

Variations in ring width density and tracheid morphology of tamarack wood (*Larix laricina*)

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Abstract

The tree genetic improvement programs focus on tree growth with little attention to wood quality despite determining the potential of wood for various applications. This study investigated the intra-ring and intra-tree variations of wood growth, density, tracheid length, and width of *Larix laricina* trees and estimated their quantitative genetic parameters of a 30-year-old progeny test using destructive and nondestructive samplings. The average ring density was 491 kg/m³. The proportion of latewood remains uniform and constant within the tree at about 24%. The tracheids were fine and long, averaging 25 µm in diameter and 2.23 mm in length for earlywood and 25 µm in diameter and 2.55 mm in length for latewood. The cambial age has a significant effect on almost all wood properties. A positive and significant phenotypic and genotypic correlation between density components was found for juvenile and mature wood. Tracheid morphological properties were positively correlated with each other and negatively correlated with wood density and growth components, except for earlywood density. Heritability estimates indicate that wood density components were under moderate to strong genetic control. These results showed that wood quality traits are important selection criteria for breeding programs to improve wood quality while maintaining a high growth rate.

Key words: *Larix Laricina*, ring density and growth, tracheid length and width, phenotypic and genetic correlations, heritability, nondestructive testing

Introduction

Tamarack (*Larix laricina* (Du Roi) K. Koch) is a fast-growing species native to North America. It is particularly common in northern regions with cold climates. Despite being one of the most widespread trees in North America, it is poorly exploited as a commercially valuable tree species (Zhang and Koubaa 2008).

Larches are valued for their durable timber and ability to thrive in diverse climates. As versatile species, they are resistant to decay and can be used for numerous purposes, such as interior and exterior lumber products. Additionally, larch wood is favored for pulp and paper production due to its long fibres, which contribute to the strength of paper products. Larch has also found its place in composite products, combining it with other materials to create innovative and durable products for various industries (Zhang and Koubaa 2008). In 1970, a larch improvement program was established in Quebec province to find the most resilient and high-quality larch trees for cultivation (Cáceres et al. 2017). The aim would have been to enhance the forestry industry and promote the growth of trees that could better withstand environmental

challenges. The tamarack, European, and Japanese larches planted at various sites in Quebec proved to be the most productive conifers when used within rotation periods of 30 years (Cáceres et al. 2017).

There is growing interest in fast-growing tree species and their use in industries. A species improvement program must consider the tree's morphological and genetic characteristics as well as the wood's final utilization. Accordingly, wood quality traits have become a serious concern among tree breeders (Perron et al. 2013). However, wood quality may involve many properties, such as density and fibre length; therefore, it can be defined only after specifying the end-use product. For example, fibre length is an indicator of paper strength (Zobel and Van Buijtenen 1989; Zhang and Koubaa 2008). Wood density, considered one of the most important quality traits, is highly correlated to its mechanical properties and in-service performance (Zobel and Van Buijtenen 1989).

This property, widely used to evaluate wood quality in tree improvement programs, varies highly with genetic, environmental, and physiological factors and silvicultural

treatments (Zobel and Van Buijtenen 1989). The within-ring wood density variation also determines its suitability for several end-uses and applications (Koubaa et al. 2002; Bouslimi et al. 2019).

Only a few investigations studied the variability in the wood properties of tamarack in North America. Yang and Hazenberg (1987) investigated the variation of growth rate, latewood proportion, specific gravity, and tracheid length of tamarack juvenile wood among locations, stands, and trees in northern Ontario at breast height. Yang et al. (1986) reported that the juvenile wood of *L. laricina* is conical in shape, tapering towards the tree top.

However, no study has investigated the variation between earlywood and latewood or between juvenile and mature wood in tamarack. Furthermore, pith-to-bark (radial) and along-the-stem (axial) variations in wood density and tracheid morphological properties in larches have not been investigated in depth. Therefore, a better understanding of this variability would help determine its suitability for various uses. Furthermore, few studies have focused on genetic and the inter-tree variation of tamarack wood properties in North America. The main objectives of this study were, therefore, (1) to investigate the radial and axial variations in ring width and density and tracheid length and width in tamarack mature wood trees and (2) to estimate the quantitative genetic parameters of its physical and anatomical wood properties.

Materials and methods

Genetic material

Trees for this study were from first-generation progeny trials for tamarack (*L. laricina*) were established in the Abitibi-Temiscamingue region in the province of Quebec, Canada, in 1989 by the “Ministère des Ressources naturelles et des Forêts”. Each site comprises 225 open-pollinated families (Perron et al. 2013). The initial spacing was 2 × 2 m and was maintained up to year 10, except in the surroundings of dead trees. No other silvicultural treatment was applied on the sampled site. A total of 40 trees from 40 families in only one site were sampled using destructive and nondestructive samplings. For the destructive sampling, 40 larch trees (one tree per family) were felled from which 5 cm thick disks were systematically sampled from each tree at 0.5 and 1.3 m stem height and every 50 cm thereafter up to the top. Disks were air-dried with fans for several months to avoid decomposition until sample preparation and measurement. These disks were used to investigate the axial and the radial variation in anatomical traits such as wood density, ring width, and tracheid length and width. A nondestructive sampling was also conducted by taking wood increment cores at breast height from 40 families for a total of 320 trees (8 trees per family). The cores were then stored in a freezer until required for analysis. The wood cores were used to estimate the ring growth and wood density and their genetic parameters.

Measurement of tracheid properties

The 40 breast height disks were analyzed to measure the radial variation of tracheid length and width. Five trees were

randomly selected for the longitudinal variation to investigate the wood properties longitudinal variations (all disks for each tree were considered). Bark to bark (passing through the pith), 2 mm thick strips were sawn from each disk for fibre quality analysis. Thin longitudinal specimens were extracted from earlywood and latewood at systematic cambial ages (3, 6, 9, 12, 15, 20, and 25 growth rings). Specimens were then macerated using Franklin's (1945) method. Each specimen was placed in test tubes, immersed in Franklin's solution (hydrogen peroxide diluted to 30% and concentrated acetic acid), and kept in hot distilled water (85–90 °C) for 7–8 h for complete delignification. The obtained delignified fibres were shaken in water using a laboratory blender to obtain a fibre suspension. The Optest The Kajani FS-300 fibre Quality Analyzer (Metso Automation Ltd., Kajaani, Finland) measured the tracheid length and width at a precision of 0.01 mm and 1 µm, respectively (Robertson et al. 1999). For each sample, 1500–5000 fibres were analyzed.

Wood density and ring width measurement

Thin strips (1.57 mm thick) were sawn from each disk and each sampled increment core (bark to bark passing through the pith) to determine the wood density and growth attributes. The strips were then extracted using a cyclohexane/ethanol solution 2:1 (v:v) and distilled water for 24 h each to remove resinous substances and water-soluble carbohydrates, and then conditioned to an equilibrium moisture content.

Ring density and growth components were measured using a QTRS-01X Tree-Ring X-ray Scanner (Quintek Measurement System, Knoxville, Tennessee) with a linear resolution step size of 0.04 mm. The maximum moisture content method (Smith 1954) determined the mass attenuation coefficient (cm²/g) to calculate the density. Pith-to-bark rings were scanned in air-dry conditions with the precaution of eliminating incomplete, false, and compression wood rings or with branch traces (Bouslimi et al. 2019). The wood density profiles served to determine the ring (RD), earlywood (EWD), and latewood (LWD) densities, the ring (RW), earlywood (EWW), and latewood (LWW) widths. Using a six-degree polynomial, the maximum derivative method determined the earlywood-latewood transition density for each annual ring (Koubaa et al. 2002). The transition density (TD) is the density at the demarcation point on the polynomial curve. The ratio of LWW to RW gave the latewood proportion (LWP). During scanning, the last ring was removed because it was hard to distinguish it from the bark, and it was never assured that the wood formation of that year had been completed.

The pith-to-bark variation in wood traits is frequently described as juvenile and mature wood zones and is used to estimate the transition age (Koubaa et al. 2002; Bouslimi et al. 2019). The juvenile wood was determined based on the radial variation profile of tracheid length, which stabilized at cambial age 12. Considering the radial pattern of variation fibre length and that of other traits, the wood produced from the pith up to the 12th ring is considered to be juvenile, the wood produced from the 13th ring to the 19th ring is considered as a transition zone between juvenile wood and mature

wood, and the remaining wood as mature wood (Yang et al. 1986).

Statistical analysis and genetics parameters

Statistical analyses were performed on R statistical software (R Development Core Team 2022). Wood density, growth components, and tracheid morphology were subjected to variance analyses (Analysis of variance (ANOVA)) using a mixed model approach (*lmer* function from the *lme4* R-package), with cambial age as the repeated measure. The cambial age and stem height were considered as fixed effects, and the tree was considered as a random effect as follows:

$$(1) \quad Y_{ijk} = \mu + \alpha_i + \beta_j + \delta_l + (\alpha\beta)_{ij} + \varepsilon$$

where Y is the dependent variable, μ is the overall mean, α_i represents the stem height fixed effect, β_j is the cambial age fixed effect, δ_l is the tree random effect, $(\alpha\beta)_{ij}$ is the stem height and cambial age interaction between, and ε is the residual error.

Graphical techniques and the Jarque-Bera test were used to check for homoscedasticity and residual normality. All dependent data were normally distributed except for the growth component (ring width, earlywood width, latewood width, and latewood proportion). Therefore, a power transformation using the exponent of 0.75 on the latter was conducted to meet model assumptions.

Wood properties' means and standard deviations were computed for each pith-to-bark annual ring and then plotted against cambial age. The wood density and width mean were calculated for each selected cambial age (3, 6, 9, 12, and 15 years). Five systematic heights (0.5, 1.3, 5.3, 7.3, and 10.3 m) were retained for the analysis. Tukey's multiple range method compared Stem heights for cambial ages 3, 6, 9, 12, and 15 years. Differences were considered statistically significant at $P < 0.05$.

Pearson's correlation coefficients determined the relationship between juvenile and mature wood's different wood density components. Genetic parameters such as narrow-sense heritability (h^2), genotypic (r_A), and phenotypic (r_p) correlations for wood density and growth components were estimated using a mixed model approach as follows:

$$(2) \quad Y_{ijk} = \mu + F_i + \beta_j + \varepsilon_{ijk}$$

where Y_{ijk} was the performance of an individual tree k in the family i in block j , μ was the overall mean, F_i was the random effect of the family i with mean zero, and variance σ_i^2 , β_j was the random effect of the block j with mean zero and variance σ_j^2 , and ε_{ijk} was the random error with mean zero and variance σ_e^2 . The 40 families were considered half-siblings, and therefore, the following relationship was assumed to estimate the additive genetic variance:

$$(3) \quad \sigma_a = 3\sigma_f^2$$

Variance components were used to estimate narrow-sense heritability (h^2). The h^2 was calculated for each trait measured

for whole wood, juvenile, and mature as

$$(4) \quad h^2 = \frac{3\sigma_f^2}{\sigma_f^2 + \sigma_e^2}$$

where σ_f^2 and σ_e^2 are the family and error variance estimates, respectively; the genetic (eq. 5) and phenotypic (eq. 6) correlations were determined using a multivariate approach.

$$(5) \quad rG_{xy} = \frac{\text{Cov}_{g(x,y)}}{\sqrt{\sigma_{g_x}^2 \cdot \rho_{g_y}^2}}$$

$$(6) \quad rp_{xy} = \frac{\text{Cov}_{p(x,y)}}{\sqrt{\sigma_{p_x}^2 \cdot \rho_{p_y}^2}}$$

where x and y are the two traits of interest, $\sigma_{p_x}^2$, $\rho_{p_y}^2$, and $\sigma_{g_x}^2$, $\rho_{g_y}^2$ are the phenotypic or genetic variance components for the x or y traits, respectively. $\text{Cov}_{p(x,y)}$ and $\text{Cov}_{g(x,y)}$ are the phenotypic and genetic covariance, respectively. The Delta method (Lynch and Walsh 1998) was used to estimate the standard phenotypic and genetic correlations and heritability errors.

Results and discussion

Tamarack wood characteristics

Table 1 presents the mean and variation of wood density components, ring width, and tracheid length, and width between juvenile and mature wood at breast height in *Larix laricina* mature trees. The mean RD for 40 tamarack families was 515 kg/m³, which was higher than what was reported previously for tamarack juvenile wood (430 kg/m³) in northern Ontario (Yang and Hazenberg 1987) for *Larix kaempferi* (Lamb.) Carr. (Japanese larch) and *Larix decidua* (European larch) (317 and 427 kg/m³, respectively) (Cáceres et al. 2017). Wood strength, durability, and combustion energy depend on wood density (Zobel and Van Buijtenen 1989).

LWD was 52% higher than EWD. The difference was 417 kg/m³, which is high compared to that reported in *Picea mariana* (382–639 kg/m³) (Pamerleau-Couture et al. 2019) and *Pinus brutia* (388–619 kg/m³) (Guller et al. 2012); however, it is slightly lower than that reported in *Pseudotsuga menziesii* (313–882 kg/m³) (Rathgeber et al. 2006), *Pinus sylvestris* (325–939 kg/m³), *Picea abies* (L.) Karst. (351–1027 kg/m³), and *Abies alba* (287–861 kg/m³) (Decoux et al. 2004).

The difference between EWD and LWD (417 kg/m³) is mainly linked to the variations in earlywood (thin) and latewood (thick) cell wall structure and chemical composition (Yang and Hazenberg 1987). According to Cáceres et al. (2017), 30% of Japanese larch water extractives were inside the cell wall, and wood density correlated to the extractive mass.

The tamarack's durability and higher density, which lead to larger wood strength, make it suitable for outdoor applications like fence posts and decking. In addition, the demarcation between earlywood and latewood in the annual ring is abrupt, as seen by the difference in color between the light-color earlywood and dark-color latewood. This contrast between earlywood and latewood confers a very aesthetic appearance, making it ideal for interior applications where

Table 1. Means and coefficients of variation (in parentheses (%)) in ring width, ring density components, and tracheid morphological properties for the whole tree, juvenile wood (rings 2–12), transition zone from juvenile to mature wood (rings 13–19), and mature wood (rings 20–27) at breast height in *Larix laricina* trees.

Ring density components (kg/m ³)				
Tree part	Ring density	Earlywood density	Latewood density	Transition density
Whole tree	515 (13)	392 (12)	809 (14)	670 (14)
Juvenile wood	488 (11)	406 (11)	772 (14)	666 (14)
Transition zone	530 (13)	380 (11)	848 (13)	688 (15)
Mature wood	557 (13)	373 (13)	841 (12)	652 (15)
Ring width (mm)				
Tree part	Ring width	Earlywood width	Latewood width	Latewood proportion
Whole tree	2.9 (58.9)	2.18 (68)	0.71 (47.8)	29.31 (43)
Juvenile wood	4.14 (34.1)	3.27 (38.6)	0.87 (37.1)	22.45 (38.5)
Transition zone	1.91 (49.5)	1.32 (57.2)	0.59 (51)	32.99 (32.6)
Mature wood	1.31 (50.1)	0.81 (61.4)	0.5 (46.7)	33.10 (32.1)
Earlywood (EW) and latewood (LW) tracheid properties				
Tree part	Length (EW) (mm)	Width (EW) (μm)	Length (LW) (mm)	Width (LW) (μm)
Whole tree	2.23 (23.5)	25.5 (10.5)	2.55 (22.9)	24.6 (9.7)
Juvenile wood	1.80 (19.2)	24.0 (12.0)	2.10 (22.2)	23.3 (9.8)
Transition zone	2.54 (11.6)	25.7 (7.8)	2.81 (12)	26.1 (6.6)
Mature wood	2.88 (9.6)	26.6 (7.6)	3.19 (7.5)	27.0 (5.7)

aesthetics is a high priority, such as visible roof structures, ceilings, walls, doors, staircases, floors, and furniture. According to Bergstedt and Lyck (2007), despite the larger contrast between earlywood and latewood, larch can, without serious problems, be worked on with all manual and mechanical tools. Dry wood is relatively easy to work with and gives a nice and clean finish if the wood is not characterized by strong spiral grain, severe knots, and wide annual rings.

The variation difference in average RD between juvenile and mature wood was low (Table 1). The difference was only 69 kg/m³, which is low compared to other species like *Pinus sylvestris* L. (161 kg/m³) and *Picea abies* (105 kg/m³) (Gryc et al. 2011), but higher than that of *Picea mariana* (3.8–17.5 kg/m³) (Alteyrac et al. 2005). Also, the LWP varies from juvenile (22.5%) to mature wood (33%), accounting for over 29% of the wood (Table 1).

Larch growth is characterized by fast development in the juvenile stage, faster than most conifers, and by an early culmination of growth at 15–25 years old (Bergstedt and Lyck 2007). The fast vegetative growth in the juvenile phase makes larch suitable for shelterwood establishment and as a supplement tree in natural regenerations or stands with severe losses (Bergstedt and Lyck 2007). The results from this study align with the previous statement. The average RW for tamarack was 2.9 mm (Table 1), with a considerable variation between juvenile (4.14 mm) and mature wood (1.31 mm).

Tamarack tracheids are long and fine (Table 1), with an average length and width of 2.23 mm and 25.5 μm in earlywood and 2.55 mm and 24.6 μm in latewood (Table 1). These values are higher in mature wood compared to juvenile wood. Tracheid width showed a small and homogenous across-tree variation (CV = 10%) compared to tracheid length (CV = 23%).

The variation between trees in mature wood was less important and homogenous, mainly for tracheid length (9%), as CV is smaller than 15%. Latewood tracheids were slightly longer than earlywood tracheids, which is similar to the previous finding for other species like *L. kaempferi* (Yoshizawa et al. 1987) and *Pinus taeda* (Dahlen et al. 2021).

As for the radial variation from juvenile to mature wood, both tracheid length and width for EW and LW increased from pith to bark, and this finding was similar to the results obtained for different species of larch (*Larix* sp.) (Fujimoto et al. 2008; Tumenjargal et al. 2020; Kim et al. 2022; Takahashi et al. 2023) and other species like *Picea glauca* (Mvolo et al. 2015), *Pinus patula* (Kamala and Missanjo 2017), *Thuja occidentalis* (Bouslimi et al. 2019), and *Pinus kesiya* (Gogoi et al. 2019).

Radial variation in ring density, ring width, and tracheid morphological properties

Figures 1 and 2 show the radial variation in ring density and width components for the 40 tamarack trees. Figure 3 shows the radial variation in tracheid length and width. The pith-to-bark variation in studied wood traits showed a gradual transition from juvenile to mature wood in tamarack. The juvenile wood RD increased rapidly from the pith to the 8th ring (Fig. 1a) and remained almost constant in the juvenile–mature wood transition zone (at about age 19). In mature wood, RD increased slightly and fluctuated after that. This pattern appears to be comparable to that of *Pinus brutia* (Guller et al. 2012), *Larix sibirica*, *Larix decidua*, *Pinus. Sylvestris* (Karlman et al. 2005), and *Picea abies* (Makinen and Hynynen 2014). The standard deviation for RD was narrower near the pith but increased slightly in mature wood, indicating more

Fig. 1. Radial variation and standard deviation of (a) annual ring density, (b) earlywood density, (c) latewood density, and (d) transition density with cambial age (from the pith) at breast height in *Larix laricina* trees.

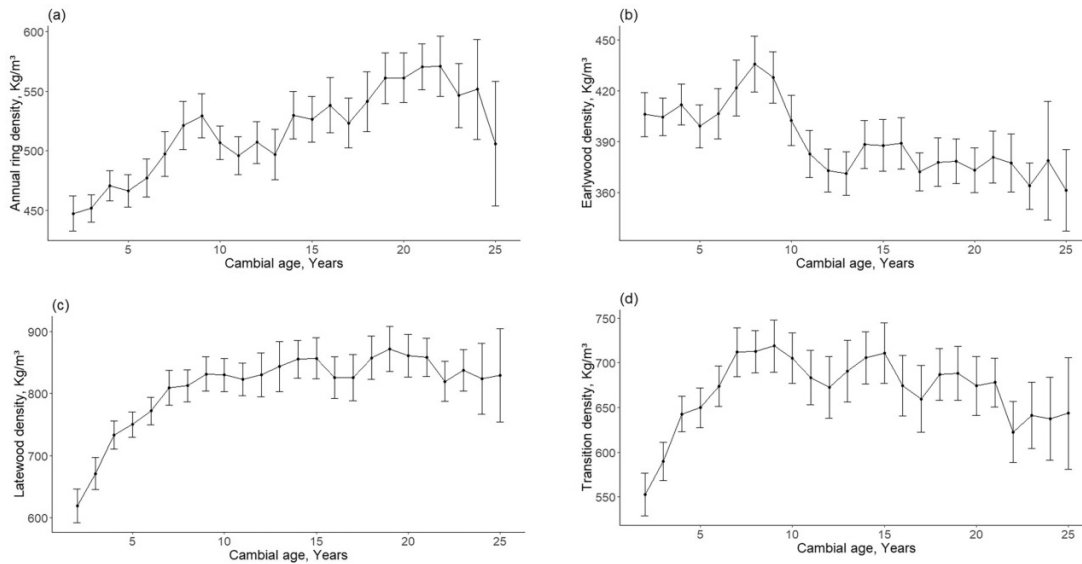


Fig. 2. Radial variation and standard deviation for (a) annual ring width, (b) earlywood width, latewood width, and (c) latewood proportion related to cambial age (from the pith) at breast height in *Larix laricina* trees.

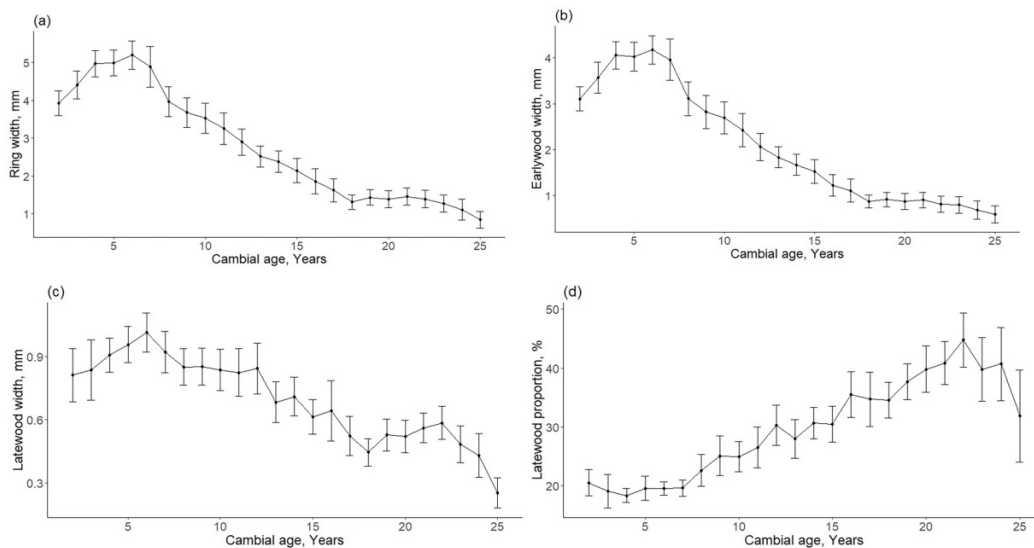
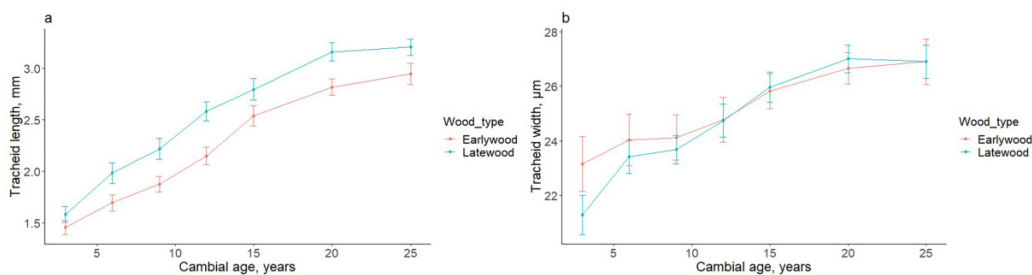


Fig. 3. Radial variation and standard deviation for (a) fiber length and (b) fiber width with cambial age (from the pith) at breast height in *Larix laricina*.



uniformity between trees in the juvenile phase, as reported with *P. brutia* (Guller et al. 2012). The between-tree variation was greater in mature wood (Fig. 1a).

The radial variation of LWD and TD showed the same pattern, increasing from a minimum near the pith to a maximum in the transition zone to mature wood and remaining relatively constant thereafter (Figs. 1c and 1d). In contrast, EWD showed a different radial pattern (Fig. 1b). EWD was constant near the pith, increased rapidly afterward to reach a maximum at the 8th ring, decreased thereafter in the juvenile–mature wood transition zone, and remained constant in mature wood. LWP also plays a major role since it increases from pith to bark (Fig. 2b).

RW increased from the pith to reach a maximum at the 6th ring (5.2 mm) rapidly and then decreased to a minimum (1.5 mm) at the 18th ring, remaining constant in mature wood (Fig. 2a). In contrast to RD, the standard deviation for RW is very high, indicating large tree-to-tree variation. The between-trees variation is more important in mature wood (50.1%) compared to juvenile (CV = 34.1%) wood (Table 1). The RW variation pattern appears to be similar to that reported for *Pinus radiata* (Adamopoulos et al. 2009; Lasserre et al. 2009), *Picea glauca* (Mvolo et al. 2019), and *Larix kaempferi* (Fukatsu and Nakada 2018). According to Bergstedt and Lyck (2007), larch growth is characterized by rapid juvenile development, faster than most conifers, and an early culmination of growth at 15–25 years old. The variation in annual RW between years might be linked to climate-related variations (Vannoppen et al. 2019) and depend on the responses of cambium phenology to many environmental and physiological factors (Rathgeber et al. 2011). According to Larson et al. (2001), crown size's relationship to the stem's length explains the within- and between-tree RW variation.

EWW showed a similar radial pattern of variation to RW, increasing in the first 8 years and decreasing rapidly to the bark (Fig. 2b). On the other hand, LWW showed almost the same pattern, as it increased near the pith and then decreased toward the bark fluctuating (Fig. 2c). The between-tree variation was greater in earlywood (CV = 68%) than in latewood (CV = 47.8%). In contrast, LWP showed a completely different radial pattern (Fig. 2d): low and almost constant (20%) near the pith up to the 6th ring and increasing thereafter to reach a maximum at the 22nd ring (40%) and decreased outer. The high standard deviation indicates a larger tree-to-tree variation (CV = 43%).

The radial variation in tracheid length for both earlywood and latewood showed a rapid increase in the first 20 years, then stabilizing in the later years, reaching 2.9 mm for EW and 3.4 mm for LW (Fig. 3). The tracheid length in the LW was higher than that of EW, and the difference increased slightly toward the bark. This pattern is observed for most of the softwoods species (Mäkinen et al. 2008; Sadegh and Kiaei 2011; Bouslimi et al. 2019; Dahlen et al. 2021). However, the age up to which tracheid length stabilizes appears to vary between species (Cai et al. 2022).

As for the radial variation for tracheid width, earlywood and latewood showed a rapid increase from pith to bark, then stabilizing somewhat in the later years, reaching a width of 27 μm . No noticeable difference between EW and LW was ob-

served except in the juvenile wood zone until the age of 12 years, where EW was slightly wider than LW. The standard errors were relatively high in the juvenile region, indicating a variation between trees, probably due to the four types of growth profiles of trees used in this study.

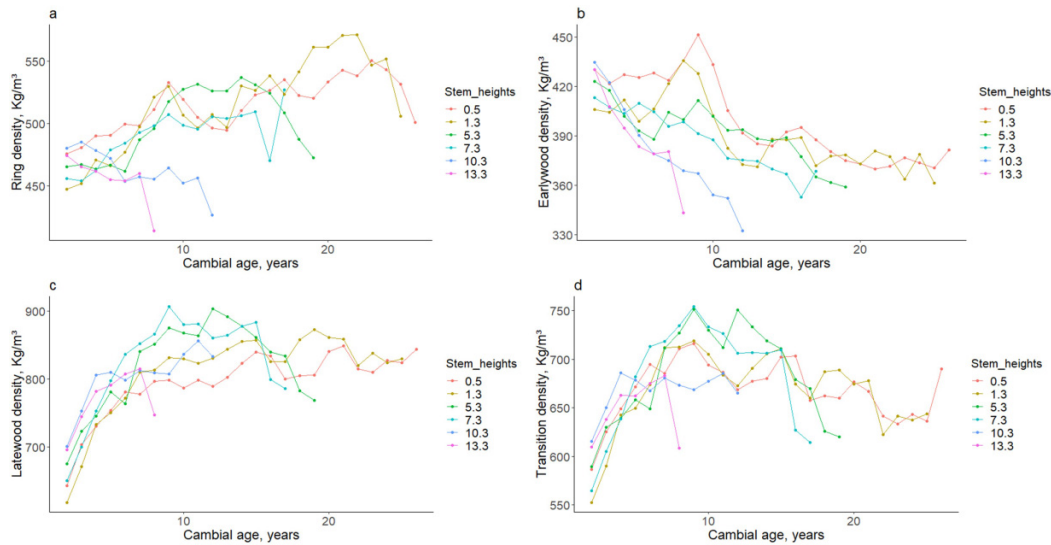
The radial variation of LWD and LWP can explain the radial ring density variation. For each annual ring, in tamarack, the gap between EWD and LWD was too high that LWD masked to some extent EWD, and the effect of LWD became more and more visible as the tree aged since LWP increased to the bark, accounting for 40%. The pattern of variation in EWD in the juvenile phase was similar to that for RD. LWD was significantly higher than EWD, indicating that a slow increase in the LWP within an annual ring directly affects RD. The major reason why density varies within the annual ring is due to the anatomical difference between EW and LW, where EW is characterized by a thin cell wall and a large lumen, thus low density; in contrast, LW is characterized by a thick cell wall and a small lumen, and hence high density (Sousa et al. 2021).

The radial variation of RW was the opposite of that for RD, and wider rings were associated with the lowest density and vice versa. This pattern is well known for most conifer species (Baltunis et al. 2007; Jyske et al. 2008; Bouslimi et al. 2019; Mvolo et al. 2019). Therefore, a slight increase in tree growth or ring width could negatively impact RD, which means that RD is the outcome of EW and LW percentage in each ring. The radial pattern of EWW was identical to RW, which is normal since EW represents two-thirds of the ring, explaining the majority of RW variation. Tracheids in the EW zone explain the low density in the juvenile zone and have a thin cell wall (Missanjo and Matsumura 2016). A negative relationship between RD and RW is found in juvenile wood when a great portion of the ring is made of EW. However, when spring drought suppresses EW formation, the late rainfall promotes the development of thick-walled latewood cells, and density is likely to exhibit a positive relationship with ring width. These results agree with what previous studies have reported for other conifers like *Pinus massoniana* (Cai et al. 2022), *Picea sitchensis* (Donnelly et al. 2017), *Pinus radiata* (Lasserre et al. 2009), and *Thuja occidentalis* (Bouslimi et al. 2019).

Variation in both RD and RW could be explained by other factors, such as competition among trees (Zhang et al. 2006; Lasserre et al. 2009; Sousa et al. 2021) and climatic and ecological conditions (Vega et al. 2021). The space a tree takes up is an extremely important factor that determines the growth rate and, therefore, the performance of the wood. The extent of surrounding vegetation and the spacing between trees determines the competition for key growth elements such as water, nutrients, and sunlight, which affects their development. The growth rate is a factor that affects wood quality. Indeed, a high growth rate means an increase in the RW, a high proportion of EW, and consequently, a low density.

The relationships between tracheid length and RW have been studied previously, and the results are contradictory for conifers. For example, Bannan (1963) showed that the maximum tracheid length is associated with a ring width of 1 mm and that tracheid length decreased in both wide and narrow rings. However, this was not the case for tamarack,

Fig. 4. The longitudinal variation in (a) annual ring density, (b) earlywood density, (c) latewood density, and (d) maximum density with cambial age at five selected heights along the stem of *Larix laricina* trees.



as tracheid length and diameter increased from the pith to the bark, and their pattern seemed independent of that of RW (Figs. 2 and 3). Still, these findings agree with a previous study on *Picea glauca* (Mvolo et al. 2019) and *Pinus kesiya* (Missanjo and Matsumura 2016). However, LW tracheids are longer within a growth ring than EW tracheids (Fig. 3). Reported values for tracheid lengths within and among conifer trees are extremely variable. Because of how cambial cells divide and the new wood cells elongate, the new population of EW and LW tracheids produced varies widely in length and width. With EW tracheids devoted to conduction, they are characterized by a large lumen and thin cell walls, and LW tracheids serve for mechanical strength; this is why they are longer than EW tracheids and have thicker cell walls (Mvolo et al. 2019). It is difficult to clearly understand the relationship between EW and LW tracheid dimensions and growth traits. Although both tracheid length and width might be used to differentiate EW from LW, they vary greatly during growth ring formation. That is, radial tracheid diameters are under the control of entirely different physiological processes (Larson 1969). Therefore, environmental or silvicultural practices might not affect the tracheid dimension. However, the EW/LW ratio and wood density values would change significantly.

Longitudinal variations in ring density, ring width, and tracheid length and width

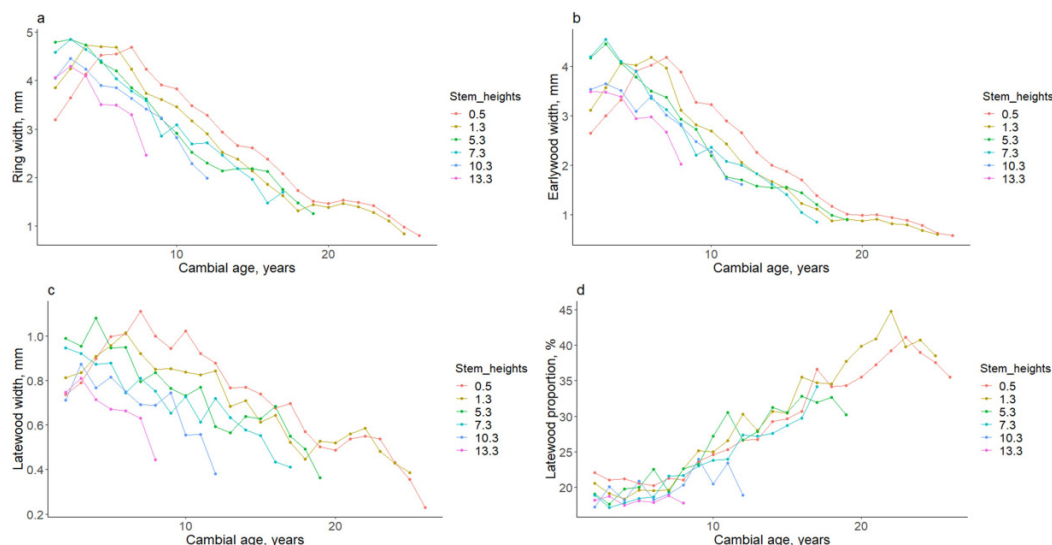
Longitudinal variation was always considered marginal and not as important as the effect of cambial age. Indeed, in most cases, tree height had no significant effect on wood properties (Park et al. 2009). A clear tree-high effect for tamarack was observed only for growth components, RD and EWD in juvenile wood. However, in mature wood, tree height had almost no effect on all wood properties (Supplementary Table S2). The tree effect was highly significant for all wood prop-

erties, which means that there is sufficient variation among trees to justify family selection to improve wood's physical properties. Average ring width and density component variations with stem height are presented in the supplementary Table S1. Averages for all density components generally decrease upward from the tree base. For instance, the average RD decreased from 514 kg/m³ at 0.5 m stem height to 447 kg/m³ at 14.8 m stem height (Supplementary Table S1). In contrast, the average ring width and EWW showed a slight increase from the base to the top of the tree, while LWW remained constant, which decreased LWP from the tree base upward. The variation in the average ring width component with stem height is higher than in ring density components. These results agree with previous findings for *Picea mariana* (Alteyrac et al. 2005), *Pinus banksiana* (Park et al. 2009), and *Thuja occidentalis* (Bouslimi et al. 2019).

Furthermore, the *F* values for stem height in juvenile wood (JW) were higher than those for mature wood (MW) and in the transition zone for almost all properties (Supplementary Tables S3, S4, and S5). These results indicate that the magnitude of the longitudinal variation depends on the wood type, in good agreement with previous findings for *Pinus banksiana* (Park et al. 2009) and *Picea mariana* (Alteyrac et al. 2005). The axial variation of wood properties is linked to many other variables, such as cambial age and RW. In our study, cambial age significantly affected all wood properties. However, based on the *F* values, the variation in juvenile wood was higher than that in mature wood and the transition zone. The high variability of juvenile wood properties explains this finding. Juvenile wood is characterized by a wide variation in chemical, physical, and anatomical properties (So et al. 2018).

The longitudinal variation was minimal near the pith for RD, EWD, LWD, and TD (Fig. 4). This variation increased, moving away from the pith (beyond ring 10) toward the bark. RD and EWD decreased rapidly with increasing tree height (Figs. 4a and 4b). However, LWD and TD show completely different

Fig. 5. The longitudinal variation in (a) annual ring width, (b) earlywood width, (c) latewood width, and (d) latewood proportion with cambial age at five heights along the stem of *Larix laricina*.



patterns; in the transition area from JW to MW (ring 12–19), LWD and TD increase until they reach a maximum at mid-height (around 880 kg/m³ for LWD and 740 kg/m³ for TD), then they decrease upwards (Figs. 4c and 4d). Beyond the cambial age of 15, LWD and TD followed the same pattern as RD and EWD, rapidly decreasing from the base to the top of the tree. These longitudinal patterns of variation are similar to those reported for *Pinus banksiana* (Park et al. 2009) and *Thuja occidentalis* (Bouslimi et al. 2019).

The overall longitudinal variation pattern for the growth component was clear, as they decreased steadily with tree height (Fig. 5). However, at a certain cambial age, growth component longitudinal variations were different depending on the wood zone (juvenile or mature). The variation for the growth component was minimal near the pith. However, in the first six rings, RW, EWW, and LWW increased slightly to the mid-height of the tree and then decreased afterward. But after cambial age 6, RW, EWW, and LWW decreased steadily from the tree base upward. These patterns indicate that at the same cambial age, the cambium will produce narrower rings at the base and the top of the tree in the first years and wider rings at the tree's base in later years. For example, at cambial age 3, RW increased by 45% from 0.5 to 7.3 m in height, then decreased by 22% from 7.3 to 13.3 m. In contrast, at cambial age 9, RW decreased significantly from 0.5 to 7.3 m in height by 31% (Table 2). The pattern of the annual variation in the RW at different stem heights and with cambial age explains the highly significant effect of the interaction between stem height and cambial age on RW.

All growth components showed the same pattern of variation (Fig. 5). Although, based on the *F* values (Supplementary Tables S2, S3, S4, and S5). *F* values for EWW and RW were close in all wood zones, which explains the high correlation between them. The *F* value for LWW was higher than those for RW and EWW, which indicates the high magnitude of the

longitudinal variation for this wood trait. LWP decreased with tree height from age 2 to 9, and the longitudinal variation was not significant. However, at 10.3 m stem height, LWP significantly differed from other stem heights (Table 2). This result could explain the low significant effect of the interaction between stem height and cambial age on LWP.

Figure 6 shows the variation in EW and LW tracheid length and width along selected stem heights with cambial age. All traits increased somewhat with stem height. However, the variation pattern was rather similar. In the juvenile zone, EW and LW tracheid length increased, but in a fluctuating manner, and in the mature zone, tracheid length increased steadily. The longitudinal variation for EW and LW tracheid width was minimal near the pith (JW) and near the bark (MW), which explains the non-significant effect of stem height on tracheid width in the juvenile and mature zones (Supplementary Table S2). Yet, in the transition zone, the ANOVA showed that stem height significantly affected the tracheid width. The longitudinal variation in wood properties has been the objective of many previous studies, and the main conclusion was that the crown location is the key to understanding these variations (Mvolo et al. 2015).

Phenotypic correlations between wood properties

The correlation coefficients between wood density and growth traits in juvenile and mature wood are presented in Table 3. Positive and significant correlations between RD, EWD, and LWD were found for juvenile and mature wood. However, these correlations were slightly higher in juvenile wood. The correlation between RD and EWD ($r_p = 0.61$ to $r_p = 0.71$) was slightly higher than that of RD and LWD ($r_p = 0.49$ to $r_p = 0.53$), probably because EW represented a large portion of the ring. A significant positive relationship was found between EWD and LWD ($r_p = 0.13$ to $r_p = 0.26$).

Table 2. Longitudinal variations in wood density properties at selected cambial age.

Stem height*	Means of ring density components						Means of ring width components					
	0.5	1.3	5.3	7.3	10.3	13.3	0.5	1.3	5.3	7.3	10.3	13.3
Cambial age*	Annual ring density (kg/m ³)						Annual ring width (mm)					
3	480a	452a	467ab	454ab	485b	466b	3.78a	4.41b	5.41c	5.48c	4.51b	4.27ab
6	499c	477abc	461ab	484bc	454a	455ab	5.01 cd	5.19d	4.46bc	4.1ab	4.14ab	3.54a
9	533c	529c	517bc	507bc	465a	412ab	4.18c	3.68bc	3.51abc	2.85a	3.15ab	1.97ab
12	496b	507b	526b	505b	430a		3.51d	2.9c	2.31ab	2.72bc	1.9a	
15	523a	527a	531a	509a			2.56b	2.14a	2.2a	1.81a		
Cambial age*	Earlywood density (kg/m ³)						Earlywood width (mm)					
	0.5	1.3	5.3	7.3	10.3	13.3	0.5	1.3	5.3	7.3	10.3	13.3
3	422a	404a	418a	407a	423a	409a	2.98a	3.57ab	4.46c	4.55c	3.64b	3.46ab
6	428c	406bc	388ab	405abc	379a	379ab	4bc	4.18c	3.51ab	3.35a	3.39a	2.86a
9	452d	428 cd	412bc	391ab	367a	341abc	3.24c	2.82bc	2.74abc	2.2a	2.42ab	1.68ab
12	392b	373b	394b	375b	333b		2.64b	2.06a	1.72a	2a	1.5a	
15	392a	388a	389a	367a			1.84b	1.53a	1.57ab	1.29a		
Cambial age*	Latewood density (kg/m ³)						Latewood width (mm)					
	0.5	1.3	5.3	7.3	10.3	13.3	0.5	1.3	5.3	7.3	10.3	13.3
3	702ab	670a	723bc	700ab	753c	741bc	0.79a	0.83a	0.95a	0.92a	0.87a	0.82a
6	781a	772a	764a	836ab	799ab	806ab	1b	1.05b	0.94b	0.74a	0.74a	0.67a
9	798a	832ab	875bc	907c	808a	737abc	0.93c	0.85bc	0.76abc	0.65a	0.73ab	0.31ab
12	789a	830ab	903c	860bc	834abc		0.87c	0.84c	0.59ab	0.72bc	0.38a	
15	840a	857a	861a				0.73b	0.61ab	0.63ab	0.53a		
Cambial age*	Transition density (kg/m ³)						Latewood proportion (%)					
	0.5	1.3	5.3	7.3	10.3	13.3	0.5	1.3	5.3	7.3	10.3	13.3
3	643abc	589a	629bc	605ab	650c	635bc	21.1a	19.1a	17.6a	17.2a	20.1a	18.3a
6	694ab	674ab	649a	713b	667ab	675ab	20.2a	19.5a	22.6a	18.7a	18.3a	17.9a
9	716ab	719ab	751b	754b	669a	615ab	23.6a	24.1a	23.2a	23a	24a	18.5a
12	668a	673a	751b	705ab	664a		26.7b	30.3b	26.6b	27.4b	19.6a	
15	702a	711a	711a	709a			29.6a	30.5a	30.5a	29a		

*Multiple comparison tests of different stem heights for each selected cambial age were performed with Tukey–Kramer adjustment. Averages followed by the same letter indicate no significant difference between stem heights.

Fig. 6. Variation in earlywood tracheid length (a), latewood tracheid length (b), earlywood tracheid width (c), and latewood tracheid width (d) at five selected stem heights in *Larix laricina*.

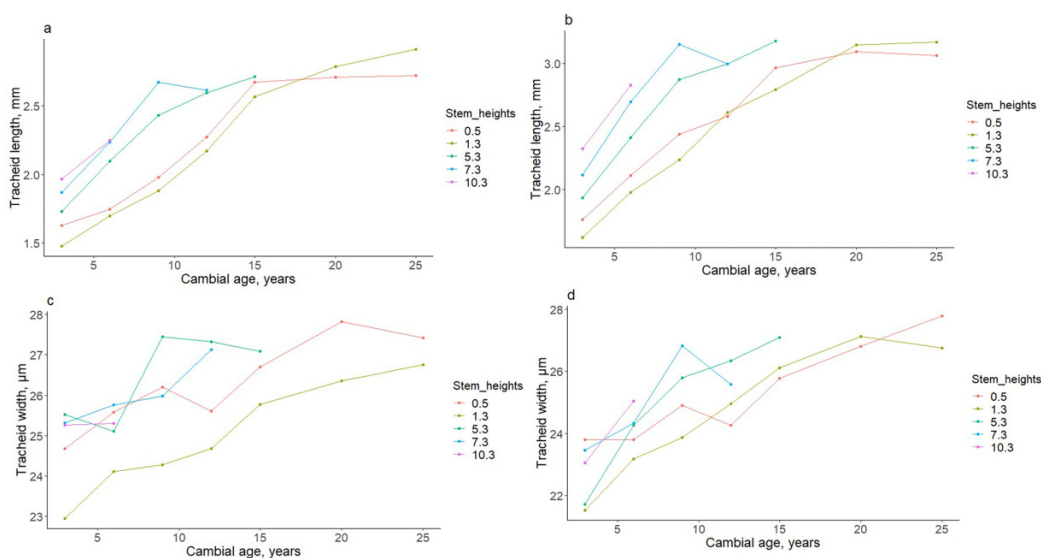


Table 3. Phenotypic correlation coefficients (standard errors in brackets) between the different traits for the juvenile (below the diagonal) and mature (above the diagonal) wood in *Larix laricina*.

Traits*	RD	EWD	LWD	RW	EW	LWW	LWP
RD	1	0.61 (0.02)	0.49 (0.02)	−0.03	−0.31 (0.03)	0.22 (0.03)	0.67 (0.02)
EWD	0.71 (0.01)	1	0.26 (0.03)	−0.19 (0.03)	−(0.03)	−0.14 (0.03)	0.18 (0.03)
LWD	0.53 (0.01)	0.13 (0.01)	1	0.14 (0.03)	0.19 (0.03)	0.01 (0.03)	−.020 (0.03)
RW	−0.14 (0.01)	0.30 (0.009)	−0.32 (0.01)	1	0.97 (0.01)	0.80 (0.01)	−0.24 (0.03)
EW	−0.19 (0.01)	0.29 (0.01)	−0.23 (0.01)	0.96 (0.00)	1	0.59 (0.02)	−0.48 (0.02)
LWW	0.09 (0.01)	0.13 (0.01)	−0.41 (0.01)	0.52 (0.01)	0.27 (0.01)	1	0.33 (0.03)
LWP	0.32 (0.01)	−0.09 (0.01)	−0.18 (0.01)	−0.29 (0.01)	−0.52 (0.01)	0.59 (0.01)	1

*Traits: RD: ring density; EWD: earlywood density; LWD: latewood density; RW: ring width; EW: earlywood width; LWW: latewood width; LWP: latewood proportion.

Similar results were found for *Picea glauca* (Mvolo et al. 2015), *T. Occidentalis* (Bouslimi et al. 2019), *Picea mariana* (Koubaa et al. 2000), *Pinus pinaster* (Gaspar et al. 2008), and *Abies balsamea* (Koga and Zhang 2002).

In juvenile wood, the correlations between RD, EWD, and LWD were higher than the correlation between density component and LWP, which means that EWD and LWD more predict RD than LWP. However, this relationship is somewhat reversed in mature wood because LWP increased. Our results showed that EWD had the strongest impact on RD, followed by LWD in JW. In MW, the LWP had the highest impact on RD, followed by the LWD.

RD was negatively correlated with RW and EWW and positively correlated with LWW for both juvenile and mature wood due to the large difference between EWD and LWD, which implies that the slight increase in LWW is sufficient to increase RD. The same observation was found in *Picea mariana* (Koubaa et al. 2000) and *Pinus pinaster* (Gaspar et al. 2008). EWD was positively correlated with growth traits in juvenile wood and negative in mature wood, which is explained by the high variability in juvenile wood, as indicated by the higher *F* values for the effect of age on RD, EWD, and LWD in juvenile wood (Supplementary Table S3). These results contradict, to some extent, previous findings for *Abies balsamea* (Koga and Zhang 2002, 2004), *Picea glauca* (Mvolo et al. 2015), *Picea mariana* (Koubaa et al. 2000), *Picea mariana* (Gerendia et al. 2007), and *Pinus pinaster* (Louzada 2003). For these mentioned species, EWD was negatively correlated with RD but positively correlated with LWD. LWD was negatively correlated with growth traits in JW. These relationships reversed in mature wood but remained very weak. The difference between JW and MW can explain this pattern. At the macroscopic level, rings are large with a small proportion of latewood. At the microscopic level, the difference lies in the latewood of JW and MW cells. In JW, cells are formed by thin-walled tracheids with a large lumen (Gryc et al. 2011). Based on these two factors, the correlation between LWD and growth traits in both JW and MW makes sense. To sum up, growth traits had a negative impact on wood density components in JW except for EWD, and the effect of radial growth on wood density decreases when the wood reaches maturity.

LWP was negatively correlated with RW in both juvenile ($r_p = -0.29$) and mature wood ($r_p = -0.24$), and a similar pattern

was observed for EWW ($r_p = -0.52$). In contrast, LWP was positively correlated with LWW in both juvenile ($r_p = 0.59$) and mature wood ($r_p = 0.33$). Correlations between growth traits were all positive and significant. As expected, a strong correlation between RW and EWW was found ($r_p = 0.96$ to $r_p = 0.97$) because RW and EWW increased from pith to bark as LWW decreased vaguely. Our results agree with previous studies on *Abies balsamea*, *Picea mariana*, and *Thuja occidentalis* (Koubaa et al. 2005; Bouslimi et al. 2019).

Tracheid length and width strongly correlated with EW and LW (Table 4). However, tracheid length and width correlated negatively with all growth components. Many previous studies investigated the relationship between tracheid morphologies and radial growth rate, and most found a negative relationship or none at all (Herman et al. 1998). Although reports are contradictory for the relationships between tracheid length and ring width in conifers, most wood scientists agree that fibre length increases with decreasing ring width along the radial axis (Mitchell and Denne 1997). For example, Gogoi et al. (2019) and Fabisiak and Fabisiak (2021) reported negative relationships between tracheid length and ring width in *Pinus kesiya* and *Pinus sylvestris* L., respectively. Similar results have been reported for *Thuja occidentalis* (Bouslimi et al. 2019) and black spruce (Bannan 1963). In contrast, Soro et al. (2023) found a positive relationship between tracheid length and ring width for white spruce (*Picea glauca*) in severe drought conditions. Diaz Váz et al. (1975) also reported a positive correlation between these traits for two softwoods.

Few investigations studied the relationship between tracheid morphology and wood density. In this study, tracheid length and width were positively and moderately correlated with RD and LWD but negatively correlated with EWD. The positive correlation between RD and tracheid length agrees with the findings of Fabisiak and Fabisiak (2021) and Dutilleul et al. (1998) for *Pinus sylvestris* and *Picea Abies*, respectively.

Genetic correlations between wood traits

The genetic correlations were generally stronger than phenotypic correlations (Table 5). The wood density components were strongly correlated with the overall ring density and were weakly correlated among themselves. For example, the mature wood showed a highly positive genetic correlation

Table 4. Phenotypic correlation coefficients between tracheid morphologies, density, and growth components (standard errors in brackets).

Traits*	ETL	ETW	LTL	LTW
ETL	–	–	–	–
ETW	0.46 (0.03)	–	–	–
LTL	0.91 (0.01)	0.50 (0.03)	–	–
LTW	0.67 (0.02)	0.66 (0.02)	0.76 (0.02)	–
RD	0.38 (0.03)	0.18 (0.03)	0.34 (0.03)	0.30 (0.03)
EWD	–0.28 (0.03)	–0.13 (0.03)	–0.32 (0.03)	–0.26 (0.03)
LWD	0.42 (0.03)	0.26 (0.03)	0.44 (0.03)	0.37 (0.03)
RW	–0.70 (0.02)	–0.26 (0.03)	–0.68 (0.02)	–0.48 (0.03)
EWV	–0.70 (0.02)	–0.27 (0.03)	–0.68 (0.02)	–0.50 (0.03)
LWW	–0.43 (0.03)	–0.10 (0.03)	–0.39 (0.03)	–0.21 (0.03)

*Traits: ETL: earlywood tracheid length; ETW: earlywood tracheid width; LTL: latewood tracheid length; LTW: latewood tracheid width; RD: ring density; EWD: earlywood density; LWD: latewood density; RW: ring width; EWW: earlywood width; LWW: latewood width. (–) correlations that could not be estimated.

Table 5. Genetic correlation coefficients (standard errors in brackets) between the different traits for the juvenile (below the diagonal) and mature wood (above the diagonal).

Traits*	RD	EWD	LWD	MaxD	MinD	RW	EWV	LWW	LWP	TransD
RD	–	–	0.92 (0.0006)	0.97 (0.0006)	–	–0.16 (0.001)	–0.36 (0.001)	–0.07 (0.001)	0.34 (0.001)	0.95 (0.0007)
EWD	1 (0.0005)	–	–	–	–	–0.16 (0.0005)	–0.13 (0.0005)	–0.24 (0.0005)	–	–
LWD	0.47 (0.00)	0.03 (0.00)	–	0.99 (0.00)	–	–0.51 (0.00)	–0.96 (0.001)	–0.36 (0.001)	–0.27 (0.001)	0.98 (0.0006)
MaxD	0.31 (0.0003)	0.15 (0.0003)	0.89 (0.0002)	–	–	–0.48 (0.001)	–0.93 (0.001)	–0.32 (0.001)	–0.16 (0.001)	0.98 (0.0006)
MinD	0.93 (0.0006)	0.88 (0.0005)	0.68 (0.0004)	0.67 (0.0004)	–	–	–	–	–	–
LWP	–	–	0.78 (0.0004)	0.36 (0.0004)	–	–	–	–	–	–

*Traits: RD: ring density; EWD: earlywood density; LWD: latewood density; MaxD: maximum density; MinD: minimum density; RW: ring width; EWW: earlywood width; LWW: latewood width; LWP: latewood proportion; TransD: transition density. (–) correlations that could not be estimated.

between LWD and RD ($r_A = 0.92$). Similar results were found for *Pinus pinaster* (Gaspar et al. 2008) and *Picea abies* (Hylén 1997). Unfortunately, due to the small sample size, genetic correlations between density and growth components were unavailable in juvenile wood. However, in mature wood, the ring growth component traits were negatively correlated with the density components, except for LWP, which was positively correlated with RD. Phenotypic and genetic correlations were close, as it has been shown that phenotypic correlations are often assumed to reflect genetic correlations (Louzada 2003).

Heritability values

Narrow-sense heritability values and standard error (in parentheses) for each juvenile and mature wood trait were estimated (Table 6). The narrow-sense heritability varies strongly between juvenile wood, mature wood, and in the transition zone JW/MW, and is lower in juvenile wood than in other zones. However, whole-tree heritability estimates for RD indicate that RD is under moderate genetic control ($h^2 = 0.18$), which is lower than values found for other species, such as *Picea glauca* and *Picea Abies* ($h^2 = 0.47$) (Hylén 1997; Lenz et al. 2010; Lamara et al. 2016). The heritability value for LWD ($h^2 = 0.37$) was higher than that of EW ($h^2 = 0.05$). These results contradict those for *Picea glauca* (Lenz et al. 2010;

Lamara et al. 2016) and *Pinus pinaster* (Gaspar et al. 2008) but agree with *Picea abies* (Hylén 1997). Ring width and other growth traits were less heritable; this is further evidence that the environment more strongly influences growth traits (Zamudio et al. 2005; Lenz et al. 2010; Lamara et al. 2016). However, the growth components in mature wood were under weak to moderate genetic control. The wood trait with the greatest change in heritability value was LWD, which increased from $h^2 = 0.02$ in juvenile wood to $h^2 = 0.39$ in mature wood. Similar results were found for other conifers (Zamudio et al. 2005; Gaspar et al. 2008; Ukrainetz et al. 2008; Hassegawa et al. 2020). Heritability of LWP appeared to increase from juvenile wood $h^2 = 0.09$ to $h^2 = 0.21$ in the transition wood and then decreased to $h^2 = 0.03$ in mature wood; these results contradict those found by Zamudio et al. (2005) for *Pinus radiata*, as they found almost no genetic effect on LWP ($h^2 \leq 0.15$) before ring 12 and a moderate genetic effect in later rings ($h^2 > 0.25$).

Based on the heritability values, our results suggest that any selection effort to obtain higher wood density will have a more direct impact on LWD than EWD. LWD showed higher heritability in the mature wood region and after ring 12. Good genetic gains would be expected when selection is based on mature wood (age 12 years or older), but additional analyses are needed to define the point of maximum selection efficiency.

Table 6. Narrow-sense heritability values for different wood properties (with standard errors given in brackets) for the whole tree, juvenile wood, and mature wood.

Traits ¹	Narrow-sense heritability			
	Whole tree	Juvenile wood	Transition zone	Mature wood
RD	0.18 (0.001)	0.15 (0.001)	0.42 (0.001)	0.17 (0.001)
EWD	0.05 (0.001)	0.02 (0.001)	0.06 (0.0007)	0.02 (0.0005)
LWD	0.37 (0.001)	0.02 (0.0003)	0.57 (0.001)	0.39 (0.001)
MaxD	0.43 (0.001)	0.05 (0.0005)	0.66 (0.001)	0.44 (0.001)
MinD	0	0.09 (0.001)	0	0
RW	0	0	–	0.12 (0.05)
EWV	0	0	0.62 (0.13)	0.02 (0.0005)
LWV	0	0	–	0.31 (0.31)
LWP	0.16 (0.01)	0.09 (0.007)	0.21 (0.008)	0.03 (0.003)
TransD	0.33 (0.001)	0.03 (0.0004)	0.65 (0.001)	0.42 (0.001)

¹Traits: RD: ring density; EWD: earlywood density; LWD: latewood density; MaxD: maximum density; MinD: minimum density; RW: ring width; EWV: earlywood width; LWV: latewood width; LWP: latewood proportion; TransD: transition density. (–) heritabilities that could not be estimated.

Conclusions

Within-tree growth variations, wood density, tracheid morphological characteristics, and quantitative genetic parameters were investigated in tamarack (*Larix laricina*). The following conclusions can be drawn: (1) the tamarack wood exhibits a large difference between earlywood and latewood densities. Tracheids were fine and long, with latewood tracheids slightly longer than earlywood tracheids; (2) cambial age showed highly significant effects on ring width, ring density, and tracheid morphological properties. Ring density increased rapidly from the pith to the juvenile-mature transition zone and remained constant afterward. Tracheid length and width increased from a minimum near the pith to a maximum in the transition zone and remained steady afterward; (3) tree height significantly affects all wood properties in juvenile wood and ring density and growth components in mature wood; (4) significant tree-to-tree variations exist for all wood properties; (5) the correlations between wood density components were high and positive, and the correlations between wood density and growth traits were negative and low except for earlywood density.

Heritability for wood density components increases appreciably from juvenile wood to mature wood, except for earlywood density. However, growth ring traits tend to be less heritable. These results will be of great importance not only for breeding programs but also to the wood industries that use tamarack as a raw material and will enable the selection of good genetic sources to ensure better wood quality.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare no conflict of interest.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfr-2024-0288>.

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