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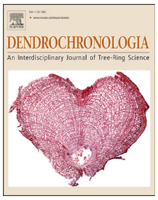

Resource utilization strategies and longevity of *Thuja occidentalis* across contrasting substrates: Insights from morphological and physiological traits

Manon Boche [a], Marc-André Lemay [a], Samuel Bouchut [a], Yves Bergeron [b,c], Christoforos Pappas [d], Miguel Montoro Girona [a,e], Valentina Buttò [b], Fabio Gennaretti [a,f,*]

[a] *Groupe de Recherche en Écologie de la MRC Abitibi, Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, Amos, Canada*
[b] *Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Canada*
[c] *Département des sciences biologiques, Université du Québec à Montréal, Montréal, Canada*
[d] *Department of Civil Engineering, University of Patras, Rio Patras, Greece*
[e] *Universdad de Huelva, Huelva, Spain*
[f] *Department of Agricultural, Food and Environmental Sciences, Università Politecnica delle Marche, Ancona, Italy*

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ABSTRACT

Understanding the interplay between environmental conditions and physiological traits is essential to explain tree longevity in resource-limited environments. We studied old (up to 466 years) *Thuja occidentalis* trees growing on contrasting rock and gravel substrates to assess how substrate type and age influence hydraulic function, resource use, and survival strategies. Using dendroanatomical and physiological measurements, we compared key functional traits across 25 trees of varying ages and site conditions in Duparquet, Quebec, Canada. Our results show that trees on drier rock substrates exhibit smaller xylem tracheids, reduced theoretical hydraulic conductivity, and lower foliage density, enabling them to resist drought stress at the cost of limited growth. These conservative traits become more pronounced as the trees age and are associated with greater longevity, with the age of trees growing on rock substrates exceeding 300 years, whereas those on gravel substrates reaching up to 200 years. In contrast, trees on gravel demonstrate greater hydraulic efficiency and radial growth potential as a result of fewer resource constraints. These findings align with the hydraulic limitation hypothesis and provide valuable insights into how substrate conditions and age-related functional acclimation shape survival strategies in long-lived trees. Moreover, they highlight the importance of local site conditions in tree resilience and underscore the need for further research into the effects of environmental variability on tree physiology and morphology to better predict tree responses to future environmental changes.

1. Introduction

The longevity of ancient trees, some of which have survived for several centuries or even millennia, makes them extremely valuable from an ecological and scientific perspective (Cannon et al., 2022). For trees to achieve extreme longevity, several factors must coincide (Cannon et al., 2022; Piovesan and Biondi, 2021). First, only certain species with specific genetic traits can survive for extended periods. Among these, conifers belonging to the Pinaceae and Cupressaceae families are especially likely to reach a very old age (Leland et al., 2018; Matthes et al., 2002). These species have evolved to thrive in harsh environments, such as mountainous regions, arid landscapes, and boreal zones (Pasques and Munné-Bosch, 2023; Piovesan and Biondi, 2021). It is the combination of their genetic makeup and the challenging environments they grow in that allows these trees to reach such remarkable ages. More generally, it is believed that species or individuals that adopt a "slower" life pace (i.e., slower growth and less intensive use of resources) are more likely to live long (Reich, 2014).

Old trees have adapted and acclimated to harsh environments through functional traits such as a resistant and resilient hydraulic system, of which the xylem is a critical component (Bhusal et al., 2021; Cannon et al., 2022; Pasques and Munné-Bosch, 2023; Piovesan and Biondi, 2021). In conifers, xylem consists of tracheids that transport water from roots to leaves thanks to cohesion-tension between water

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* Corresponding author at: Groupe de Recherche en Écologie de la MRC Abitibi, Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, Amos, Canada.

E-mail address: fabio.gennaretti@uqat.ca (F. Gennaretti).

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molecules and a negative pressure gradient (Brodribb, 2009; Zimmermann, 2013). The pressure within the xylem, known as water potential, is influenced by environmental factors such as soil moisture, temperature, and air humidity (Tyree and Ewers, 1991). If this pressure reaches a critical threshold, the cohesion of the water column can break due to the formation of gas bubbles, leading to embolism and possibly tree mortality due to hydraulic failure (Klein et al., 2018). Resistance strategies that mitigate this risk include narrower tracheids with thicker walls (Klein et al., 2018) or strip-bark morphology (Leland et al., 2018), where partial cambium loss can optimize resource allocation and reduce metabolic demands. However, there is a trade-off between safety against hydraulic failure and efficient water transport, which can ultimately impact growth (Hacke and Sperry, 2001; Sperry et al., 2008). For example, given a fixed number of conduits, reducing the size of the conduits decreases water transport capacity.

Studying hydraulic system trade-offs through tree rings and their cellular structure can help identify the traits that contribute to resistance and longevity at the cellular level (Fonti et al., 2010; von Arx et al., 2016). Dendroanatomy, the study of wood cells, is critical for elucidating tree growth patterns and their responses to local site conditions, such as substrate type and water availability. The structural characteristics of wood cells, particularly the size and arrangement of tracheids, are shaped by water availability, temperature, soil conditions, and changes in tree size throughout tree ontogeny (Carrer et al., 2015; Fonti et al., 2010; Matisons et al., 2019; Piermattei et al., 2020). For instance, anatomical traits must evolve with increasing tree height to maintain effective hydraulic functioning (Liu et al., 2019; Olson et al., 2018; Petit et al., 2011). When such size-related changes are controlled for, the analysis of wood cell anatomy can reveal how long-lived trees differ for their growth processes and how they respond or remain vulnerable to external climatic drivers and environmental conditions. However, focusing solely on individual wood anatomical traits can lead to incomplete interpretations that may even contradict initial hypotheses, as single traits often fail to capture the trade-off between tree resistance and efficiency (Hajek et al., 2016). To improve interpretation, multiple traits should be considered together, for example, lumen area and pit architecture, to fully understand drought resistance and vulnerability to cavitation (Mrad et al., 2018). Additionally, anatomical traits should preferably be complemented by other physiological measurements, including xylem pressure, leaf morphology, crown structure, and sapwood area (Hajek et al., 2016).

Our study aims to describe the anatomical and functional traits of old (up to > 400 years old) eastern white cedars (*Thuja occidentalis* L.) at Lake Duparquet, Canada, across two different substrates to understand the factors contributing to their remarkable longevity. Eastern white cedar is a member of the Cupressaceae family and is widespread throughout the northeastern part of North America from the United States to Canada, thriving on various substrate types (Burns et al., 2016). It is a late-successional species following fire disturbances (Bergeron, 2000). Very old specimens are found on the Niagara Escarpment (> 1300 years old; Matthes-Sears et al., 2008) and on certain islands in Lake Duparquet (> 800 years old; Archambault, 1989; Archambault and Bergeron, 1992), situated at the northern limit of the species range in Abitibi, Quebec, Canada. Although eastern white cedar has a long potential lifespan, this longevity is realized only under rare, specific conditions, often on rocky outcrops. In the boreal region, trees older than 200–300 years are considered old, as favorable microsite conditions are uncommon and the short fire-return interval drastically reduces the likelihood of reaching such ages (Bergeron, 2000). In this study, we hypothesize that cedar trees on the rocky, nutrient-poor, and dry escarpments along Lake Duparquet have developed hydraulic traits that enable them to persist for centuries. We predict that the dry environment of the rocky escarpments promotes acclimation through specific resistance traits increasing hydraulic safety, and that these traits become even more pronounced as the trees undergo ontogeny in these challenging conditions.

2. Materials and methods

2.1. Study site and sampled trees

The study eastern white cedars (*Thuja occidentalis* L.) population is located on an island on Lake Duparquet (Abitibi region, Quebec, Canada). According to the nearest weather station (Rouyn-Noranda), this area has a continental boreal climate with mean annual precipitation between 800 mm and 900 mm, average winter (December to February) temperature of −18°C, and average summer (June to August) temperature of 17°C. The site climate was also characterized using ERA5 reanalysis data (Copernicus Climate Change Service; Hersbach et al., 2020) for specific analyses, including the description of climatological conditions (Fig. S1), drought indices (Standardized precipitation evapotranspiration index, SPEI, Fig. S2), weather during relevant days (Fig. S3), and tree growth sensitivity to drought (Fig. S4).

Lake Duparquet hosts over one hundred islands, some of which support populations of ancient white cedars (Archambault, 1989). Three of these islands are part of the “Reserve écologique des vieux arbres” (Old trees ecological reserve), which was created to protect some of the oldest trees in northeastern North America (Archambault, 1989). The study population is located outside the ecological reserve (48.461° N, 79.276° W) but contains old (> 400 years old) trees, with some growing on mesic substrate primarily composed of shallow till/gravel beaches (referred to as “gravel” from now onwards), and the oldest ones on dry rocky outcrops (referred to as “rock” from now onwards). We sampled the first line of trees adjacent to the lake shore, where the oldest trees are typically found. All sampled trees were adults, each over two meters in height (Table 1). In total, we sampled 25 trees: 12 on gravel and 13 on rock. For each tree, we measured tree height, diameter at breast height, and age. We measured the diameter at breast height using a measuring tape and tree height with a measuring pole. Additional variables are described in more detail in the following sections and include dendroanatomical traits, sapwood width, midday water potential, and foliage interception of light.

2.2. Dendrochronology

For each tree, we extracted two cores at the tree base (30 cm height) using a 4-mm Pressler borer in the direction transverse to the slope to avoid reaction wood. We glued the cores onto boards and sanded them until 600-grit sandpaper prior to scanning them at a resolution of 4800 DPI (Epson Perfection 4800, Seiko Epson Corporation, Suwa, Japan) (Fig. S5). We then used the CooRecorder software (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden) to measure ring widths and date the cores. When necessary, we used Duncan's method to estimate the number of missing rings up to the pith and calculate tree age (Duncan, 1989). We crossdated the cores using the Past5 (SCIEM, Vienna, Austria) and COFECHA (Holmes, 1983) software. In addition to calculating tree age and average growth, the sensitivity of ring-width chronologies to drought was evaluated by focusing on the SPEI at a 1-month scale for August, which showed the strongest correlation with tree-ring width data (Fig. S4). Chronologies were obtained by individually standardizing the raw ring-width series using basic functions from the *dplR* package and applying the spline detrending method (Bunn, 2008).

Table 1
Characteristics of the old cedars (*Thuja occidentalis* L.) sampled at Lake Duparquet by growing substrate.

Substrate	Age (years) Mean (min-max) ± SD	Height (cm) Mean (min-max) ± SD	DBH (cm) Mean (min-max) ± SD
Rock	274 (90−466) ± 124	495 (230–740) ± 180	21.0 (4.5–48) ± 13.5
Gravel	110 (52−178) ± 43	541 (260–1130) ± 236	15.5 (6–34) ± 9.2

2.3. Wood anatomy

We sampled one additional 10-cm long wood core per tree at breast height with a 5-mm Pressler increment borer and used those cores for wood anatomy analysis. The outermost three centimeters of each core were cut using a razor blade and then boiled in water until they sank to the bottom of the beaker. The water was replaced when it turned brown to prevent the cores from being stained by secondary compounds, which are abundant in cedar wood.

We prepared the samples for image acquisition by slicing 10-µm thick transverse sections using a microtome (Leica RM2245, Germany), staining with safranin (0.5 %), dehydrating with ethanol (progessive concentrations of 50 %-75 %-95 %), and mounting between slides and coverslips using Permount (Fisher Chemical). We scanned the 15 most recent annual rings of each sample (Aperio LV1 scanner, Leica, Germany) at 20x magnification to measure anatomical traits at the oldest age of each tree (Fig. S6).

We conducted an initial image analysis to date the samples. For this, we traced the rings using WinCell software (Regent Instruments Inc, Québec, Canada) on the scanned microscope slides and confirmed their dating with the results from the Past5 software (see above) using our dendrochronological reference curve. We selected the rings from 1999 to 2005 for downstream analyses as they were common to all samples. Despite the collection of the cores in 2022, the cored portion of the trunk had already died earlier for some of the samples due to the modular growth typical of the species.

For dendroanatomical analyses, we used a tangential width of approximately forty radial files to obtain average measurements for each ring (Seo et al., 2014). We identified radial files using the RAPTOR R package (Peters et al., 2018). We computed Mork's index (Denne, 1988) to distinguish between latewood and earlywood. Cells falsely detected as latewood were semiautomatically filtered out by comparison with their neighbouring cells. Other false latewood cell detections were visually filtered by plotting the cells and their dimensions. The measured anatomical parameters included traits describing the water and carbon functioning of the study trees (Table 2).

In addition to the measured tracheid lumen diameter (LD), we computed the theoretical hydraulic conductivity (Kh) and the hydraulic carbon use efficiency (HCUE). Kh estimates the water transported per unit time per pressure gradient and was used as proxy for hydraulic efficiency. For the theoretical hydraulic conductivity, we used the equation:

$$Kh = \frac{\pi}{64} * \frac{a^3 * b^3}{a^2 + b^2} \tag{1}$$

where a is the major diameter of the cell and b is the minor diameter of the cell, assuming the shape of an ellipse. This equation assumes that the viscosity of the liquid and the length of the cells are constant across different trees (Tyree and Zimmermann, 2002).

Table 2
List of all traits used in this study, including quantitative wood anatomy traits and other functional traits.

Parameters	Acronym	Unit	Mesured (M) Derived (D)	Portion of tree-ring used
Theoretical hydraulic conductivity	Kh	μm^4 $Pa^{-1} \cdot s^{-1}$	D	Earlywood
Lumen diameter	LD	µm	M	Earlywood
Hydraulic carbon use efficiency	HCUE	μm^2 Pa^{-1} s^{-1}	D	Earlywood
Tree-ring width	TRW	µm	M	All Ring
Sapwood width	SpW	cm	M	-
Foliage density	FD	None (ratio)	D	-
Midday stem water potential	SWP	bar	M	-

HCUE was used as proxy for the hydraulic return per carbon investment (Prendin et al., 2018). HCUE was calculated for each radial file as the ratio of the accumulated theoretical conductance of all tracheids (Kh) to the accumulated cell well area of all tracheids within the radial file (CWA_{RF}) using the equation:

$$HCUE = \frac{Kh}{CWA_{RF}} \tag{2}$$

2.4. Sapwood width

During the sampling of tree cores, we measured the sapwood width to the nearest millimeter using a measuring tape. The sapwood was easily distinguishable due to its moist, more translucent appearance compared to the rest of the core (Pappas et al., 2022). Since we collected two cores per tree, the average of the two measurements was used in analyses.

2.5. Midday stem water potential

We measured stem water potential following Williams et al. (2012) using a portable pressure chamber (Model 600, PMS Instrument Co., Oregon). For each tree, two mature terminal portions of branches at about 2-m height, oriented towards the lake, were wrapped in aluminum foil 30–40 min prior to measurement. The terminal portions were subsequently cut and immediately placed in the pressure chamber for assessment. The pressure recorded corresponded to the point at which a droplet emerged from the end of the stem. All measurements were conducted at midday on a sunny summer day (July 27, 2022). The two measurements per tree were averaged for analysis.

2.6. Foliage density

We measured light attenuation by the crown of a specific tree to obtain an index related to its foliage density using a LAI-2200 Plant Canopy Analyzer (LI-COR, Nebraska). We took four measurements per tree in the early morning of a clear-sky day on the 180° of the crown facing the lake with a 45° view cap on the sensor to assess the attenuation of the photosynthetic active radiation passing through the crown. For each measurement, an initial reading was taken below the crown at ground level as close to the trunk as possible, followed by a second reading along the same axis, outside the crown, and always at ground level. Light attenuation was measured with the equation:

$$\text{Foliage density} = \frac{\sum_{rep=1}^{4} \sum_{ring=1}^{2} \frac{PAR_{above} - PAR_{below}}{PAR_{above}}}{n_{rep} * \quad n_{ring}} \tag{3}$$

where PAR_{above} is the photosynthetic active radiation outside the crown, PAR_{below} is the photosynthetic active radiation below the crown, *rep* is one of the four measurements, and *ring* is one of the two rings of the sensor considered in this analysis. Indeed, we only considered the first two rings of the sensor corresponding to the most vertical angles to ensure that we captured light attenuation in a region that passes through the crown.

2.7. Statistical analysis

To examine the relationships between various tree traits, ontogeny and environmental factors, we employed linear models specified as:

$$\text{Trait} = \beta_0 + \text{Height} + \text{Age} : \text{Substrate} + \varepsilon \tag{4}$$

where Trait represents the tree trait being analyzed (mean of the 1999–2005 period), β_0 is the intercept, Height is tree height included to control for changes in trait values linked to tree size, Age is tree age, Substrate is the growing substrate (gravel or rock), and ε denotes the residual error, which follows a normal distribution. Age:Substrate represents the interaction between tree age and substrate. To determine if the age slopes differ significantly between substrates, we used the general linear hypotheses test (glht) function from R package multcomp (Hothorn et al., 2008). This method was applied to analyze theoretical hydraulic conductivity (Kh), lumen diameter (LD), hydraulic carbon use efficiency (HCUE), sapwood width (SpW), and ring width (TRW) (Table S1). For additional traits where the impact of tree age was not significant, such as tree height, stem water potential, and foliage density, Wilcoxon rank-sum tests or Student's *t*-tests were used depending on the distribution of the data to assess shifts in these traits as a function of the growing substrate (Table S1). All statistical analyses were performed using R version 4.3.3 (R Core Team, 2024) using data available in Table S2.

3. Results

3.1. Linking tree age, tree height and type of growing substrate

The sampled trees were significantly older on rock than gravel ($W = 15$, $p < 0.001$; Fig. 1a, Table S1), but no relation was identified between tree height and substrate (Fig. 1b, Table S1) or between tree height and age (Fig. 1c, Table S1). Only trees on rocky substrates exceeded 200 years of age, with the oldest individual reaching 466 years (Table 1).

3.2. Type of substrate and physiological stress

The midday stem water potential differed significantly between trees on gravel and those on rock ($t = 2.52$, $df = 22.9$, $p < 0.05$; Fig. 2, Table S1). Trees growing on gravel exhibited a higher mean midday water potential (mean $= -10.63$ bar) compared to those on rock (mean $= -11.64$ bar). The day on which stem water potential was measured was sunny but not particularly warm or dry compared with typical summer days in July–August (Fig. S3). Consequently, the results indicate that, under normal summer conditions, trees growing on rock experience higher water stress than those growing on gravel.

3.3. Theoretical hydraulic conductivity

Theoretical hydraulic conductivity (Kh) increased significantly with height (slope $= 0.121$, $p < 0.001$; Table S1), indicating that taller trees had higher hydraulic conductivity. The interaction between tree age and substrate type also influenced Kh (Fig. 3a). A positive relationship was observed in gravel (slope $= 0.428$, $p < 0.01$; Table S1), suggesting that the effect of age on Kh is substrate dependent. In contrast, no significant effect of age on Kh was found in rock (slope $= -0.042$, $p > 0.05$; Table S1).

3.4. Lumen diameter

Lumen diameter (LD) increased significantly with height (slope $= 0.00551$, $p < 0.001$; Table S1), indicating that taller trees had larger radial lumen diameters. The interaction between tree age and substrate type also affected LD (Fig. 3b), with a stronger relationship observed on gravel (slope $= 0.0288$, $p < 0.001$; Table S1) than on rock (slope $= 0.00829$, $p < 0.01$; Table S1), suggesting that the effect of age on LD is more pronounced on gravel.

3.5. Slower increase of hydraulic carbon use efficiency on rock

The hydraulic carbon use efficiency increased significantly with tree height (slope $= 1.36 * 10^{-5}$, $p < 0.05$; Table S1), suggesting that taller trees exhibit more efficient carbon use. Substrate type also played a key role, with trees on gravel becoming markedly more efficient with age (slope $= 8.44 * 10^{-5}$, $p < 0.01$; Table S1) compared to those on rock (slope $= 3.75 * 10^{-5}$, $p < 0.01$; Table S1). This indicates a pronounced effect of substrate type on hydraulic carbon use efficiency (Fig. 3c).

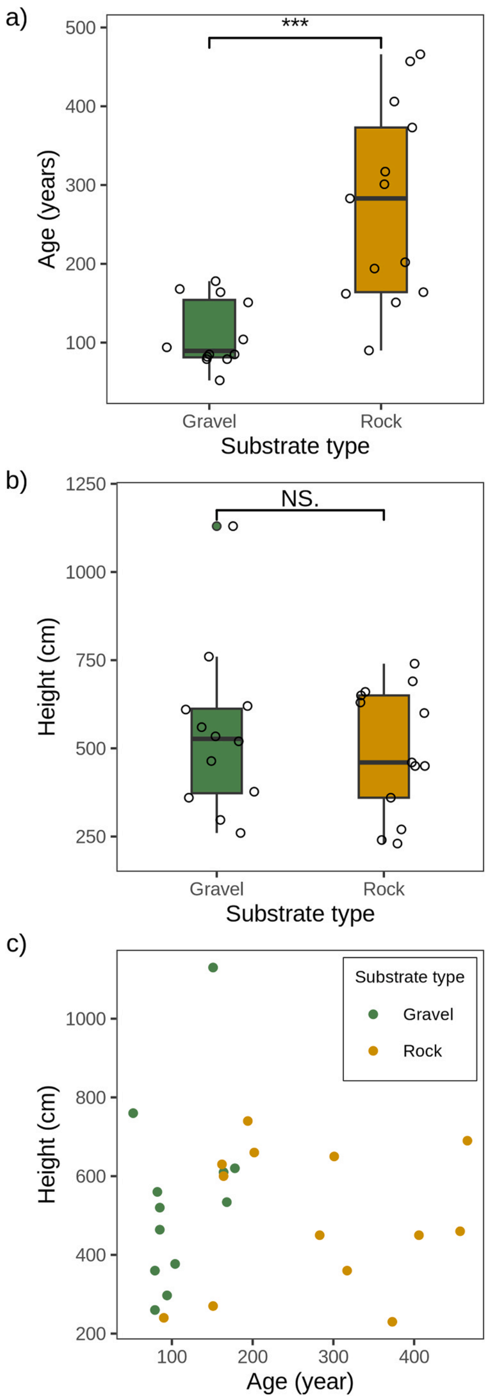

Fig. 1. Relation between (a) substrate and tree age, (b) substrate and tree height, and (c) age and height. The full distribution of values is shown on top of the boxplots as points jittered along the x-axis. NS: non-significant difference according to *t*-test. *** Statistically significant difference with $p < 0.001$ according to Wilcoxon test.

3.6. Sapwood width

Sapwood width (SpW) was different between the two substrate types ($t = 6.88$, $df = 20.7$, $p < 0.001$; Table S1). The effect of age on SpW was marginally significant on gravel (slope $= 0.00237$, $p < 0.1$; Table S1), suggesting a slight increase in sapwood width with age (Fig. 4). In

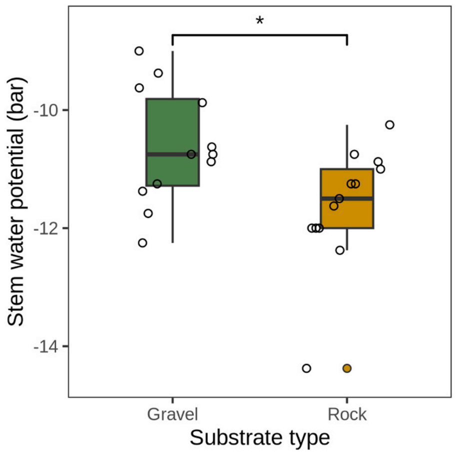

Fig. 2. Relation between stem water potential and substrate type. The full distribution of values is shown on top of the boxplots as points jittered along the x-axis. * Statistically significant difference with $p < 0.05$ according to *t*-test.

contrast, a significant negative effect was observed on rock, where SpW decreased with age (slope = −0.00128, $p < 0.05$; Fig. 4, Table S1).

3.7. *Reduction of foliage density on rock*

Foliage density was significantly higher in trees growing on gravel (mean = 0.839) than those growing on rock (mean = 0.533) substrate (W = 137, p-value < 0.001; Fig. 5; Table S1). The foliage density increases with age on gravel (slope = 0.00224, $p < 0.05$; Table S1) but not on rock (slope = $6.58 * 10^{-5}$, $p > 0.05$; Table S1).

3.8. *Reduction of radial growth on rock*

Ring width increased significantly with height (slope = 0.509, $p < 0.01$), indicating that taller trees had wider rings. The substrate type also affected ring width, with a significant reduction observed on rock compared to gravel (estimate = −402.7, $p < 0.001$; Fig. 6, Table S1). This suggests that rings of trees on rock are considerably narrower than those on gravel. Analysis of year-to-year variations in ring width relative to drought indices (SPEI) shows that *Thuja occidentalis* growing on gravel is correlated with the August SPEI, exhibiting reduced growth during dry years (1940–2020), whereas no such correlation is found for *Thuja occidentalis* growing on rock (Fig. S4).

4. Discussion

Our results indicate that dry sites on rocky substrate, where the oldest cedar trees are found, can significantly alter tree hydraulic functioning. These effects become more pronounced as the trees age and correlate with growth reduction. These mechanisms remain detectable even when accounting for changes in tree size over time (i.e., height) and seem crucial for longevity, promoting a conservative use of available resources.

4.1. *Influence of local site conditions on key traits enhancing tree longevity*

Our results, obtained from old trees used as a case study, effectively demonstrate how acclimation to resource-poor local site conditions can enhance tree longevity. Although the overall site climate is not particularly dry during summer (Fig. S1), *Thuja occidentalis* growing on rock at Duparquet experience extremely dry substrate conditions, where water drains rapidly (Archambault, 1989; Archambault and Bergeron, 1992). In such dry, rocky and nutrient-poor environments, trees exhibit lower water potential, indicating a constant state of hydric stress associated

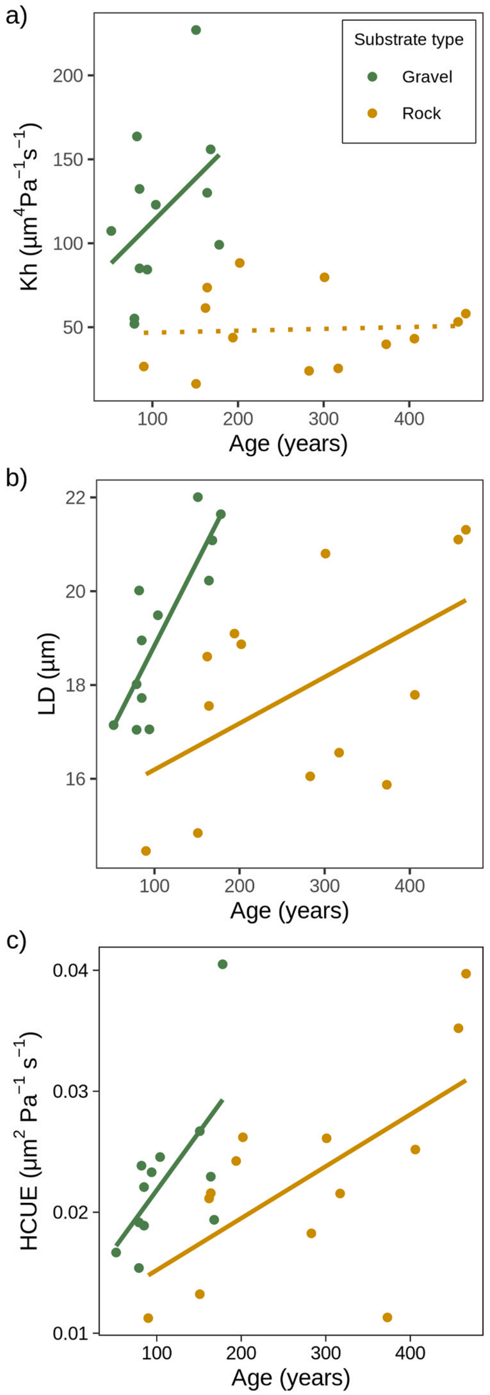

Fig. 3. Relation between (a) theorical hydraulic conductivity (Kh) and age, (b) lumen diameter of earlywood (LD) and age, and (c) hydraulic carbon use efficiency (HCUE) and age on the two growing substrates, gravel and rock. The points represent the sampled trees, and the linear regressions are indicated by the corresponding-colored lines. Solid lines denote statistically significant slopes at α = 0.05 whereas the dotted line is a non-significant slope.

with this substrate (Hacke et al., 2001; McDowell et al., 2008). Adaptations to such conditions include reduced hydraulic conductivity and narrower lumen diameters. Consequently, trees on rocky sites produce growth rings composed of fewer, smaller cells, enhancing their resistance to limited water availability (Gleason et al., 2016). This pattern is also supported by the annual climate–growth correlation analysis. *Thuja occidentalis* growing on gravel are negatively affected by summer drought, whereas this is not the case for the better-acclimated

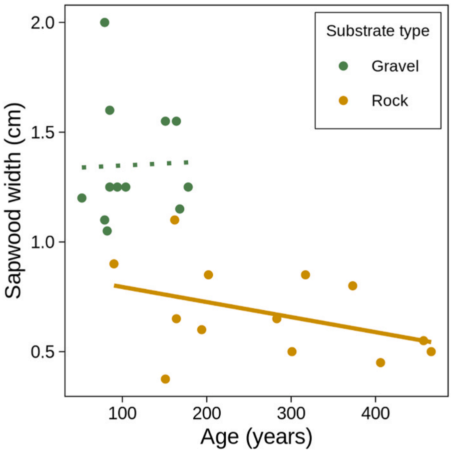

Fig. 4. Relation between sapwood width and age on the two growing substrates, gravel and rock. The points represent the sampled trees, and the linear regressions are indicated by the corresponding-colored lines. The solid line denotes a statistically significant slope at $\alpha = 0.05$ whereas the dotted line is a non-significant slope.

individuals growing on rock, which experience dry conditions regardless of yearly variability. The changes in conductive surface area, as measured by the width of the sapwood, also reflect acclimatization to low water conditions (Gartner and Meinzer, 2005). By reducing conduit size and conductive surface area on rock, these trees are able to maintain water transport even during periods of drought (Brodribb, 2009; Sperry et al., 2008; Tyree and Zimmermann, 2002). Additionally, trees on rocky substrates demonstrate significantly lower foliage density. This reduction in foliage limits evapotranspiration due to a smaller leaf surface area and decreases the resource allocation needed for foliage maintenance (Niinemets, 2010; Sala et al., 2012). Such a reduction in foliage density may also be associated with the loss of living cambium, as has been observed by Archambault (1989). However, this limitation in both conductivity and foliage also likely results in reduced resource assimilation through photosynthesis, leading to a permanent state of low resource availability (Chhajed et al., 2024; Deans et al., 2020; Mencuccini et al., 2019; Ryan et al., 2006).

It is known that trees in dry environments may acclimate to nutrient-poor conditions by modifying their resource utilization strategies (McDowell, 2011; Meinzer et al., 2011; Piovesan and Biondi, 2021). These adaptations include increased resistance to embolism and careful management of water and nutrients, which enable them to withstand both inter-annual and intra-annual variations in precipitation. This resource conservation capability plays a crucial role in the longevity of trees in dry habitats, allowing them to thrive in challenging conditions (Issartel and Coiffard, 2011; Pasques and Munné-Bosch, 2023; Piovesan and Biondi, 2021). The Hydraulic Limitation Hypothesis elucidates this trade-off: as trees face difficulties in efficient water transport, they reduce their photosynthetic activity to conserve resources, which ultimately results in limited growth potential (Issartel and Coiffard, 2011; Pasques and Munné-Bosch, 2023; Rötheli et al., 2012; Ryan et al., 2006). By balancing the need for hydration with the constraints imposed by their environment, these trees effectively navigate the challenges of dry habitats. Our results are in line with the Hydraulic Limitation Hypothesis because they reveal that trees growing in dry environments exhibit physiological and morphological responses that balance water transport limitations with resource conservation.

A key factor contributing to tree longevity in dry environments is the

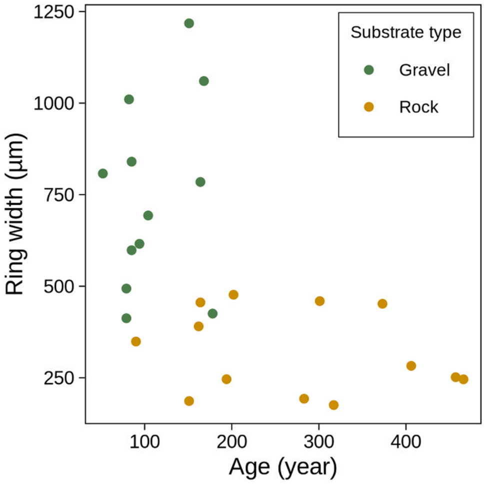

Fig. 6. Relation between ring width and age on the two growing substrates, gravel and rock. Regression was non-significant for both tree groups (rock and gravel).

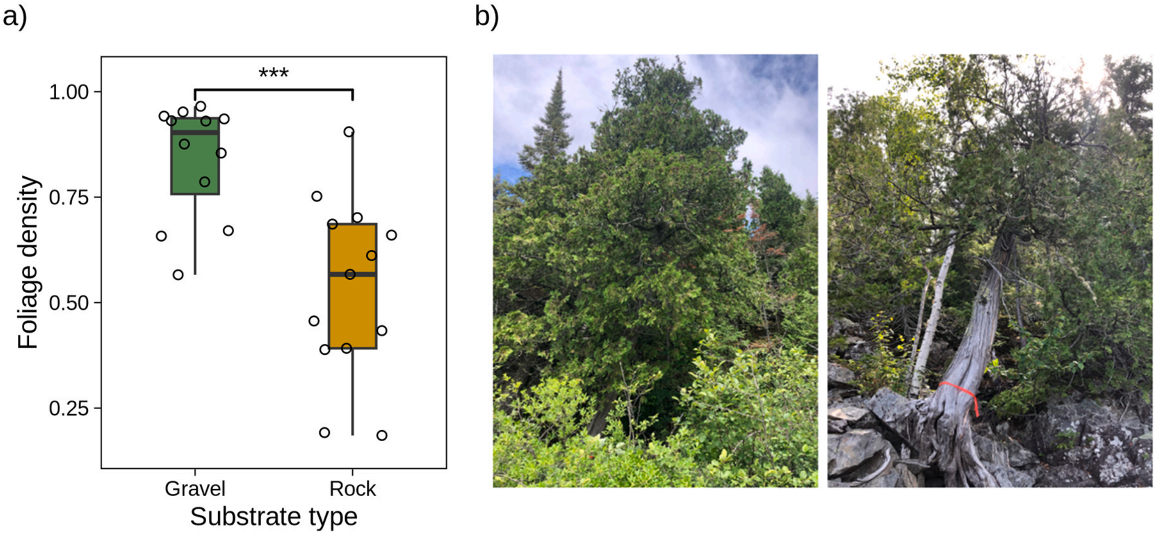

Fig. 5. (a) Relation between foliage density and growing substrate. The full distribution of values is shown on top of the boxplots as points jittered along the x-axis. (b) Pictures of white cedars growing on gravel (left) and on rock (right). The lower foliage density of the cedar growing on rocks is apparent. *** Statistically significant difference with $p < 0.001$ according to Wilcoxon test.

strong link between slow growth and increased wood density. It is well established in dendrochronology that the oldest trees are often those that exhibit the slowest growth rates, as rapid growth can lead during unfavorable periods to an early attainment of the photosynthetic efficiency threshold, limiting long-term survival potential (Bigler and Veblen, 2009; Black et al., 2008; Rötheli et al., 2012). In the studied cedar trees growing on rocky substrates, the production of small-diameter tracheids and, more importantly, the reduced ring width, may result in increased wood density, a trait associated with greater resistance to decay, fungal pathogens, and insect attacks (Arnič et al., 2022; Bouslimi et al., 2022; Franceschi et al., 2005; Larson et al., 1993; Schulman, 1954). This enhanced structural integrity reduces the likelihood of mechanical failure and prolongs tree lifespan under harsh environmental conditions.

4.2. *The evolution of resistance traits during ontogeny*

The observed variation in functional traits between trees growing on gravel and rocky substrates appears to be influenced not only by substrate conditions but also by significant ontogenetic changes, while no clear trend is evident in atmospheric dryness over the last 80 years (See Fig. S2 showing the SPEI at a 1-month scale for August, which showed the strongest correlation with tree-ring width data). As trees age, those rooted in gravel display increases in both hydraulic conductivity and lumen diameter. In contrast, trees established in rocky soils exhibit an increase in lumen diameter over time, albeit slower, without a corresponding rise in overall theoretical hydraulic conductivity, attributable to the reduction in the number of formed tracheids per year over time and, consequently, to narrower growth rings (Hacke et al., 2001). This suggests that lumen enlargement with age occurs independently of substrate type and is predominantly driven by trunk growth (Liu et al., 2019; Olson et al., 2018; Petit et al., 2011). To ensure the upward transport of sap to the canopy, conducting tracheids must expand annually to maintain effective capillarity and water potential gradients. In dry soils, in addition to the stable Kh per growth ring, the sapwood area of trees tends to decrease with age, reflecting an adaptation to drier environmental conditions (Gartner and Meinzer, 2005). Additionally, hydraulic carbon use efficiency (HCUE)—interpretable as the hydraulic return per carbon investment—increases with age in both substrate types, but again the increase is more pronounced in trees growing on gravel as their Kh rises much faster. Trees on rocky substrates seem to suffer from resource depletion as they age, as their HCUE increases even with a stable Kh, indicating a slight decrease in cell wall area. In contrast, trees in gravel substrates may experience less hydraulic stress, enabling them to allocate resources more efficiently toward both hydraulic function and structural carbon. All these patterns are consistent with a previous study based on carbon isotopes, which showed that the same old-growth cedars on rock did not increase their growth rate despite higher atmospheric carbon concentrations from anthropogenic emissions and a concurrent rise in their intrinsic water-use efficiency (Giguère-Croteau et al., 2019).

The development of hydraulic safety traits in older trees may be influenced by their exposure to multiple extreme climatic events over their life span, including droughts and fluctuations in temperature associated with historical periods like the Little Ice Age (Archambault and Bergeron, 1992; Briffa et al., 1995; Gleason et al., 2016; Schulman, 1954). Surviving these severe conditions may imprint distinct functional traits, differentiating older trees from younger ones and enhancing their ability to cope with chronic hydric stress (Balducci et al., 2015; Hereş et al., 2014; Martin-Benito et al., 2017). This interpretation is also supported by our climate–growth correlation analysis, which shows a reduced sensitivity of trees growing on rock to dry years (Fig. S4). Alternatively, it could be that we are observing the result of the survivorship bias, i.e., only those trees that met specific criteria were able to survive until an old age (Duchesne et al., 2019).

4.3. *Implications and limitations of the study*

We present a comprehensive analysis of tree traits which were measured across multiple scales within individual trees. Our approach, combining dendroanatomical data with other physiological traits, provides valuable insights into resource utilization strategies in the studied old-growth trees. This analysis confirms and enhances our understanding of key tree functional processes and offers a foundation for comparison with other tree species or under different environmental conditions.

Understanding the interplay between environmental conditions and tree functional traits is crucial, particularly in the context of climate change. Numerous studies have shown that trees in dry environments exhibit distinct anatomical traits, such as altered hydraulic characteristics and variations in leaf density (Hereş et al., 2014; Hochberg et al., 2018; McDowell, 2011; Mencuccini et al., 2019). For instance, research has indicated that trees facing water stress develop narrower xylem vessels and sparser foliage to enhance drought resilience (Greenwood et al., 2008; Martin-Benito et al., 2017). These adaptations not only help in conserving water but also improve the trees ability to manage embolism, thereby prolonging their lifespan despite the challenges posed by their harsh surroundings (Álvarez-Yépiz et al., 2014; Piovesan and Biondi, 2021).

Our study contributes to this body of knowledge by highlighting how the effects of age intertwine with environmental influences on tree traits. It demonstrates how environmental factors shape tree anatomy and underscores that tree age also plays a significant role in the acclimation process (Groover, 2017; Johnson and Abrams, 2009; Meinzer et al., 2011). However, a limitation of our study lies in its approach: rather than examining temporal series within individual trees, we compare trees of different ages. While this approach allowed us to simultaneously evaluate the effects of substrate type and tree age on a sufficient number of trees, it does not fully account for ontogenetic changes, and trait comparisons cannot be made at the same age across individuals. In addition, we sampled only trees with the highest potential for longevity, which in our case were always located in the first line of trees adjacent to the lake, without implementing a fully randomized, stratified, and representative sampling design for each substrate type. To thoroughly investigate how traits evolve with age, future studies should increase sampling depth, standardize procedures and sampling design, and focus on analyzing complete temporal series from individual trees growing under different environmental conditions (Babst et al., 2018; Klesse et al., 2018). Our findings on changes in functional traits with age should therefore be interpreted with this nuance in mind.

5. Conclusion

As the studied cedar trees age, acclimations to local conditions become more evident, suggesting complex interactions between longevity, environmental stressors, and functional traits. The study of age-dependent changes is vital for understanding how trees might respond to future climate challenges (Allen et al., 2010; Carrer and Urbinati, 2004; Matisons et al., 2019). Notably, the risk of functional decline and mortality may increase as older trees reach their physiological limits under sustained stress, especially if conditions become gradually more and more severe. Recognizing both environmental and age-related factors is essential for predicting the resilience of these emblematic trees.

Our study demonstrates that trees on rocky substrates exhibit adaptations such as reduced hydraulic conductivity, narrower conduits, and lower foliage density compared to those in less restrictive environments. These hydraulic adjustments come at the expense of radial growth but likely promote longevity. Moreover, as trees on rock age, they exhibit a shift in resource allocation strategies, such as reduced sapwood area and earlywood hydraulic conductivity (Kh) that remains stable rather than increasing with age. These findings underscore how environmental stress and ontogenetic changes shape tree longevity, reveal insights into resilience of such trees under current and future climates, and support the active conservation of this natural heritage, given their delicate internal balance. We may conclude that the sampled white cedars maintain a delicate balance between growth and survival and lie on the "slow" end of the plant economics spectrum (Reich, 2014).

Supporting information

Supplementary file 1.docx: supplementary figures S1-S6 as well as supplementary table S1 and S2.

CRediT authorship contribution statement

Valentina Buttò: Writing – review & editing. **Fabio Gennaretti:** Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Samuel Bouchut:** Writing – review & editing, Formal analysis. **Yves Bergeron:** Writing – review & editing, Supervision, Resources. **Christoforos Pappas:** Writing – review & editing. **Miguel Montoro Girona:** Writing – review & editing. **Manon Boche:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Marc-André Lemay:** Writing – review & editing, Visualization, Validation, Formal analysis, Data curation.

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Declaration of Competing Interest

The authors declare no competing interests.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2026.126484.

Data Availability

The dataset used in statistical analyses is available in supporting information.

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