

# Maximizing growth without compromising wood density: Selecting superior Norway spruce clones

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## Abstract

The study examined a free-growing (initial stand density 400 trees ha<sup>-1</sup>), 50-year-old grafted clonal Norway spruce plantation in Eastern Latvia to assess the genetic control and variability of growth traits and wood density. The latter was used as a proxy for structural timber strength. Results showed moderately high heritability in growth traits and moderate variability in wood density among clones, with an estimated genetic coefficient of variation  $CV_g$  of 8.6%. Even when grown at a very low density on nutrient-rich soil, 85% of the trees met the density requirements for construction timber (C18 in accordance with EN 338). The negative correlation between growth traits and wood density was weak at both individual tree and clonal levels ( $-0.08 < r_p < -0.06$ ;  $-0.16 < r_G < -0.09$ ), making it feasible to select fast-growing clones with wood density required for structural timber. The observed variation underscores the importance of selective breeding to ensure optimal timber quality, with implications for enhancing sawn wood strength grades and promoting climate-resilient forestry practices.

**Keywords:** tree breeding; structural timber; clonal forestry; wood properties; plantation forestry; climate-smart forestry

## Introduction

In the Baltic Sea region, forests have a pivotal role in the economy, with the forest industry being a cornerstone sector in the Nordic and Baltic countries (Ruotsalainen 2014, Hetemäki 2020). Managed forests are vital sources of raw materials for various products, including timber for construction, pulp, paper, and biofuel, meeting the increasing demand driven by the bio-based economy (Hetemäki 2020, Lutter et al. 2021). Expanding forested areas, including the afforestation of non-forested land, may be a solution to meet the rising demand for wood biomass while mitigating conflicts with conservation objectives (Lutter et al. 2021). Sawn timber, a primary product utilized in construction, not only sequesters carbon but also substitutes fossil-based materials, contributing to climate change mitigation efforts (Brunet-Navarro et al. 2021, Jonsson et al. 2021).

In this context, Norway spruce (*Picea abies* (L.) H. Karst.) emerges as a pivotal species for achieving both economic and environmental objectives. Norway spruce is one of the main tree species in commercial forestry operations (Pfister et al. 2007, Katrevičs et al. 2018, Jansone et al. 2020a). Proper management, like using sparse plantations, can help it quickly reach its desired size, leading to shorter rotation and better profits (Katrevičs et al. 2018, Routa et al. 2019). This approach also lessens the chance of damage from environmental and biological threats, such as wind, drought, and pests, crucial for its management amid

climate change-induced risks (Arhipova et al. 2011, Allikmäe et al. 2017, Donis et al. 2018, Zeltiņš et al. 2018, de Groot et al. 2019, Samariks et al. 2020).

Concerns arise regarding the quality and suitability of spruce timber for structural applications from fast-growing plantations on more nutrient-rich soil (Jansons et al. 2016, Jansone et al. 2020b), characterized by lower wood density and mechanical strength due to the prevalence of juvenile wood (Hannrup et al. 2004, Chen et al. 2014). Additionally, the relationship between wood density and hydraulic vulnerability suggests that fast-growing trees may face limitations in hydraulic performance under extreme drought conditions. This highlights the need for a balanced approach in breeding for growth, wood quality and resilience to uncertain future climate (Zubizarreta-Gerendiain et al. 2009, Rosner et al. 2014). Competition for resources within a stand affects growth and wood properties, indicating the need for careful selection of genotypes that can maintain high growth rates and desired wood properties after canopy closure (Zubizarreta-Gerendiain et al. 2009). Norway spruce breeding has been shown to enhance productivity and stem quality, leading to higher financial returns compared to utilizing unimproved forest reproductive material (Ruotsalainen 2014, Jansons et al. 2015, Jansson et al. 2017, Ahtikoski et al. 2020, Haapanen 2020, Marcu et al. 2020). However, achieving a balance between growth and sufficient wood density poses a significant challenge for tree breeding, as these traits are unfavourably corre-

lated (Hysten 1997, Steffenrem et al. 2007). Still, breeders often have the possibility of finding genotypes that exhibit good performance in both traits without compromising too much one for the other (Zubizarreta-Gerendiain et al. 2007, Levkoev et al. 2017).

We studied a 50-year-old Norway spruce plantation, which has reached dimensions for sawn timber, hence serving as a valuable case study due to the scarcity of information regarding clone performance at such advanced ages. By utilizing vegetatively propagated clones at a wide-spaced ( $5 \times 5$  m) setup, we aimed to maximize genetic consistency, capturing a spectrum of the genetic variability within the studied population (White et al. 2007, Rosvall et al. 2019, Chen et al. 2020). Along with growth traits, we also studied wood density as a proxy for structural timber characteristics (Ridley-Ellis et al. 2016), considering its tight link to other wood density components, strength and stiffness (Zobel and Van Buijtenen 1989, Hysten 1997, Steffenrem et al. 2007, Hautamäki et al. 2014). Parameters such as wood density, modulus of elasticity (MOE), and modulus of rupture (MOR) are customarily used to categorize timber into strength grades (classes), dictating its suitability for structural applications (Gil-Moreno et al. 2023). Thus, we aimed to explore the phenotypic and genotypic variation of growth traits and wood density, as well as the relationship between them in a sample of Norway spruce clones from the local eastern Latvian population. This research assists forming a breeding population for climate-smart management of vegetatively propagated productive Norway spruce stands by identifying clones capable of higher vitality and fast diameter development without compromising structural wood properties.

## Materials and methods

The study material was obtained from a Norway spruce clonal plantation situated in eastern Latvia ( $56^{\circ}42'N$ ,  $25^{\circ}53'E$ ), characterized by fertile mineral soil under mesotrophic conditions akin to the *Oxalidos* forest type (Buss 1997). Climatic conditions in the study area featured a mean annual temperature of approximately  $+6.0^{\circ}C$ , with monthly temperatures ranging from  $-6.4^{\circ}C$  in February to  $+17.1^{\circ}C$  in July. Annual precipitation averaged around 700 mm (Harris et al. 2020).

Established in 1964 and originally intended as a seed orchard, the plantation utilized vegetatively propagated (grafted) planting material sourced from 21 selected fast-growing plus trees of local origin, with a planting density of 400 trees  $ha^{-1}$  at a spacing of  $5 \times 5$  m. A total of 421 grafts were planted in randomly distributed single-tree plots, with 11–31 replications (ramets) per clone. Weed control measures were implemented during the planting year and the subsequent year, while no pruning and thinning activities were conducted before sampling.

All mature trees aged 50 years were measured for diameter at breast height (DBH) and height. From the measu-

rement data, height-to-diameter ratio (H/D ratio) and green crown length-to-height ratio (hereinafter green crown ratio) were estimated. Growth and yield data for the plantation were previously reported by Katrevičs et al. (2018). Cores extending from pith-to-bark at breast height (1.3 m) collected from 230 trees aged 50 years were available, representing 21 clones (with 7–19 ramets per clone). Core sampling excluded trees with stem defects such as visible crown asymmetry, double leaders, or severe browsing damage. The cores were stored indoors and air-dried to a moisture content of 12%. Annual ring width data were obtained using high-frequency densitometry with a LignoStation (Spiecker et al. 2003). All sample cores were cross-dated and validated through graphical inspection using the COFECHA software (Holmes 1983). Ring width weighted mean density (WD) was estimated and its lower fifth percentile value was calculated for characterizing variability and rough comparison with characteristic values used in strength grading (Ridley-Ellis et al. 2016).

## Data analysis

Pearson correlations ( $r_p$ ) were calculated using R package Hmisc (Harrel 2024) to assess the relationships between the variables studied. The coefficient of variation (CV%) was estimated as the ratio of the standard deviation to the mean, expressed as a percentage. The genetic variance components were estimated using the following model:

$$y_{ij} = \mu + C_i + \varepsilon_{ij} \quad (1)$$

where

$y_{ij}$  is the observation on the  $i$ th tree of the  $j$ th clone,

$\mu$  is the overall mean, and

$C_i$  is the random effect of the clone.

Broad-sense heritability ( $H^2$ ) of the studied traits was estimated as follows:

$$H^2 = \frac{\hat{\sigma}_G^2}{\hat{\sigma}_G^2 + \hat{\sigma}_\varepsilon^2} \quad (2)$$

where  $\hat{\sigma}_G^2$  and  $\hat{\sigma}_\varepsilon^2$  are the estimated variance components of clone and residual, respectively.

The genotypic coefficient of variation ( $CV_g$ ) was calculated as:

$$CV_g = \sqrt{\frac{\hat{\sigma}_G^2}{\bar{x}}} \cdot \frac{100}{\bar{x}} \quad (3)$$

where

$\bar{x}$  is the phenotypic mean.

Genotypic correlations between traits were calculated as follows:

$$r_G = \frac{\widehat{Cov}_{(xy)}}{\sqrt{\hat{\sigma}_{(x)}^2 \cdot \hat{\sigma}_{(y)}^2}} \quad (4)$$

where

$\hat{\sigma}_{(x)}^2$  and  $\hat{\sigma}_{(y)}^2$  are the family variances for two traits, and  $\widehat{Cov}_{(xy)}$  is the genotypic covariance between two traits (Falconer and Mackay 1996), estimated from the multivariate model extending the univariate mixed model in Equation 1.

Standard errors were calculated employing Dickerson's approximation method (Dickerson 1969).

Data analysis was conducted using R software, version 4.0.3 (R Core Development Team 2020), using package sommer (Covarrubias-Pazarán 2016) to estimate genetic parameters.

## Results

In the studied clonal plantation, a mean height of 25.1 m and a mean DBH of 36.3 cm resulted in a mean stem volume of 1.182 m<sup>3</sup> at the age of 50 years. On average, H/D ratio and green crown ratio reached 0.701 and 0.754, respectively. From increment cores, the mean ring width was 4.12 mm, and the WD was 400.9 kg m<sup>-3</sup> with a corresponding 5<sup>th</sup> percentile value of 274.9 kg m<sup>-3</sup>. At the trial level, tree height, H/D ratio, and green crown ratio showed the lowest variation (*CV*% = 9.0–11.9%), while reaching *CV*% of 37.4% for the height of the lowest green branch (Table 1).

The growth traits – height, DBH, and stem volume – possessed the highest broad sense heritability estimates

**Table 1.** Summary statistics of the traits studied in the 50-year-old Norway spruce clonal plantation in Eastern Latvia

Trait	Mean	Min	Max	SD	CV%
Height (m)	25.1	16.8	30.0	2.3	9.0
Diameter at breast height (cm)	36.3	22.0	53.0	5.4	14.9
Height of the lowest green branch (m)	6.2	1.5	12.3	2.3	37.4
Stem volume (m <sup>3</sup> )	1.182	0.301	2.740	0.388	32.8
Height to diameter ratio	0.701	0.512	0.919	0.082	11.7
Green crown length to height ratio	0.754	0.498	0.937	0.09	11.9
Weighted mean density (kg m <sup>-3</sup> )	400.9	212.7	581.2	77.4	19.3
Ring width (mm)	4.122	2.345	7.436	7.60	18.4

Note: ‘Min’ denotes minimum value, ‘Max’ denotes maximum value, *SD* is the standard deviation, *CV*% denotes coefficient of variation (%).

**Table 2.** Broad-sense heritability (*H*<sup>2</sup>) with standard error (*SE*) and genotypic coefficient of variation (*CV*<sub>g</sub>) for the studied traits in the 50-years-old Norway spruce clonal plantation in Eastern Latvia

Trait	<i>H</i> <sup>2</sup>	<i>SE</i>	<i>CV</i> <sub>g</sub> (%)
Height	0.35	±0.128	5.15
Diameter at breast height	0.30	±0.116	8.12
Stem volume	0.37	±0.135	19.47
Height of the lowest green branch	0.02	±0.035	5.76
Height/diameter at breast height ratio	0.23	±0.095	5.59
Green crown ratio	0.02	±0.033	1.51
Weighted mean wood density	0.20	±0.087	8.63
Ring width	0.22	±0.092	8.59

**Table 3.** Trait-trait genotypic correlation coefficients (*r*<sub>G</sub>) with standard errors in the brackets (upper right triangle) and the Pearson correlation coefficients (*r*<sub>P</sub>, lower left triangle) between the studied traits in the 50-years-old Norway spruce clonal plantation in Eastern Latvia

	Height	DBH	Height of lowest green branch	Stem volume	H/D ratio	Green crown ratio	Weighted mean wood density	Ring width
Height		0.69 (0.240)	0.40 (0.125)	0.84 (0.282)	0.02 (0.140)	0.46 (0.329)	-0.09 (0.136)	0.40 (0.100)
DBH	0.60 ***		0.58 (0.330)	0.97 (0.332)	-0.73 (0.280)	0.05 (0.268)	-0.16 (0.127)	0.79 (0.291)
Height of lowest green branch	0.28 ***	-0.07		0.56 (0.279)	-0.29 (0.339)	-0.61 (1.105)	0.33 (0.258)	0.63 (0.454)
Stem volume	0.77 ***	0.96 ***	0.03		-0.56 (0.202)	0.22 (0.240)	-0.16 (0.123)	0.73 (0.263)
H/D ratio	0.01	-0.79 ***	0.30 ***	-0.59 ***		0.47 (0.528)	0.11 (0.142)	-0.65 (0.252)
Green crown ratio	-0.06	0.21 **	-0.97 ***	0.15 *	-0.32 ***		-0.42 (0.301)	-0.14 (0.301)
Weighted mean wood density	-0.06	-0.08	0.01	-0.08	0.07	-0.03		-0.16 (0.358)
Ring width	0.31 ***	0.69 ***	-0.20 **	0.64 ***	-0.61 ***	0.28 ***	-0.12	

Note: \* *p* < 0.05; \*\* *p* < 0.01; \*\*\* *p* < 0.001.

of 0.35, 0.30, and 0.37, respectively, while the height of the lowest green branch and green crown ratio had the lowest heritability (*H*<sup>2</sup> = 0.02) (Table 2). Ring width and WD had comparable heritability of 0.20–0.22. The genotypic coefficient of variation followed the patterns of *CV*% yet being somewhat lower (Table 2) – the *CV*<sub>g</sub> of wood density was 8.63%, being similar to ring width (8.59%) and DBH (8.12%).

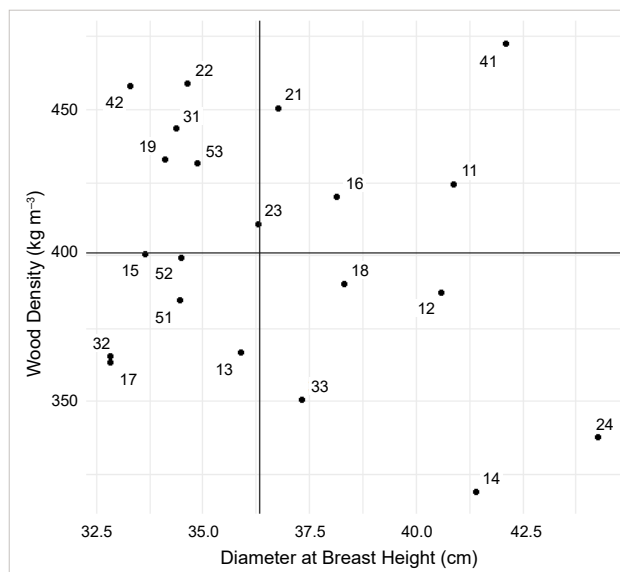
Strong correlations between growth traits were found at both individual tree (*r*<sub>P</sub> = 0.60–0.96) and clonal (*r*<sub>G</sub> = 0.69–0.97) levels (Table 3). H/D ratio showed strong negative correlations with DBH (*r*<sub>P</sub> = -0.79, *r*<sub>G</sub> = -0.73), yet almost non-existent relation to height (*r*<sub>P</sub> = 0.01, *r*<sub>G</sub> = 0.02). The WD showed both negative and positive, yet statistically nonsignificant and practically negligible correlations with other studied traits (-0.08 < *r*<sub>P</sub> < 0.07); also, at the genotypic level these relations remained weak. Only a negative moderate genotypic correlation was found between WD and green crown ratio (*r*<sub>G</sub> = -0.42). For ring width, we observed a strong positive correlation with DBH and stem volume (*r*<sub>P</sub> = 0.64–0.69, *r*<sub>G</sub> = 0.73–0.79), and a strong negative correlation with H/D ratio (*r*<sub>P</sub> = -0.61, *r*<sub>G</sub> = -0.65).

## Discussion

Our study revealed insights into the genetic control and expression of growth and wood density traits. The growth traits exhibited higher heritability than the other traits, with stem volume showing the highest broad-sense heritability estimate of 0.37. Ring width and WD demonstrated comparable heritability estimates ( $H^2 = 0.20\text{--}0.22$ ). Similarly, moderate to high heritability of WD was obtained earlier for Norway spruce (Silva et al. 2000, Hannrup et al. 2004, Steffenrem et al. 2007, Chen et al. 2014, Högborg et al. 2014).

While growth traits were strongly interrelated, indicating that selection for one is likely to affect the others positively, WD's correlation to these traits was less pronounced and generally weak at both phenotypic and genotypic levels (Table 3). Chen et al. (2014) and Hylén et al. (1997) reported a more negative genotypic correlation between wood density and growth traits compared to phenotypic correlations, similar to our findings. The weak correlations between WD and growth traits suggest that selecting these traits concurrently does not necessitate significant compromise. This is notable given the often-reported negative correlation between growth rate and WD (Hylén 1997, Hannrup et al. 2004, Steffenrem et al. 2009, Chen et al. 2014, Levkoev et al. 2017, Luostarinen et al. 2017), a relationship that poses a challenge for breeding programmes to improve both traits simultaneously. Such fast-growing clonal spruce plantations on fertile sites may provide economic gains from volume growth – one of the fundamental elements of tree breeding – if sufficient sawn wood quality is maintained. In our study, we could select among the most productive clones with WD above the plantation mean (e.g. clones No. 41, 11 or 16; Figure 1). Similarly, despite the general pattern of negative relation between growth and WD, clones with both high DBH and mean wood density were selected in a Finnish trial (Zubizarreta-Gerendiain et al. 2007, Levkoev et al. 2017). Such results restricted to single-site analysis may be biased due to the lack of genotype  $\times$  site interaction considered (Hylén 1997), hence should not be generalized. Nevertheless, sufficient differences among the clones even from very limited geographic area with virtually no elevation in the central part of Norway spruce distribution range, where high genetic variation is typically found (Kapeller et al. 2017), demonstrate the potential for successful breeding for desired combination of growth and wood quality traits.

Overall, the rather wide annual rings (on average, 4.12 mm; Table 1) possessed a WD of 400.9 kg m<sup>-3</sup>, generally comparable to values obtained in other studies. For instance, Cukor et al. (2020) found similar wood density on agricultural land in Central Europe (399 kg m<sup>-3</sup>), while Gil-Moreno et al. (2023) reported 406.5 kg m<sup>-3</sup> in Great Britain. In Ireland, stand mean wood density varied from 420 to 485 kg m<sup>-3</sup> with corresponding ring width of 5.16 to 3.95 mm (Krajnc et al. 2019). Hylén (1997) reported wood



**Figure 1.** Genotypic values of clones for diameter at breast height (DBH) and ring width-weighted mean wood density at the age of 50 years

Numbers denote clones, solid lines represent overall trial means for DBH and wood density.

density of 300 kg m<sup>-3</sup> at 28-years-old progeny trial in Norway, while Raiskila et al. (2006) found higher mean density of 461 kg m<sup>-3</sup> for average annual ring width of 3.15 mm in Finnish trials. In Lithuania, wood density ranged from 408 to 431 kg m<sup>-3</sup>, with decreasing initial stand density from 3,100 to 1,100 trees ha<sup>-1</sup> (Šilinskas et al. 2020). In a Romanian study of 60 to 105-year-old stands with different thinning regimes, a mean estimate of 378 kg m<sup>-3</sup> was indicated without decreasing trend with increased thinning intensity (Vlad et al. 2022).

In our study, the variation in WD ( $CV\% = 19.3\%$ ) was similar to the variation in ring width (Table 1) and about two to four times higher than in earlier studies (Hylén 1997, Zubizarreta-Gerendiain et al. 2007, 2009, Chen et al. 2014, Levkoev et al. 2017). Despite the high mean WD, the high variation led to a low 5<sup>th</sup> percentile density ( $\rho_{0.05} = 274.9$  kg m<sup>-3</sup>) which is critical for grading structural timber according to EN 338 (CEN 2016). This is likely due to the exceptionally low tree spacing, which allows for fuller expression of heritability with less inter-tree competition (Zeltniš et al. 2022). However, the rejection rate for Norway spruce to meet common structural timber grades C16 and C18 (with threshold  $\rho_k = 310$  kg m<sup>-3</sup> and  $\rho_k = 320$  kg m<sup>-3</sup>, respectively, according to EN 338 (CEN 2016)) would be only 11 and 15%, respectively, indicating that 89 and 85% of the material would meet the density requirements for these grades, assuming other key properties like moduli of elasticity and bending strength meet the corresponding requirements too. In practice, the selected clones for utilization in plantation forests would be planted at a higher initial density of about 1,000–1,200 trees per hectare, which would likely result

in higher wood density. A Lithuanian study reported a rejection rate of 0% for grade C16 in Norway spruce stands (2,100–3,100 trees ha<sup>-1</sup>), and a rejection rate of 5% for C14 in the stand of 1,100 trees ha<sup>-1</sup> (Šilinskas et al. 2020). An Irish study found variation from grade C18 to C22 in thinned and unthinned Norway spruce stands (593–1,552 trees ha<sup>-1</sup>) (Krajnc et al. 2019). Nonetheless, spruce wood with lower WD has various applications in non-supporting structures and may benefit from reduced swelling, shrinking, and cracking (Luostarinen et al. 2017).

We acknowledge that our results may not be directly comparable with estimated wood density in machine strength grading due to differing sampling methods (Ridley-Ellis et al. 2016), although both methods – high frequency densitometry (used in this study) and X-ray (commonly used in machine grading) – might give comparable results (Wassenberg et al. 2014). Mechanic properties and density differ between air-dried samples and timber for grading, which may have any moisture content (Niklas and Spatz 2010). Still, reference moisture content in grading is 12%, requiring adjustments and ensuring comparability (Ridley-Ellis et al. 2016).

Difficult and costly sampling of numerous trees per genotype largely limits breeding studies of sawn timber quality (Högberg et al. 2014). Nevertheless, in both cases a specific population is sampled (Ridley-Ellis et al. 2016), with substantial wood density variation among trees, annual rings and heights (Repola 2006, Jyske et al. 2008, Fischer et al. 2016, Gil-Moreno et al. 2023). Still, the average estimates and variation of the studied trial give a valuable insight into the tendency of selected clones from the local eastern Latvian population at fertile conditions with untypically wide space for individual trees, manifesting their genetic potential of growth and wood properties, when dimensions of logs for sawn wood are reached. The grafted clones are uncommon as planting stock, yet growth differences among genetic varieties are generally independent of plant type (Liziniewicz et al. 2018), and the fast growth observed suggests no negative effects from cyclophysis (Olesen 1978, Viherä-Aarnio and Rynänen 1994, Wendling et al. 2014). Although the high phenotypic variation indicates critically low (for structural purposes) WD for separate trees and is partially in line with observations of reduced wood density at fertile sites with wider spacing or intensive thinning (Krajnc et al. 2019), the unaffected average estimate compared to trials with conventional spacings imply minor effect. Cukor et al. (2017, 2020) found higher radial growth on relatively fertile former agricultural land compared to forest land up to the age of 23 years and argued that a higher growth rate resulted in denser stands, hence subsequent higher wood density (399 kg m<sup>-3</sup>).

The observed substantial genotypic variation ( $CV_g = 19.3\%$ ) suggests the potential to select among the clones with higher WD without compromising productivity, as indicated by practically inconsiderable genotypic corre-

lations (Table 3). We also stress that the spacing in the particular case study is untypically low (400 trees ha<sup>-1</sup>), and more realistic initial conditions of at least 1,000 trees ha<sup>-1</sup> would result in higher inter-tree competition, hence increased wood density with less pronounced variation regardless of the clonal structure (Zubizarreta-Gerendiain et al. 2009). In turn, culling of clones with inferior wood density would not only improve the potential for higher sawn wood strength grade of the breeding population but also contribute to climate-smart forestry practices, as suggested by higher drought sensitivity of trees with low wood density due to limited hydraulic conductivity during extreme summer drought events (Rosner et al. 2014).

## Conclusions

In conclusion, our study of a 50-year-old grafted clonal Norway spruce plantation highlights the significant genetic control of growth traits, while also revealing considerable variability in wood density among free-growing clones collected from a very limited geographical area, in trees that have reached dimensions for sawn timber. Despite the commonly reported negative correlation between growth rate and wood density, our findings suggest opportunities for selecting clones with higher wood density without compromising productivity, aimed at forming a breeding population of elite clones for vegetative propagation. Even under the given conditions of a eutrophic site and untypically low initial stand density, 89% of the wood samples would meet the wood density criteria for a common structural timber grade C16 according to EN 338.

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