seasonal correlation analysis, *A. pseudoplatanus* shows significant negative correlations at the first quantile (Q1) with temperature for the months of July, August, and September, and with precipitation for July only, when considering lagged pairs ranging from one to four months. This indicates that the period from July to October is affected. No significant correlations are observed at Q2.

At the third quantile (Q3), significant correlations with temperature are identified for the months of September, October, and November, again for lagged pairs of one to four months, corresponding to a period extending from September to January of the following year.

For the fourth quantile (Q4), significant correlations are observed exclusively with temperature, from March to May, across lagged pairs of one to four months, thus covering the period from March to August (Figure 40).

For *A. glutinosa* (Figure 41), no significant correlations are observed at the seasonal level, either with temperature or with precipitation.

Finally, for the seasonal correlation analysis of *C. betulus*, significant positive correlations with temperature are consistently observed across the first three quantiles (Q1, Q2, and Q3) from April to August, when considering lagged pairs ranging from one to four months. This indicates that the period from April to October is affected. Additionally, at Q3, a significant negative correlation is detected for the two-month lag corresponding to the March–April period.

No significant correlations with precipitation are observed for Q1 and Q2. However, at the fourth quantile (Q4), no significant correlation is found with temperature, while significant negative correlations with precipitation are identified over the period from March to June (Figure 42).

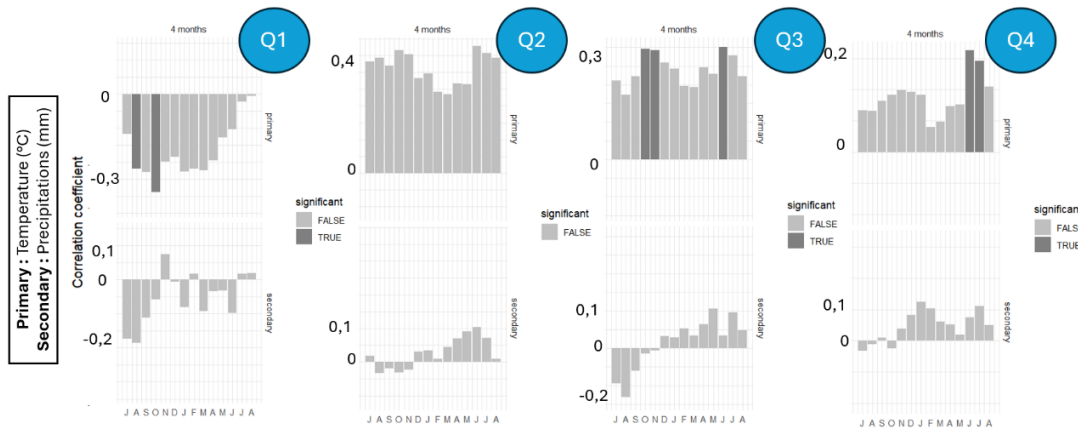


Figure 40- *Acer sp.* Quantile seasonal correlation analysis with temperature (°C) and precipitation (mm) for the 1951-2025 period

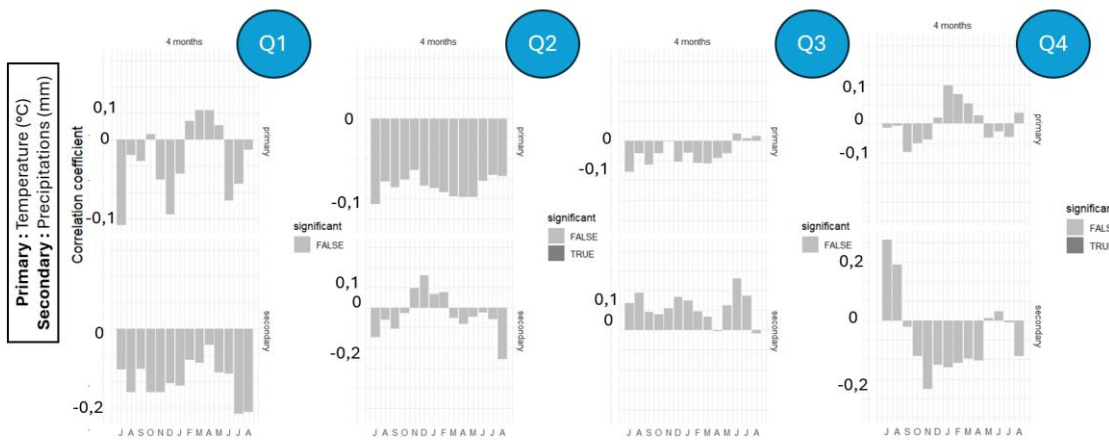


Figure 41- *Alnus sp.* Quantile seasonal correlation analysis with temperature (°C) and precipitation (mm) for the 1951-2025 period

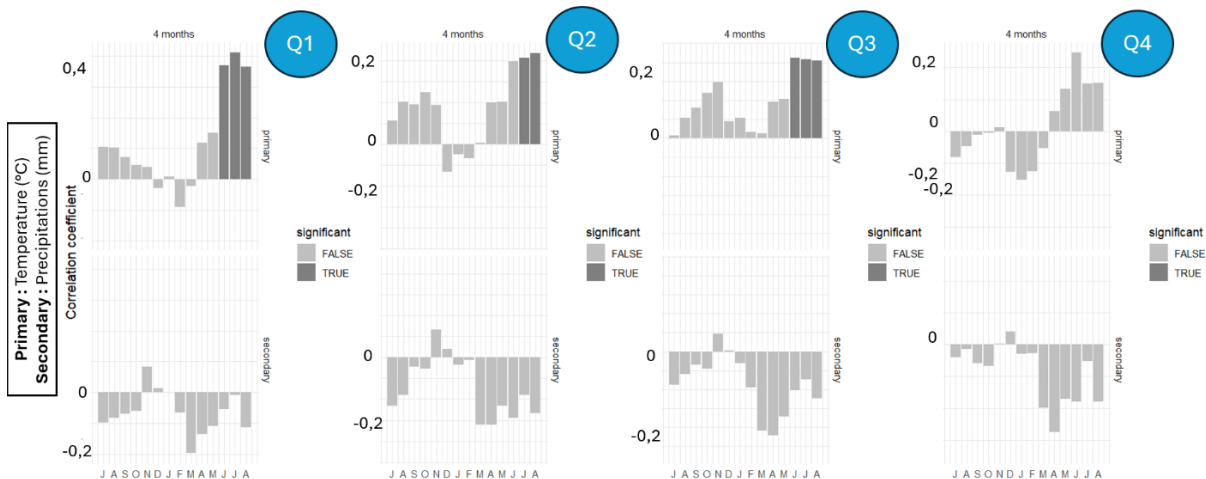


Figure 42- *Carpinus sp.* Quantile seasonal correlation analysis with temperature (°C) and precipitation (mm) for the 1951-2025 period

### 3.1.6 Preliminary study (Belgium)

The results of the preliminary study conducted in Gembloux are presented in the Appendix, as its primary objective was simply to assess the feasibility of carrying out a dendrochronological study on a larger scale. However, despite the limited number of samples analysed, this study still made it possible to identify certain trends and draw relevant observations.

First, a grouped graphical representation of the ring width index and the maximum density index for small and large-scale studies is presented in Appendix 8 and 9.

Regarding the statistical analysis of the chronologies, the EPS value exceeds the commonly accepted threshold of 0.850 for ring width in *A. pseudoplatanus* (0.877). However, this result should be interpreted with caution given the limited number of samples, especially since the EPS calculation is directly dependent on the number of cores ( $n = 6$ , Equation 3). The corresponding values of  $\bar{R}$  ( $>0.350$ ) and SNR ( $>1$ ) are also satisfactory for this species.

In contrast, for *A. glutinosa* and *C. betulus*, the EPS values are significantly below the 0.850 threshold, which is not surprising considering the small sample size ( $\text{EPS} < 0.500$  in both cases). This limitation is even more pronounced for MXD and quantile density, where EPS values fall below 0.250.

Appendix 10 presents the ring width index (RWI) as a function of time, using a detrended function, along with the associated sample depth. The limited number of samples explains the relatively weak effect of the detrending process on the resulting curve. Correlation graphs with temperature and precipitation are provided in Appendix 11 for the three species.

For *A. pseudoplatanus*, a significant correlation with temperature is observed during the month of May. A similar correlation appears for December; however, this should be interpreted as a false positive, as tree growth is halted during winter. No correlation was observed with precipitation.

In contrast, *A. glutinosa* shows no correlation with temperature, but a correlation with precipitation is observed in January and November. These results should be interpreted with caution, as they correspond to periods when growth is reduced or absent.

Finally, *C. betulus* shows a positive correlation with temperature in October, which, again, likely represents a false positive. Regarding precipitation, positive correlations are observed in March and May.

The maximum density index (MXDi) of the three species is presented in Appendix 12. Appendix 13 highlights a positive correlation between MXD and temperature for *A. pseudoplatanus*, particularly in April. Seasonal correlations are also presented, showing a positive relationship

with temperature over the April–May–June period. No correlation with precipitation is observed, either at the monthly or seasonal scale.

For *A. glutinosa*, a strong positive correlation between MXD and precipitation is observed in April, and a negative correlation in February. No relationship with temperature is detected. However, strong seasonal patterns emerge for precipitation, with negative correlations during the early months of the year, regardless of whether two-, three-, or four-month periods are considered.

Finally, *C. betulus* exhibits negative correlations with precipitation in February, as well as at the seasonal scale during the early part of the year. In contrast, strong positive correlations with temperature are observed for January, April, May, June, and July. This trend is also visible at the seasonal scale, although it is not statistically significant.

Appendix 14 presents the correlations between temperature and precipitation, both at the monthly and seasonal scales, for the different density quantiles (Q1–Q4).

For *A. pseudoplatanus*, no significant correlation with precipitation is observed for any of the quantiles. In contrast, temperature shows positive correlations at the beginning of the year across all four quantiles. In the seasonal analysis, the positive correlation with temperature is most pronounced for quantile 3, particularly during the early months of the year.

For *A. glutinosa*, a positive correlation with precipitation is observed in March for all quantiles except Q4. No correlation with temperature is detected, except for Q4 in September. At the seasonal scale, significant negative correlations with precipitation are observed, while a significant positive correlation with temperature appears only for Q4 when considering four-month periods.

Finally, *C. betulus* exhibits positive correlations with precipitation across the different quantiles between February and June, depending on the quantile considered. Regarding temperature, strong and significant positive correlations are observed for most of the growing season months. The same pattern is evident in the seasonal analysis for temperature. Precipitation also shows positive correlations for Q2 to Q4 between April and June, regardless of the length of the multi-month periods considered.

# 4. Discussion

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## 4.1 Consistency Between Preliminary and Large-Scale Dendroclimatic Analyses Across Species

The preliminary small-scale study in Belgium broadly aligns with the large-scale German analysis, although with notable differences in robustness and clarity due to sample size limitations (Appendix 5, 8 and 9).

For *A. pseudoplatanus*, both studies consistently identify temperature as the primary climatic driver, with a significant positive relationship in spring, particularly in April–May for density-related parameters. The absence of a clear precipitation signal is also consistent across scales. However, the small-scale study suggests additional correlations (e.g., May temperature in ring width) that are not confirmed at the larger scale, indicating that these may reflect local or sample-size effects rather than robust regional patterns.

For *A. glutinosa*, both studies agree on the weak or absent relationship with temperature. The large-scale study identifies a negative response to summer precipitation in ring width and a temperature signal in density (negative in April), whereas the small-scale study instead highlights correlations with precipitation, often during non-growing periods. These discrepancies suggest that the preliminary results are less reliable for this species and may be influenced by limited replication or spurious correlations.

For *C. betulus*, the two studies show strong convergence. Both indicate a clear positive response to temperature during the growing season (spring to early summer), particularly for density parameters and, to a lesser extent, ring width. Some inconsistencies exist regarding precipitation signals, but the dominant temperature control is robust across scales.

Overall, the small-scale study mainly corroborates the large-scale results (Appendix 8 and 9). However, the preliminary study also contains several likely artefacts (e.g., winter correlations), highlighting that only the strongest and biologically meaningful patterns are confirmed at the larger scale.

## 4.2 Influence of Ecological Traits on Tree Growth Sensitivity to Climate

### 4.2.1 Sycamore maple

The dendroclimatic results are broadly consistent with this ecological profile, first highlighting the absence of a significant overall correlation between ring width and either temperature or precipitation (Figure 32). This suggests that radial growth in *A. pseudoplatanus* is not strongly

driven by interannual climatic variability (*Pliūra, 2007*), which is in line with its preference for buffered microclimates such as shaded slopes and ravines. In such environments, both temperature and water availability tend to be relatively stable, reducing the direct influence of climatic fluctuations on growth.

Nevertheless, the significant positive correlation between MXD and temperature observed in April indicates that early-season thermal conditions play a key role in stimulating physiological activity. This period corresponds to budburst, leaf expansion, and cambial reactivation, all of which are temperature-dependent processes. Warmer conditions in April likely enhance photosynthetic capacity, leading to increased growth rate and higher maximum density (Figure 36). This response is typical of temperate broadleaved species whose growth initiation is constrained by spring temperatures (*Pasta, 2016*).

The quantile analysis further refines this interpretation by revealing differentiated responses depending on growth conditions. At the intermediate quantile (Q2), the positive correlation with temperature between April and August suggests that, under average growth conditions, warmer temperatures throughout the growing season promote sustained cambial activity and carbon assimilation (Appendix 6). This is consistent with the species ecological preference for moderately warm and moist conditions, where growth is optimized without significant stress (*Pasta, 2016*).

At the lower quantile (Q1), however, significant negative correlations with temperature during the summer months (July to September), as well as with precipitation in July, indicate that under limiting growth conditions, *A. pseudoplatanus* becomes sensitive to climatic stress (Figure 40). Higher summer temperatures may increase evapotranspiration and induce water deficits, to which the species is known to be vulnerable due to its limited drought tolerance (*Fichier écologique des essences*). The negative correlation with precipitation in July may appear counterintuitive but could reflect periods of excessive or poorly timed rainfall, potentially associated with reduced radiation or transient soil saturation, both of which can limit photosynthetic activity and root function (*Pliūra, 2007*).

At higher quantiles (Q3 and Q4), the significant correlations with temperature over extended periods, ranging from late summer and autumn (Q3) to spring and early summer (Q4), suggest a prolonged influence of thermal conditions on growth processes (Figure 40). For Q3, the relationships extending into autumn and early winter may reflect carry-over effects, such as carbohydrate storage and reserve accumulation, which are essential for the following year's growth. For Q4, the strong dependence on temperature from March to May highlights the importance of favourable early-season conditions in years of high growth, where rapid cambial activation and sustained physiological activity drive increased ring formation (*Pasta, 2016*).

Overall, these results depict a species with a relatively plastic but moisture-dependent growth strategy, in which temperature acts as a key driver primarily during the onset and peak of the growing season, while water availability becomes limiting under stressful summer conditions (Pasta, 2016). This behaviour is fully consistent with the ecology of *Acer pseudoplatanus*, which thrives in cool, moist, and buffered environments but exhibits sensitivity to drought and, to a lesser extent, to hydric imbalances during critical periods of the growing season.

#### **4.2.2 Black alder**

The absence of a significant overall correlation between ring width and temperature suggests that radial growth in *A. glutinosa* is not primarily limited by thermal conditions (Figure 33). This is consistent with its ecological niche in riparian and wetland environments, where water availability generally buffers the effects of temperature and reduces evaporative stress (Claessens, 2010). However, the significant negative correlation between TRW and temperature observed around April indicates that higher temperatures at the onset of the growing season may have a constraining effect on growth. This could be explained by an earlier increase in evapotranspiration demand, potentially leading to an imbalance between water supply and demand during certain periods, even in typically moist environments, or to a phenological mismatch affecting the resumption of growth (Pliūra, 2004).

More strikingly, the significant negative correlations with precipitation observed in June and August indicate that excessive rainfall during the summer period is associated with reduced ring width (Figure 33). Although *A. glutinosa* is highly dependent on water (Claessens, 2010), this result highlights an important ecological nuance: while the species tolerates and even requires high soil moisture, excessive or prolonged flooding during the active growing season can impair physiological functioning. Waterlogged conditions may reduce oxygen availability in the root zone, limiting respiration and nutrient uptake despite the species adaptations to such environments. This can ultimately constrain cambial activity and radial growth.

The lack of significant correlations at the quantile level (Figure 41) further emphasizes the relatively stable response of *A. glutinosa* across a range of growth conditions (Pliūra, 2004). Unlike more mesophilic or drought-sensitive species, its growth does not appear to be strongly modulated by interannual climatic variability, which is consistent with its specialization in hydrologically buffered habitats. Similarly, the absence of significant relationships in the seasonal correlation analysis suggests that its growth dynamics are less influenced by short-term climatic fluctuations and more by consistently high moisture availability throughout the year.

Overall, these results describe a species whose growth is weakly dependent on temperature but sensitive to hydrological extremes, particularly excess water during the growing season. This

behavior is fully consistent with the ecology of *A. glutinosa*, which, despite being highly hygrophilous, requires a balance between sufficient moisture and adequate soil aeration (Durrant, 2016). Its deep rooting system, nitrogen-fixing capacity, and adaptation to wet environments allow it to thrive in conditions unsuitable for many other species.

#### 4.2.3 Common hornbeam

The dendroclimatic results are consistent with the ecological profile of Hornbeam. The absence of a significant overall correlation between ring width and temperature suggests that radial growth in *C. betulus* is not strongly constrained by annual thermal variability (Figure 34). This aligns with its shade tolerance and frequent occurrence in understory environments, where microclimatic buffering reduces exposure to climatic extremes (Sikkema & al., 2016). However, the significant positive correlations observed between April and June indicate that growth is stimulated by higher temperatures at the beginning of the growing season. This period corresponds to cambial reactivation and earlywood formation, which are particularly sensitive to temperature. Under these conditions, moderately warm temperatures enhance physiological activity (photosynthesis, cell division), leading to increased ring width and potentially higher wood density (Figure 38; Sokołowski & al, 2024).

According to Emaminasab (2023), *C. betulus* growth is linked to precipitations, especially during fall. However, this study was conducted in Iran, where environmental conditions are considerably more arid than in the Greater Region. During our study, negative correlation was observed with precipitation in March. This can be interpreted considering the species ecological requirements: excess water at the end of winter and early spring may lead to soil saturation, limiting root oxygen availability. Despite its moderately deep rooting system, *C. betulus* remains sensitive to hypoxic conditions, which can delay cambial reactivation and subsequently reduce growth. This response is consistent with its classification as a mesophilic species that prefers well-drained soils (Sokołowski & al, 2024).

Quantile analysis further reveals differentiated responses depending on growth conditions. The significant positive correlations observed at lower quantiles (Q1 to Q3) from March to August suggest that under limiting growth conditions, increased temperatures play a key role in alleviating physiological constraints, particularly by accelerating leaf development and cambial activity. In contrast, the absence of significant temperature correlations at the upper quantile (Q4) indicates that during years of high growth, other factors become limiting, especially water availability (Figure 42).

This is supported by the significant negative correlations with precipitation observed at Q4 between March and June. Under otherwise favourable growth conditions, excess water may again induce detrimental effects related to soil waterlogging or reduced aeration, thereby

constraining root function. This response highlights the mesophilic, but not hygrophilous, nature of the species, which tolerates moderate variability in water availability but remains sensitive to prolonged excess moisture (Sikkema & al., 2016).

Finally, the influence of temperature over an extended period from April to August, and even up to October when considering lag effects, reflects the relatively long growing season of *C. betulus* (Figure 42). This is consistent with its marcescent foliage and its capacity to take advantage of favourable conditions over an extended time window. Nevertheless, the presence of occasional negative correlations, particularly in late summer or early spring, indicates complex physiological adjustments in response to specific climatic conditions.

Overall, these results describe a relatively plastic species whose growth is primarily enhanced by moderately warm temperatures in spring and early summer, while remaining sensitive to excess water during early growth stages. These findings are fully consistent with the ecology of *C. betulus*, characterized by a mesophilic strategy, high shade tolerance, and strong hydraulic safety (Sikkema & al., 2016).

### 4.3 Species-specific climatic responses in tree growth and wood structure

The comparison between the literature and the dendrochronological results highlights a general agreement on the absence of a universal climate–growth response, while refining species-specific patterns of sensitivity (Section 1.6).

Overall, the literature emphasizes that tree growth and wood structure are climate-sensitive but highly dependent on species ecology, hydraulic strategy, and local conditions. This is reflected in the results, where climatic signals are clearly expressed in some species but weak or absent in others, confirming that anatomical and growth responses are not uniform across taxa.

*A. pseudoplatanus* shows a weak climatic signal in ring width, which is consistent with its described high phenotypic plasticity. However, the detected positive effect of spring temperature on maximum density suggests that climate sensitivity is expressed more at the level of wood structure than radial growth. This indicates a partial decoupling between growth and anatomical response, with climate influencing internal wood properties rather than overall growth rate (Pliūra, 2007).

*A. glutinosa* also exhibits a limited and inconsistent response to climate, with no clear temperature effect on growth and a counterintuitive negative relationship with summer precipitation. This suggests that local environmental constraints or site-specific hydrological conditions may override broader climatic controls, reinforcing the idea of strong short-term physiological buffering in this species (Pliūra, 2004).

In contrast, *C. betulus* shows a coherent and statistically robust response to temperature, particularly during the early growing season, affecting both ring width and wood density. This confirms a stronger climatic control on cambial activity and wood formation compared to the other two species, consistent with its intermediate ecological strategy and sensitivity to seasonal climatic conditions (Schmucker & al., 2023).

Taken together, these results support the idea that climatic sensitivity is strongly species-dependent and more reliably detected in wood density than in ring width. They also suggest that phenotypic plasticity can mask or modulate climatic signals in some species, while in others, such as *Carpinus*, climate exerts a clearer and more direct control on wood formation.

## 4.4 Structure of the Dendrochronological Signal

As outlined in Section 1.2.1, the dendrochronological signal can be described as the sum of several components following the formulation of Cook (1987; Equation 1).

### 4.4.1 Climatic influence and individual tree factors

Regarding climatic factors, both climate-related information and individual tree responses are presented in the *Results* section and further examined in the *Discussion*. These aspects are addressed through several subsections: Section 4.1, which explores links between small- and large-scale processes; Section 4.2, which focuses on growth sensitivity to climate; and Section 4.3, which examines wood responses to climatic conditions. Additional concepts are also discussed in detail, including extreme years, growth memory and autocorrelation (Section 4.6).

### 4.4.2 Age related trend

A closer examination of the age-related trend reveals several relevant insights. The mean age of the sampled trees in Germany, presented in Table 1, ranges between 60 and 80 years depending on the studied species. More notably, the oldest individuals reached approximately 136 years for *A. pseudoplatanus*, 160 years for *C. betulus*, and over 193 years for *A. glutinosa*, the latter representing an exceptionally rare and remarkable sample for the region.

Considering the detrended ring-width index (RWI) series (Figures 31), distinct temporal patterns emerge. For *A. pseudoplatanus*, certain periods appear particularly favourable for growth, such as 1920–1940 and 1970–1990, whereas others show reduced growth, including 1910–1915, 1950–1970, and a similar declining tendency after 2015.

In contrast, *A. glutinosa* exhibits a detrended curve that remains consistently close to a value of one, suggesting relatively stable growth over time with limited interannual variability and a weaker sensitivity to external fluctuations.

A similar pattern is observed for *C. betulus*, although values more frequently fall below one than above, indicating a slight tendency toward reduced growth conditions compared to the mean, while *A. glutinosa* displays a more balanced distribution around the mean over time.

Figure 30 shows the average growth curves of the studied individuals. From these graphs, it is found that the study species have not yet reached a plateau in their growth, which suggests that their population has not reached its maximum growth potential. In addition, the variations and slowdowns in growth validate the findings made from the other data and figures presented above.

The MXD index (MXDi) also provides insights into age-related growth dynamics over time (Figure 35). For *A. pseudoplatanus*, the series is characterized by generally favourable conditions, with values frequently above one, interrupted by distinct negative anomalies, notably around 1935, 1951, and 1977. These downturns likely reflect periods of environmental stress affecting wood density formation.

*A. glutinosa* shows an overall pattern that is more frequently below one, indicating comparatively lower density values relative to the mean, punctuated by occasional positive peaks, such as in 1935, 1954, and 1973. The 1935 peak is particularly notable as it contrasts with the negative anomaly observed for *A. pseudoplatanus*, suggesting species-specific responses to climatic or environmental conditions.

Finally, *C. betulus* displays relatively stable oscillations around the value of one, indicating moderate variability in maximum latewood density. Its temporal dynamics broadly align with those of *A. pseudoplatanus* and *A. glutinosa*, with all three species exhibiting a marked decline after 2015, pointing to a potential common external driver affecting recent growth conditions.

These growth patterns should be put in relation with major European drought events, notably 1976, 2003, 2015, 2018, 2019, and 2022, which are widely recognized as periods of strong hydric stress. The potential impact of these climatic extremes on tree growth is further addressed and discussed in Section 4.6 (Ramonet & al, 2020; Büntgen & al, 2021).

#### **4.4.3 Stand factors**

In the studied stands, the sampled trees have already reached the dimensional thresholds required for the effective application of the dimensioning phase. This implies that they are no longer subject to the intense competitive pressures characteristic of early stand development. On the contrary, they have been selectively released, allowing their crowns to expand freely and ensuring optimal access to light. As a result, these individuals can be considered with growth conditions that are no longer significantly constrained by neighbouring trees (Wilhelm, 2025).

Although basal area and stem density values remain relatively high, these figures should not be interpreted as indicative of limiting silvicultural conditions. Instead, they reflect the intentional maintenance of relatively dense stands in earlier stages to promote strong competition and natural selection. Once the target trees reach sufficient dimensions, competition is locally reduced through targeted interventions. This dual dynamic, initially high competition followed by selective release, ensures both the selection of high-potential individuals and the optimization of their subsequent growth (*Wilhelm, 2025*).

Consequently, silvicultural factors do not appear to be limiting in these stands. The current structure results from a management strategy explicitly designed to support production objectives while maintaining favourable growth conditions for selected trees. Even under seemingly high stand densities, the trees benefit from adequate resource availability due to their dominant status and the interventions carried out. This suggests that their development is primarily driven by intrinsic growth potential and site conditions, rather than constrained by stand structure.

## 4.5 Linking Tree-Ring Quantiles to Seasonal Growth Dynamics: A Literature and Dendrometer Based Framework

A theoretical growth curve can be constructed to link the defined ring quantiles with successive phases of seasonal development. As illustrated in Figure 42, this framework provides a robust basis for interpreting intra-annual variations in tree growth by anchoring anatomical subdivisions of the ring to their corresponding temporal windows.

For *A. glutinosa*, the seasonal timing was established using data reported in the literature (*Vacek, 2022; Sebastian, 2009*), whereas for the two other species, the temporal framework was derived from dendrometer measurements collected during the study period (*INRAE, 2026*).

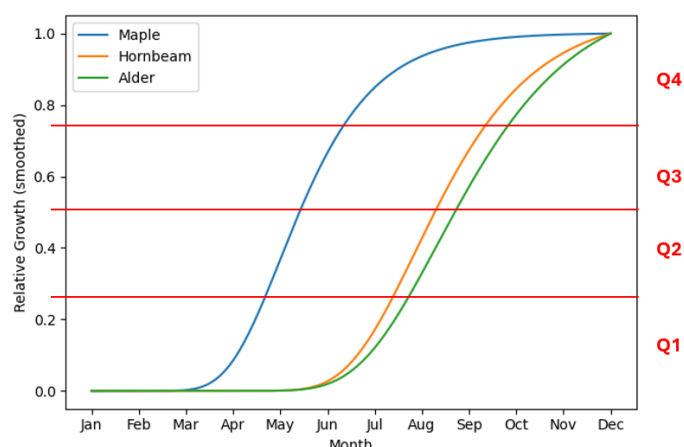


Figure 42-Smoothed Intra-Annual Growth curves of the species of study, with quantiles boundaries (Author)

Dividing each annual tree ring into equal quantiles (Q1 to Q4) raises an important question regarding the temporal correspondence of these segments, particularly the months to which

they can be attributed, and how this relationship may vary depending on the species under study. Addressing this issue is essential for the accurate interpretation of intra-annual variability in tree-ring structure.

Extensive scientific literature provides valuable insights into this question, notably through high-resolution measurements obtained from dendrometers, which enable precise monitoring of radial growth dynamics throughout the growing season (Bouriaud, 2005). Such data make it possible to establish meaningful relationships between specific portions of the ring and distinct periods of the year.

## 4.6 Integrating Tree-Ring Autocorrelation to Reveal Climatic Memory and Forest Growth Responses

### 4.6.1 Climatic Stress: dendrochronological Evidence

Drought episodes can induce growth reductions that persist for several years, even after favourable conditions return. Such legacy effects arise from sustained physiological constraints, including depletion of carbon reserves, hydraulic dysfunction, and foliage loss (Marquès & al, 2022). In species such as *F. sylvatica* and *Quercus* spp., these processes can significantly delay recovery and prolong the impact of past stress events.

Consequently, it is plausible to hypothesize that stress occurring in a given year may influence tree growth over subsequent years. This phenomenon is expressed as temporal autocorrelation in growth series: trees exhibiting high growth in one year tend to maintain relatively high growth in following years due to their physiological status and competitive position (Cook, 1990). At the same time, environmental constraints such as drought and temperature exert continuous pressure on growth, leading to persistent reductions when disturbances alter internal resource dynamics or hydraulic functioning. These effects are directly recorded in tree rings, which capture both the immediate impact of stress and its temporal extension, making wood a natural archive of past climatic influences.

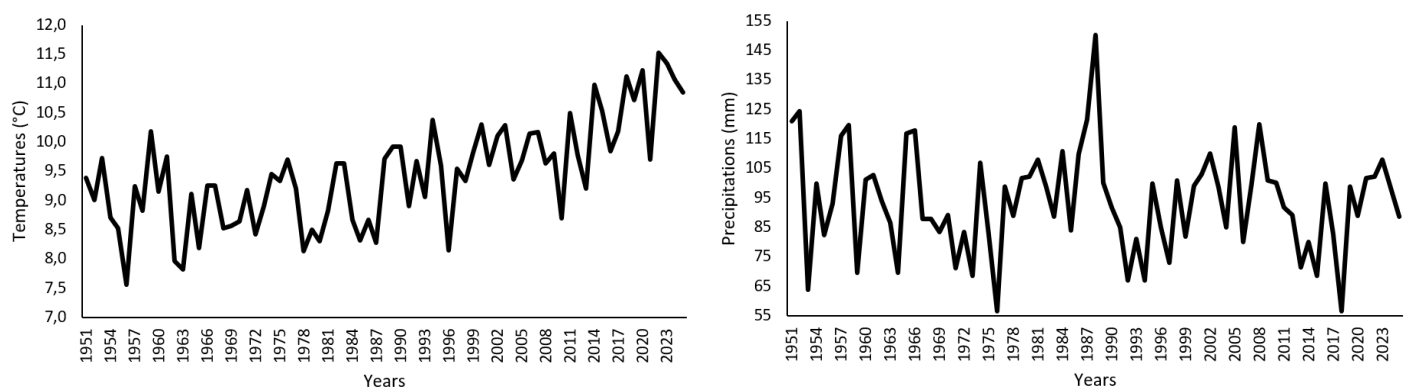


Figure 43-Average annual temperatures (°C) and precipitations (mm) between 1951 and 2025 (station of Saarbrücken-Ensheim; CDC, 2026)

The annual climatic averages are consistent with the dendrochronological patterns identified in this study, particularly in distinguishing favourable growth periods from phases of stress (Figure 43).

The 1970–1990 period, identified as favourable for growth, is characterized by moderate mean annual temperatures (8.1–11.4 °C) and relatively variable but overall sufficient precipitation (57–150 mm). These conditions likely reflect a generally balanced hydrothermal regime, with temperatures high enough to stimulate spring cambial activity while maintaining adequate water availability, thus supporting sustained growth (CDC, 2026).

In contrast, the 1951–1970 period, associated with reduced growth, shows slightly lower mean annual temperatures (7.6–10.2 °C) and a narrower precipitation range (64–124 mm). These cooler conditions may have limited early-season physiological processes, resulting in overall reduced growth (CDC, 2026).

Extreme years further highlight the role of climatic stress. The year 1976 (9.7 °C; 57 mm) corresponds to the lowest annual precipitation and reflects severe drought conditions, consistent with negative growth anomalies. Similarly, 2015 (10.5 °C; 69 mm), 2003 (10.3 °C; 99 mm) and the 2018–2022 period (9.7–11.5 °C; 57–102 mm) combine relatively high temperatures with reduced or variable precipitation, indicating recurrent drought stress. These conditions are known to limit growth, especially through increased evapotranspiration and reduced water availability during the growing season (CDC, 2026).

The pointer years method was applied, complemented by a detailed analysis of extreme years (Buras & al, 2020; Appendix 15). These results further refine species-specific responses to climatic stress. In 1976, growth was negative for *A. glutinosa* and *C. betulus*, while *A. pseudoplatanus* showed a positive response. The period 2015–2022 was generally associated with negative growth in *A. pseudoplatanus*. In contrast, *C. betulus* exhibited positive growth signals in 2018 and 2022, whereas *A. glutinosa* showed negative responses in 2019 and 2022.

Overall, growth appears to be favoured under moderately warm and sufficiently moist conditions, while higher temperatures combined with low or unstable precipitation led to growth reductions. The increasing frequency of such warm and dry conditions after 2015 is consistent with the observed decline in growth across species.

#### **4.6.2 Autocorrelation as an Expression of Growth Memory**

Table 2 reveals marked differences in growth memory between species and proxies. For RWI, *C. betulus* exhibits the highest autocorrelation (AC = 0.829), followed by *A. glutinosa* and *A. pseudoplatanus*, indicating a strong dependence of radial growth on previous years conditions in *C. betulus*, likely reflecting pronounced biological inertia. *A. glutinosa* shows intermediate persistence, whereas *A. pseudoplatanus* appears more responsive to current-year conditions,

with weaker temporal memory. A similar pattern is observed for MXD in *A. glutinosa* and *C. betulus* ( $AC > 0.600$ ), while *Acer* displays a much lower value ( $AC = 0.195$ ), suggesting that latewood density in this species is primarily driven by contemporaneous climatic factors (Robert & al, 2001; Brienen & al, 2006).

#### 4.6.3 Climatic Memory and Tree Growth Dynamics: A Dendrochronological Perspective

TRW series exhibit higher autocorrelation than MXD series, regardless of species. This difference is attributed to internal biological processes such as storage and remobilization of reserves, which enhance interannual dependence in radial growth, whereas MXD is more directly controlled by climatic conditions during the year of formation (Bradley, 2015).

From an interspecific perspective, *A. glutinosa* tends to grow under relatively stable, water-dependent site conditions, which may promote continuity in growth and thus higher autocorrelation. In contrast, *C. betulus* and *A. pseudoplatanus*, often described as mesophilous species with broad ecological amplitude, exhibit growth patterns more directly modulated by interannual climatic variability, particularly temperature and precipitation. This sensitivity to current conditions reduces the persistence of growth signals and leads to lower autocorrelation, especially in standardized series.

Overall, while species-specific differences are evident, existing dendrochronological studies suggest that variability in autocorrelation is more strongly influenced by the type of proxy (TRW versus MXD) than by taxonomy alone. Together, these findings highlight a common message: the legacy effects of past climatic stress can persist in tree growth for several years, emphasizing the importance of integrating both short-term indicators and long-term biological memory in the interpretation of forest responses to climate variability (Esper & al, 2015; Bunn & al, 2020; Vacek & al, 2022).

### 4.7 Comparative Dendroclimatic Responses of Studied Species in Relation to Beech and Oak

The comparison provides an opportunity to highlight the similarity between *C. betulus* and *Fagus sylvatica*, as both species exhibit a clear temperature-driven growth pattern, with positive responses to warmer conditions during the growing season. Although the similarity is less pronounced for precipitation, this convergence suggests that *C. betulus* may function ecologically in a manner comparable to beech under similar climatic constraints (Šimůnek & al, 2019; Drobyshev & al, 2010).

In contrast, the other two species, *A. pseudoplatanus* and *A. glutinosa*, display markedly different responses when compared not only to beech but also to *Quercus sp.* While oak is typically limited by water availability, *Alnus* shows negative responses to increased precipitation, indicating that excessive moisture rather than drought may constrain its growth, likely due to

already humid site conditions. *A. pseudoplatanus*, on the other hand, exhibits weak and inconsistent climatic signals, suggesting a lower sensitivity to both temperature and water availability compared to both beech and oak (Rozas, 2005).

These differences underline the interest of the studied species: *C. betulus* as a functional analogue to beech under temperature control, *A. glutinosa* as a species potentially limited by excess water rather than deficit, and *A. pseudoplatanus* with buffered growth responses. Together, they illustrate a broader spectrum of dendroclimatic strategies than the classical beech–oak contrast.

## 4.8 Addressing the Research Questions

The results of this study demonstrate that sycamore maple, black alder and hornbeam can be successfully used for dendrochronological research. Despite being less frequently investigated, all three species exhibit sufficiently distinct and synchronous growth-ring patterns to allow reliable cross-dating and the construction of robust chronologies. Furthermore, their growth records contain meaningful climatic information, confirming their potential for dendroecological applications and for investigating species-specific responses to environmental change.

The findings also highlight that tree-ring width alone does not fully capture the complexity of tree responses to climate. While ring-width chronologies provide valuable information on annual growth variations, wood density profiles reveal additional anatomical and physiological signals that may remain undetected using conventional approaches (Figures 1 & 24).

In this context, X-ray Computed Tomography represents a major methodological advance. Beyond its non-destructive nature, XCT enables the automated extraction of large quantities of data, allowing growth processes to be analysed in much greater detail than ring-width measurements alone. By combining traditional dendrochronological methods with XCT-derived density analyses, it becomes possible to strengthen common growth signals, improve the characterization of climate-growth relationships, and gain deeper insights into the mechanisms underlying tree responses to environmental variability.

## 5. Conclusion

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Based on the dendroclimatic analyses, *Acer pseudoplatanus*, *Alnus glutinosa*, and *Carpinus betulus* all exhibit a certain degree of resilience to climate change, although through contrasting strategies. *A. pseudoplatanus* shows limited climatic sensitivity but may become vulnerable to increasing summer drought. *A. glutinosa* remains relatively stable under current conditions, yet its dependence on hydrological balance could make it sensitive to future changes in water availability. *C. betulus* appears the most responsive to climate, benefiting from warmer growing seasons while remaining sensitive to excessive soil moisture.

Overall, no species can be considered fully resilient to climate change. Their complementary climatic responses nevertheless highlight the importance of mixed-species forests for enhancing ecosystem resilience under future environmental conditions.

This thesis demonstrates the dendrochronological potential of three underexplored species and highlights the value of X-ray computed tomography (XCT) as a high-resolution, non-destructive tool for tree-ring analysis. Beyond the methodological advances achieved, the results provide a basis for future research on species-specific growth dynamics, climate-growth relationships, and the further integration of XCT approaches into dendrochronological studies.

## 6. Contributions to the Master thesis

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This thesis was defined and supervised by Tom De Mil, Professor at Gembloux AgroBioTech, who also helped during the sampling phase (in Belgium and Germany) and contributed to the critical review of the report and oral presentation. Jan Van den Bulcke, Professor at Ghent University (UGent), also supervised this work and participated in the analysis of samples using the X-ray scanner, in collaboration with Louis Verschuren.

Victor Sibille, a fellow student and friend, helped with the sampling campaign in Belgium.

Hugues Claessens, a member of the jury, provided valuable support in the identification and selection of trees to be sampled in the Rondeux Forest. Bernard Longdoz, also a jury member, offered new perspectives in the analysis of environmental stresses and in introducing the concept of "growth memory."

Finally, Georg Josef Wilhelm enabled the collection of samples in Germany and provided a dataset related to the silvicultural QD method.

Additionally, artificial intelligence (ChatGPT) was used as an assistance tool for the rephrasing of certain passages and the translation of texts into English (OpenAI, 2023).

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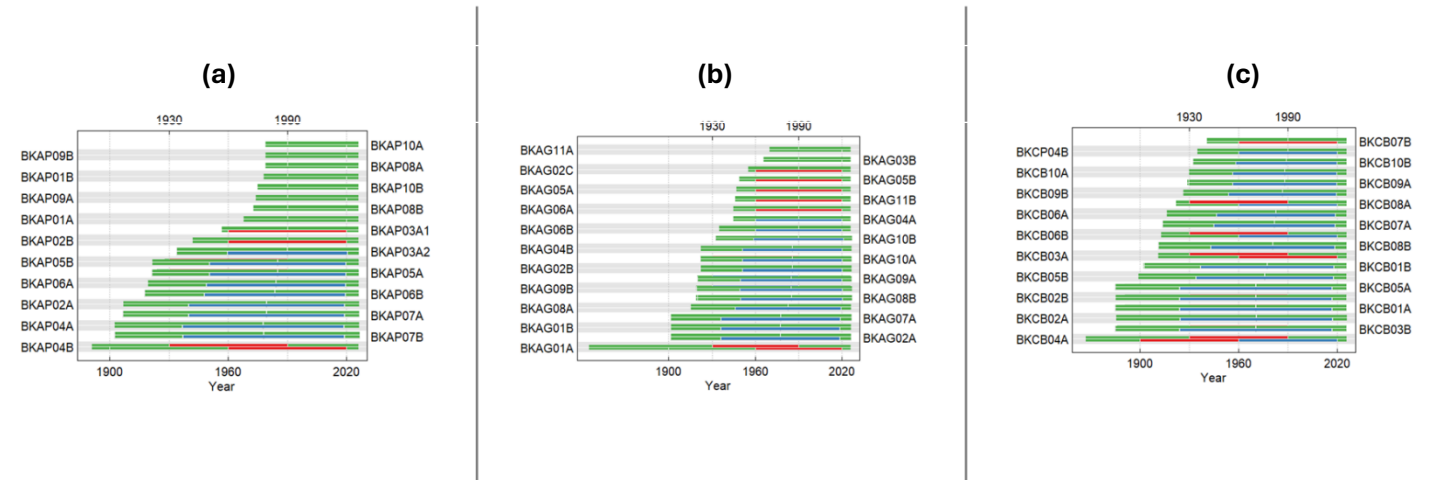
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# 8. Appendix

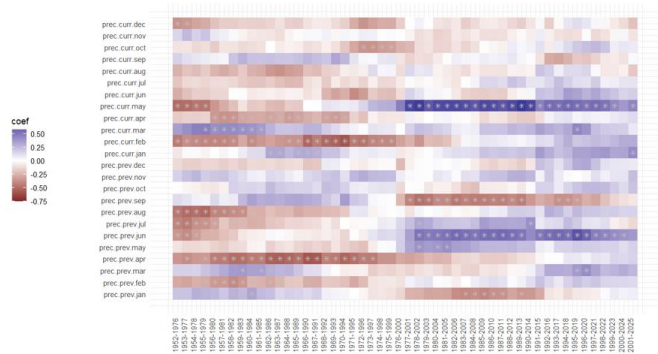
Appendix 1: Table with an Inferior calorific value (at a 0% moisture content) and wood density (Kg/m<sup>3</sup>) comparison between the main hardwood firewood species (Ollivier, 2010; Buche, 2022)

| Tree species            | Inferior calorific value <sub>0%H</sub><br>(MJ/Kg) | Wood mean density<br>(kg/m3) |
|-------------------------|----------------------------------------------------|------------------------------|
| <i>Quercus sp.</i>      | 18,39                                              | 900                          |
| <i>Fagus sylvatica</i>  | 18,29                                              | 750                          |
| <i>Carpinus betulus</i> | 18                                                 | 731                          |
| <i>Acer sp.</i>         | 17,50                                              | 599                          |
| <i>Alnus glutinosa</i>  | 17                                                 | 489                          |



Appendix 2: Segment-wise Correlation of Ring-Width Index (RWI) Series for *A. pseudoplatanus* (a), *A. glutinosa* (b) and *C. betulus* (c) (Large-scale study)

**(a)**



(b)

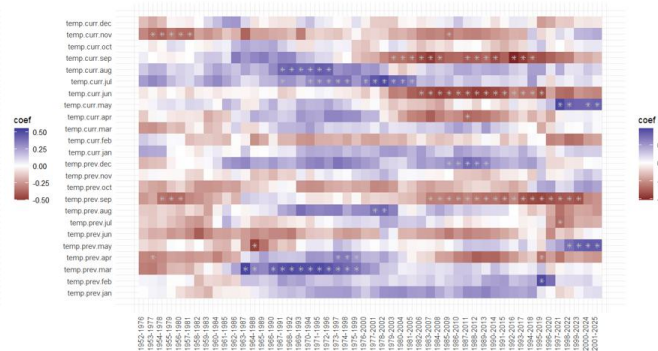
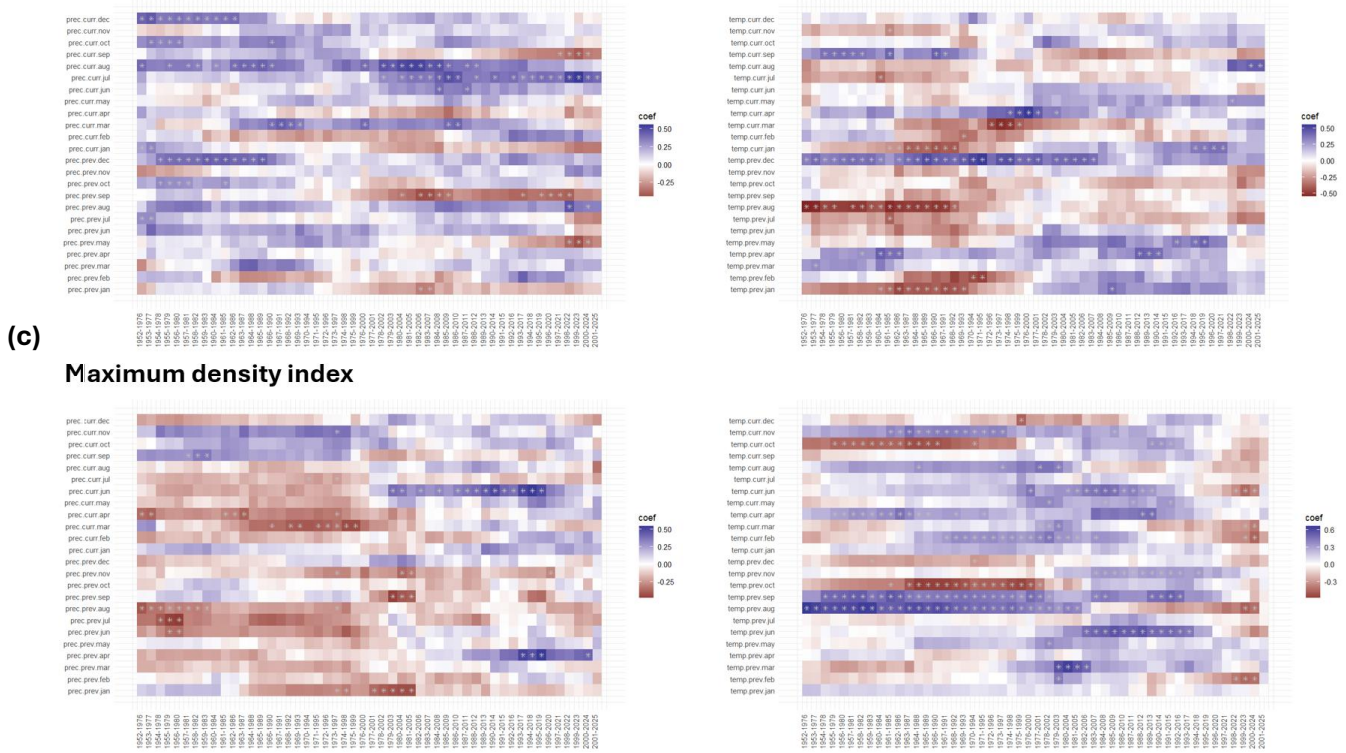


Figure 1 is a heatmap illustrating the correlation between the current and previous year's temperature anomalies for various months. The y-axis lists 24 temperature anomaly series (e.g., temp curt dec, temp prev nov). The x-axis lists 24 years (1950-1975). A color scale on the left indicates correlation values from -0.25 (red) to 0.50 (blue). The heatmap shows that correlations are generally higher (blue) for the current year's temperature anomalies and lower (red) for the previous year's temperature anomalies.

## Ring width index



Appendix 3: Moving Climate–Growth Relationships for Ring-Width Index (RWI) and Maximum density index (MXDI) for *A. pseudoplatanus* (a), *A. glutinosa* (b) and *C. betulus* (c). Significant correlations are highlighted by a white star ( $p > 0.05$ ), the Figure on the right is precipitations, the one on the left is temperatures.

Appendix 4: Correlation matrix featuring the RWI, the MXDI and the Quantiles index for the study species (Large-scale study)

| <i>A. pseudoplatanus</i> | RWI  | MXDI | Q1   | Q2   | Q3   | Q4   |
|--------------------------|------|------|------|------|------|------|
| RWI                      |      | 0.17 | 0.16 | 0.15 | 0.13 | 0.12 |
| MXDI                     | 0.17 |      | 0.15 | 0.16 | 0.12 | 0.35 |
| Q1                       | 0.16 | 0.15 |      | 0.23 | 0.17 | 0.14 |
| Q2                       | 0.15 | 0.16 | 0.23 |      | 0.29 | 0.18 |
| Q3                       | 0.13 | 0.12 | 0.17 | 0.29 |      | 0.24 |
| Q4                       | 0.12 | 0.35 | 0.14 | 0.18 | 0.24 |      |

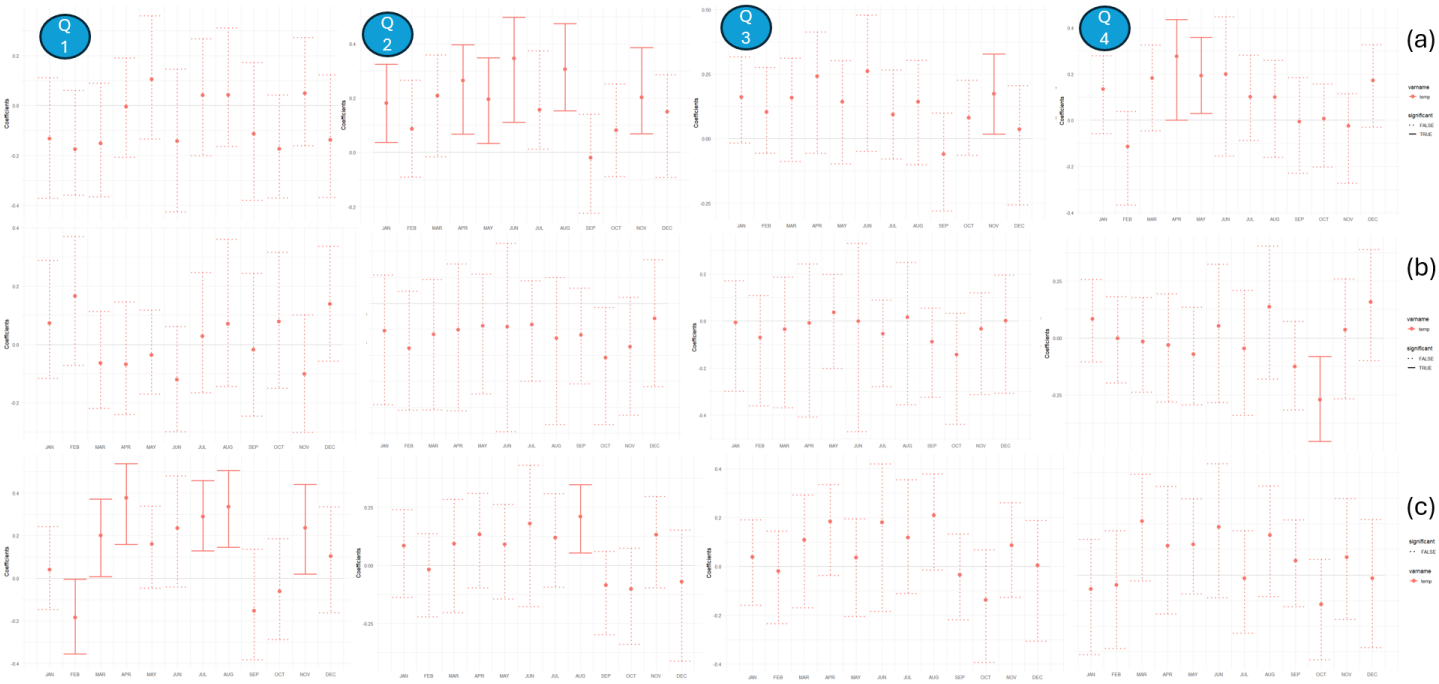
| <i>A. glutinosa</i> | RWI  | MXDI | Q1   | Q2   | Q3   | Q4   |
|---------------------|------|------|------|------|------|------|
| RWI                 |      | 0.35 | 0.22 | 0.23 | 0.23 | 0.21 |
| MXDI                | 0.35 |      | 0.20 | 0.24 | 0.25 | 0.33 |
| Q1                  | 0.22 | 0.20 |      | 0.22 | 0.22 | 0.23 |
| Q2                  | 0.23 | 0.24 | 0.22 |      | 0.27 | 0.23 |
| Q3                  | 0.23 | 0.25 | 0.22 | 0.27 |      | 0.30 |
| Q4                  | 0.21 | 0.33 | 0.23 | 0.23 | 0.30 |      |

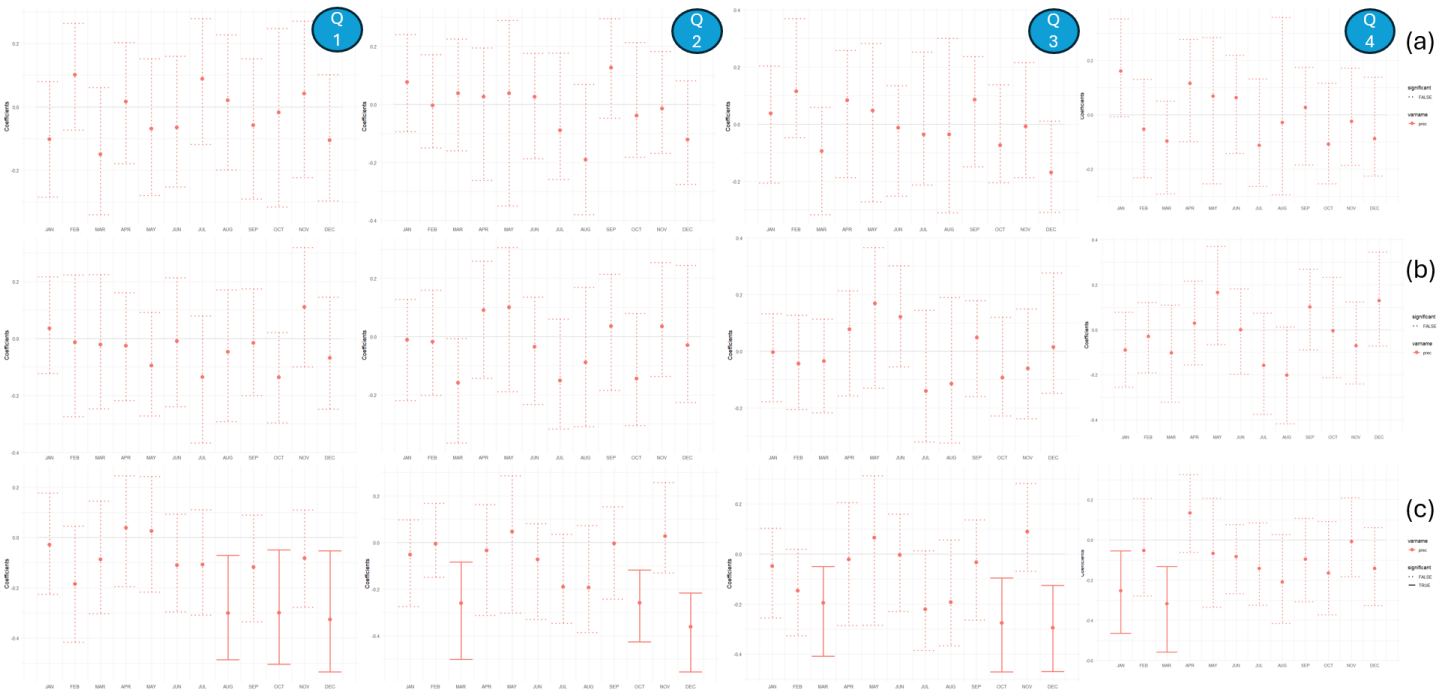
| <i>C. betulus</i> | RWI  | MXDI | Q1   | Q2   | Q3   | Q4   |
|-------------------|------|------|------|------|------|------|
| RWI               |      | 0.40 | 0.35 | 0.34 | 0.35 | 0.33 |
| MXDI              | 0.40 |      | 0.33 | 0.33 | 0.36 | 0.40 |
| Q1                | 0.35 | 0.33 |      | 0.29 | 0.28 | 0.27 |
| Q2                | 0.34 | 0.33 | 0.29 |      | 0.35 | 0.31 |
| Q3                | 0.35 | 0.36 | 0.28 | 0.35 |      | 0.37 |
| Q4                | 0.33 | 0.40 | 0.27 | 0.31 | 0.37 |      |

Appendix 5: Correlation significance of RWI, MXDI and Quantiles index between the data from the small-scale and from the large-scale study over their overlapping period

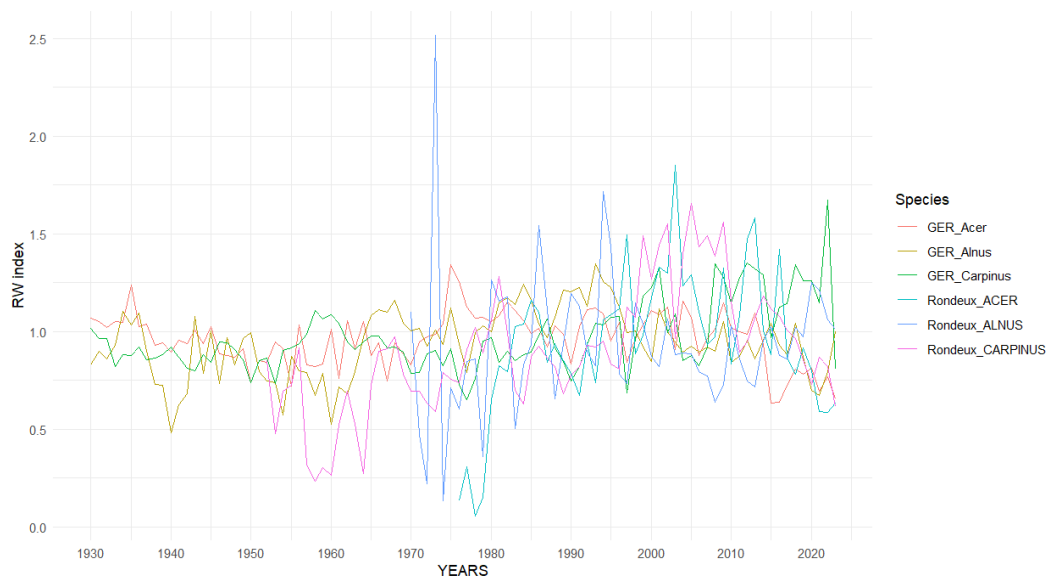
| Species           | RWI              | MXDI             | Q <sub>1-4</sub> |
|-------------------|------------------|------------------|------------------|
| A. pseudoplatanus | r= 0.55 (p>0,05) | r= 0.52 (p>0,05) | r= 0.18 (p>0,05) |
| A. glutinosa      | r= 0.61 (p>0,05) | r= 0.44 (p>0,05) | r= 0.21 (p>0,05) |
| C. betulus        | r= 0.57 (p>0,05) | r= 0.42 (p>0,05) | r= 0.22 (p>0,05) |



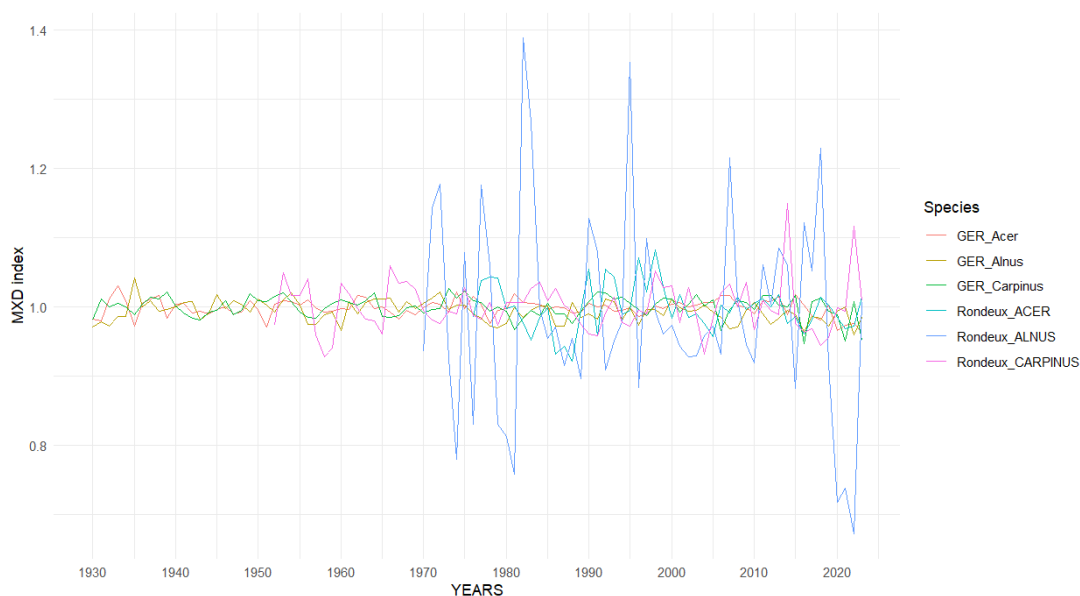
Appendix 6: *A. pseudoplatanus* (a), *A. glutinosa* (b) and *C. betulus* (c) Quantile Density analysis and its monthly correlation with temperatures (°C) for the 1951-2025 period (Large-scale study)



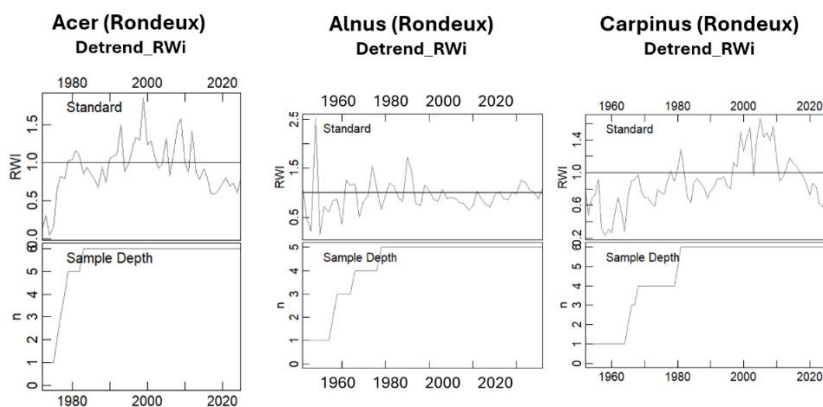
Appendix 7: *A. pseudoplatanus* (a), *A. glutinosa* (b) and *C. betulus* (c) Quantile Density analysis and its monthly correlation with precipitations (mm) for the 1951-2025 period (Large-scale study)



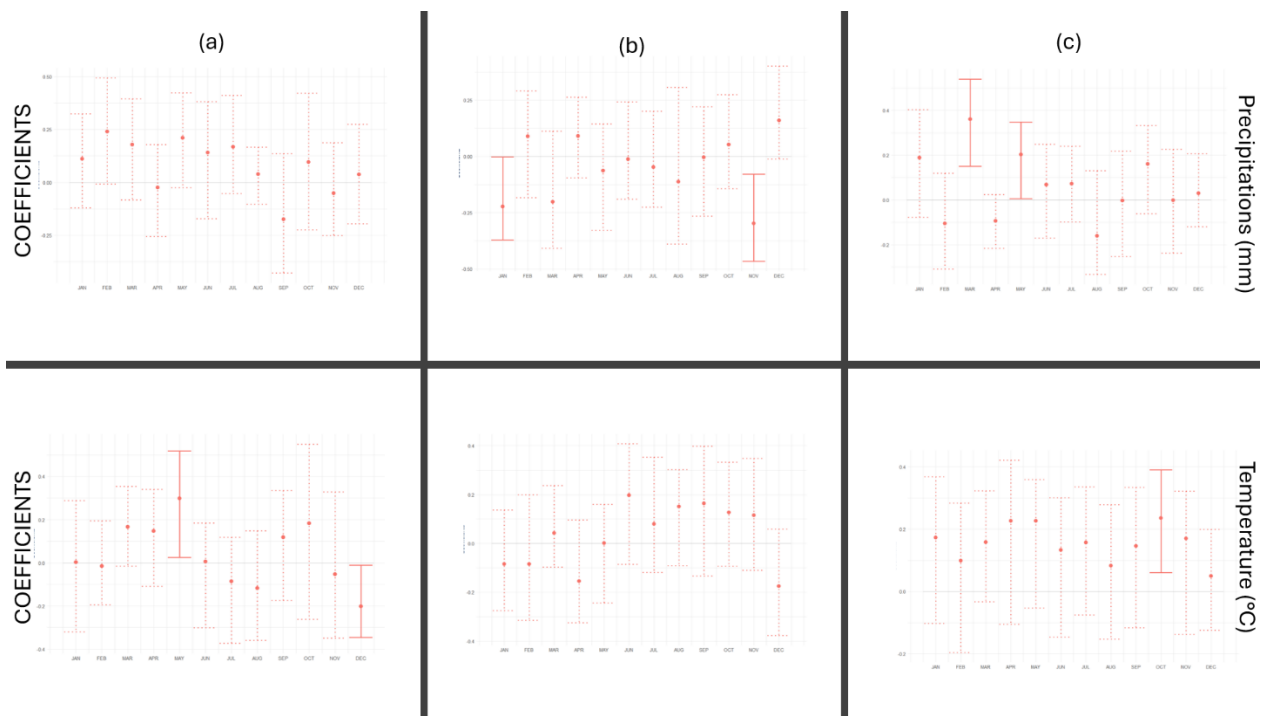
Appendix 8: grouped graphical representation of the ring width index for small and large-scale studies



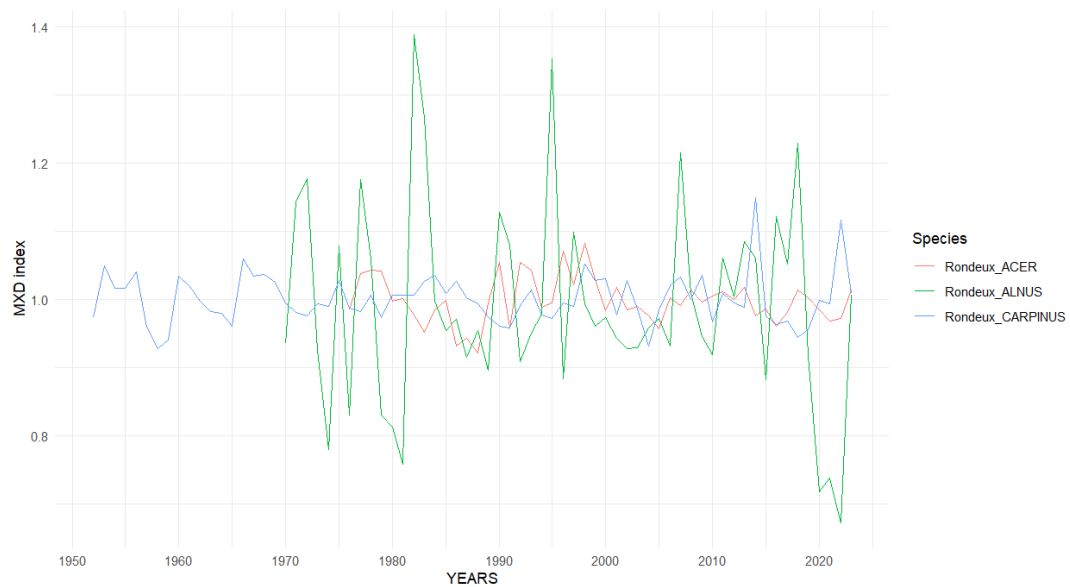
Appendix 9: grouped graphical representation of the maximum density index for small and large-scale studies



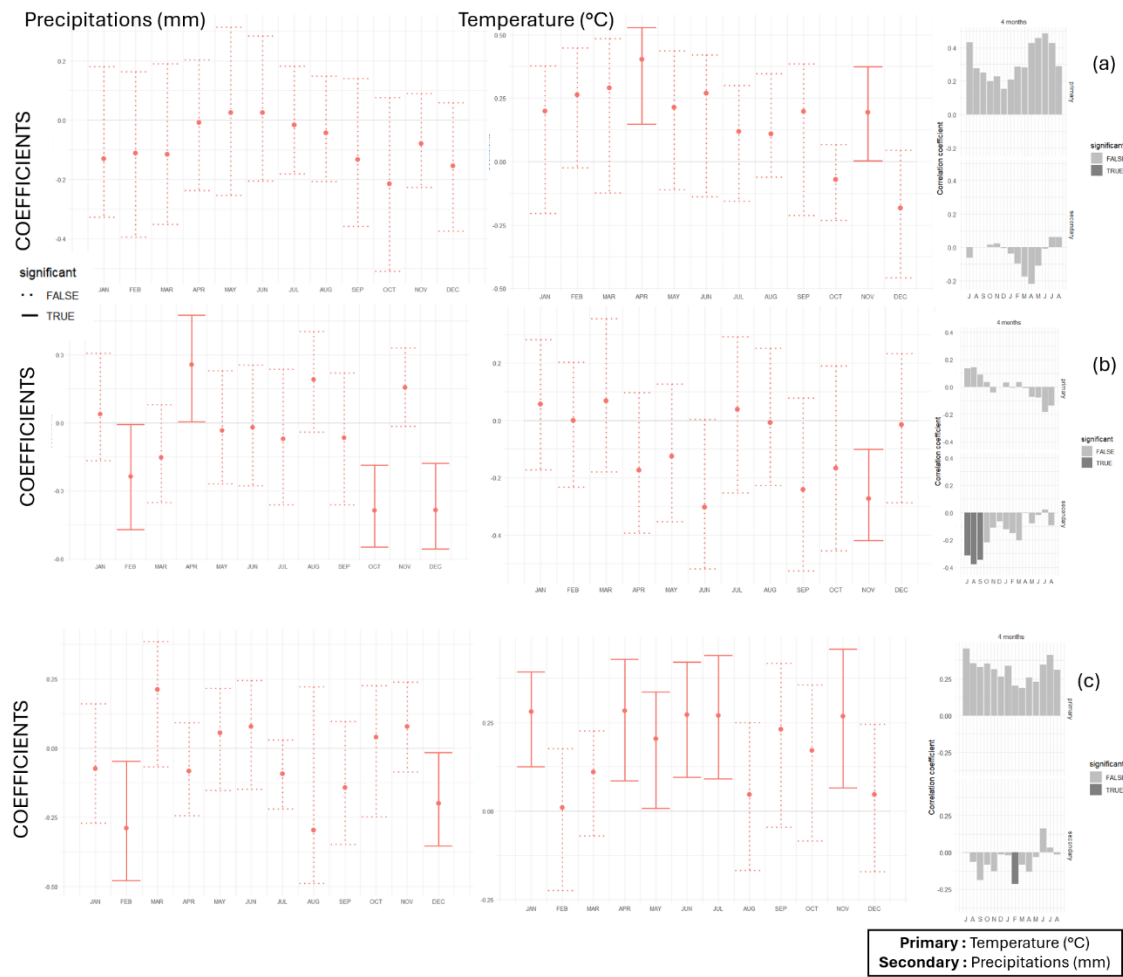
Appendix 10: detrended Ring Width Index (RWI) graph of the species of study (Preliminary study)



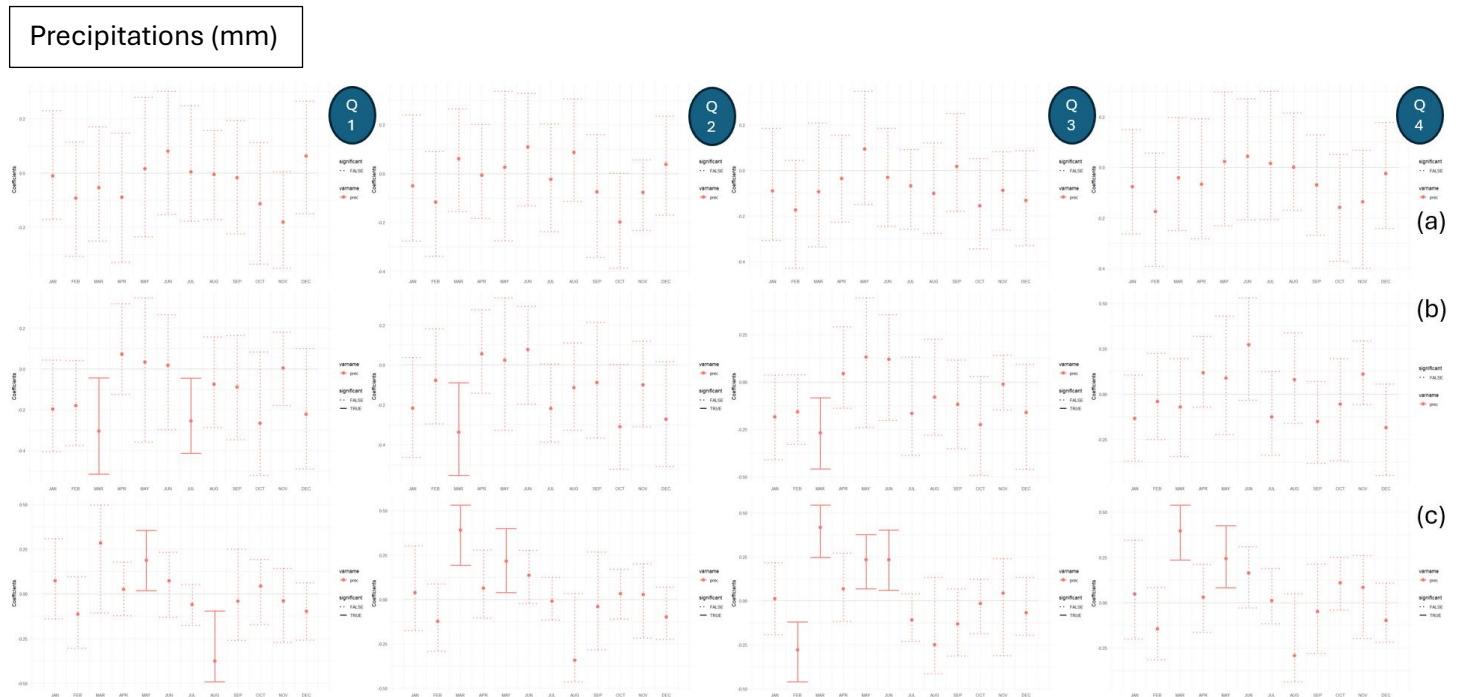
Appendix 11: correlation graphs between Ring Width and precipitations and temperatures (Preliminary study) for *A. pseudoplatanus* (a), *A. glutinosa* (b) and *C. betulus* (c)



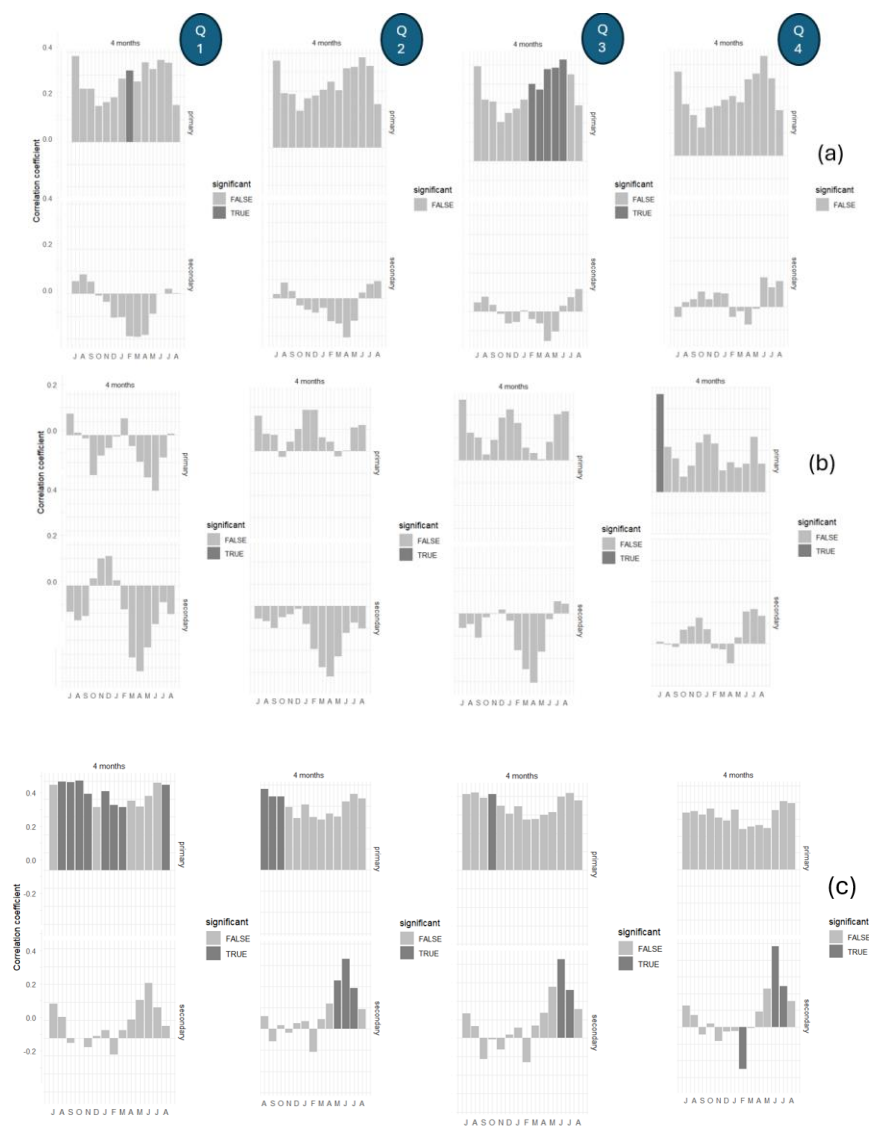
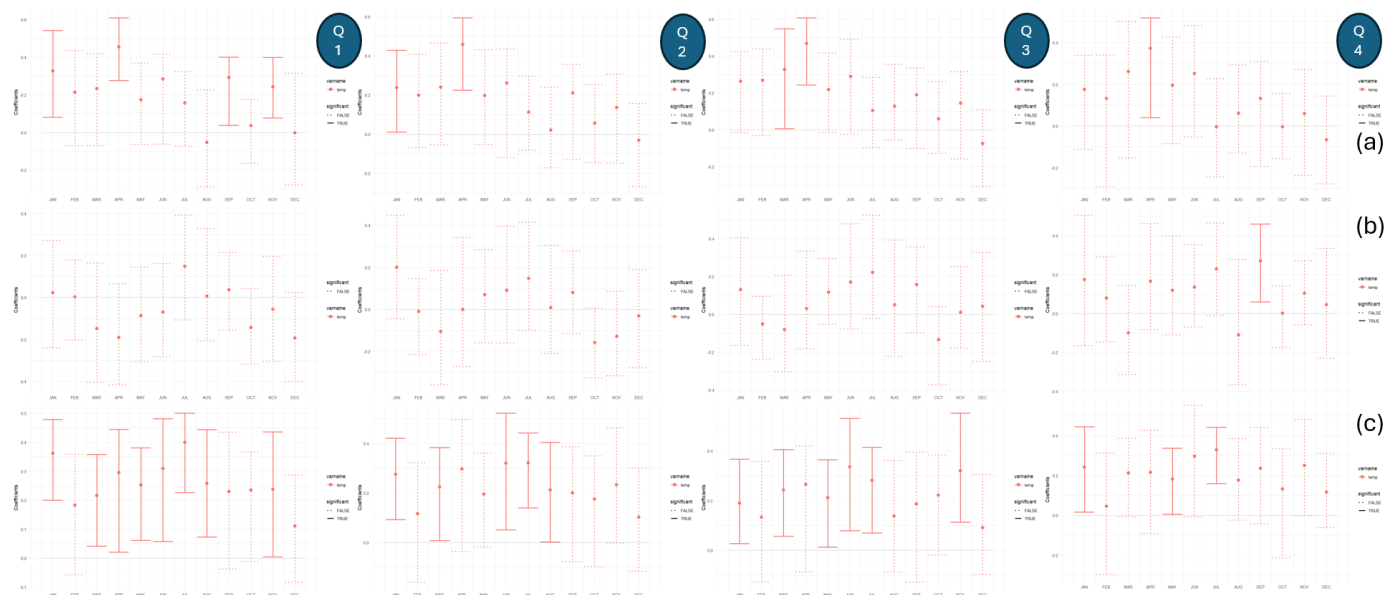
Appendix 12: Maximum density index (detrended) graphs for the species of study over time (Preliminary study)



Appendix 13: Overall and Seasonal Correlations Between Maximum Density and Temperature/Precipitation (Preliminary study) for *A. pseudoplatanus* (a), *A. glutinosa* (b) and *C. betulus* (c)



## Temperature (°C)



**Primary : Temperature (°C)**  
**Secondary : Precipitations (mm)**

Appendix 14: Overall and Seasonal Correlations Between Quantile Density and Temperature/Precipitation (Preliminary study) for *A. pseudoplatanus* (a), *A. glutinosa* (b) and *C. betulus* (c)

Appendix 15: characterization of the impact of extreme years on growth using the pointer years method (Buras & al, 2020). A black circle indicates a positive extreme year while a white circle indicates a negative extreme year (Large-scale study).

| Species                  | Extreme years |      |      |      |      |      |
|--------------------------|---------------|------|------|------|------|------|
|                          | 1976          | 2003 | 2015 | 2018 | 2019 | 2022 |
| <i>A. pseudoplatanus</i> | ●             |      | ○    | ○    | ○    | ○    |
| <i>A. glutinosa</i>      | ○             |      |      |      | ○    | ○    |
| <i>C. betulus</i>        | ○             |      |      | ●    |      | ●    |