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Consequences of faster growth for wood density in northern red oak (*Quercus rubra* Liebl.)

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The objective of this study was to establish whether the relationships between wood density, growth rate and ring number from the pith were equivalent in the contrasting conditions of a natural forest and an intensively managed plantation of northern red oak (Quercus rubra Liebl.). The radial X-ray densitometry profiles of 14 natural forest trees and 18 plantation trees growing in the southwest of Québec, Canada, were studied in detail using a linear mixed-effects modelling approach. In the natural stand, the effect of faster growth on overall ring density changed from a slightly negative relationship at a ring number 5 to a strongly positive effect at ring 40. In the plantation trees, the overall ring density remained almost constant along the range of observed ring widths. For the range of ring numbers common to both stand types (i.e. rings 1–15) the relationship was almost equivalent. Overall, our results suggest that because trees are harvested at a target diameter, silvicultural interventions specifically designed to improve radial growth rate in northern red oak will not be detrimental to overall wood density.

Introduction

To maintain wood production while promoting forest conservation, an approach gaining interest is to divide forest areas into different management zones consisting of (1) full protection areas; (2) low-intensity management areas, where forest composition and structural characteristics of the natural forest mosaic are maintained according to the principles of ecosystem-based management[1], and (3) intensive management areas, where priority is given to fibre production.[2] In eastern Canada, fast-growing plantations have been proposed with the specific intention of accelerating the growth of individual trees to shorten rotation age. However, such practices raise concerns about wood quality, which may decrease with increasing radial growth rate. Several physical and mechanical properties of wood are strongly influenced by wood density, which is therefore considered a major wood quality attribute.[3,4] Although the concept of wood quality is specific to end-use requirements, higher wood density is generally seen as a desirable attribute as it is associated with increased strength and stiffness of sawn timber. A key characteristic of wood density is its high variability, which has its origins in several factors, including genetics,[5] tree growth (ring number from the pith, ring width and silviculture),[6,7] and environmental influences, such as climate,[8] elevation[9] and site fertility.[10,11]

In the past few decades, the impact of growth rate on wood density has been investigated using a statistical modelling approach.[12–15] However, little information exists on the relationship between growth rate and wood density in northern red oak (*Q. rubra* Liebl.). This is important because red oak provides significant ecological and economic value in the eastern deciduous forests of North America where it is among the most valuable species for wood products.[16]

Wood density has been studied extensively for pedunculate (*Quercus robur* Liebl.) and sessile oaks (*Quercus petraea* Liebl.) growing in France.[7,10,15,17,18] Through these studies, it has been established that the wood density of European oaks is positively related to ring width and negatively related to ring number from the pith. The ring porous wood found in oak species is characterized by the division of each annual ring into low-density earlywood and high-density latewood zones, the latter containing smaller vessels and therefore a higher proportion of fibres than earlywood.[19] Within a tree, earlywood width and density are generally constant in pith-to-bark profiles, while latewood width and density vary with both ring number and ring width.[15,18] The latter studies attributed the positive relationship between ring width and ring density to the increase in latewood proportion with increased growth rate. They thus concluded that European oak would benefit from intensive silviculture, whereby faster growth would produce denser wood with improved mechanical properties. However, this conclusion was based on observations from just one commonly applied silvicultural treatment (high forests). Therefore, if the positive correlation between wood density and growth rate is bounded, these limits might not have been observed due to the limited range of variation in growth rate within the sampled populations.[15,18]

This study investigates wood density variation in northern red oak as a function of ring number from the pith and growth rate. More specifically, we aim to examine whether or not a positive relationship between wood density and growth rate can be observed in two contrasting management scenarios i.e. both in a natural forest and an intensively managed plantation. To achieve this, we have divided the analysis into two components that together determine the average density of a growth ring: (1) the respective proportions of earlywood and latewood within an annual ring and (2) earlywood and latewood densities, respectively. We hypothesized that a positive relationship between ring width and ring density would be observed in the natural forest, but not in the intensively managed plantation, which is associated with a faster radial growth rate. Gaining a better understanding of the relationships between radial growth and wood density will help forest practitioners to evaluate the potential of fast-growing northern red oak plantations for the production of high quality timber.

Material and methods

Study sites

The study area is located in the southwest part of the province of Québec, Canada. The climate is continental, with an average annual temperature of 6.2°C and seasonal mean temperature of 20.6°C in July and −9.7°C in January. The annual frost-free period is 140 days with 2066 growing degree-days (above 5°C). Average annual rainfall is 929mm, of which 17% falls as snow. The sampling period for the available climate data covers 30 years (Environment Canada 2011). Two sampling sites were chosen to represent two contrasting silvicultural strategies, which would produce logs of similar dimensions over different time periods.

The first, a natural forest stand dominated by northern red oak, was situated at the top of Covey Hill near Havelock (N 45°01.33′; W073°47.53′). Sugar maple (*Acer saccharum*, Marsh.), black cherry (*Prunus serotina* Ehrh.) and white ash (*Fraxinus americana* L.) were the associated species. The soil is a well-drained sandy loam with gravel (46% sand, 38% loam, 15% clay),[20] and forest canopy cover ranged from 70% to 90%. The average height of trees was 12–17 m and the trees ranged from 30 to 50 years of age.

The second stand was a 21-year-old plantation site near Saint-Anicet, which is located 40 km west of Covey Hill on an unstable deposit of tardiglacial sand. The soil is a very well-drained sandy loam (76% sand, 8% loam, 16% clay). Slope and stoniness were negligible and ground-water table depth was 90cm. The experimental plantation was established, after soil plowing and harrowing, in the spring of 1989[21] from 2-year-old bare-root red oak stock seedlings. Trees were planted manually in a complete randomized block design.[22] Each of the three blocks was divided into three plots, and each plot was randomly assigned to one of three weed control treatments (1 m^2 black plastic mulch, glyphosate herbicide and a control). In each plot, 49 trees were planted in a 2 m^2 spacing equivalent to an initial stand density of 2500 stem/ha. Trees from the mulch treatment, which were selected for this study, had an estimated survival rate of 75% at 21 years after planting. All trees in the experiment were pruned after 3, 5, 7, 10, 12 and 16 years.

Tree sampling

In July 2008, 14 red oak trees were harvested from the natural forest stand near Havelock and 18 trees from the plantation near Saint-Anicet. The main tree characteristics for each site are given in Table 1. The sample trees were selected to represent the range of tree basal areas in each stand. Mean diameter at breast height (DBH) was 22.6 ± 3.8 cm in

Table 1 Mean characteristics of the sample trees from each stand type

	No. of trees	No. of rings (total*)	No. of rings per tree* (min–max)	Tree age[†] (years)	Stem diameter at breast height (cm)	Tree height (m)	Base live crown (m)	Density (kg m^{-3})	Width of each wood type (mm)
Natural stand	14	515	31–40	46 (1)	22.6 (17.1–31.5)	15 (12.0–18.0)	10.7 (8.2–12.6)		
EW								585 (61)	0.74 (0.2)
LW								887 (57)	1.15 (0.6)
Ring								760 (56)	1.89 (0.6)
Plantation	18	218	9–14	22 (0)	20.6 (16.5–26.4)	15.3 (13.5–17.3)	7.6 (6.75–8.65)		
EW								542 (56)	1.3 (0.5)
LW								807 (53)	3.8 (1.5)
Ring								734 (46)	5.0 (1.6)

Values shown are the mean and standard deviation (parentheses).
Explanation of abbreviations: EW = earlywood; LW = latewood; Ring = overall ring (earlywood + latewood).
*Number of rings used in the study from samples taken at 2.5 m. In most trees, the first and second growth rings near the pith were removed from the analysis because their segment did not exactly reach the pith (risk of measurements errors).
[†] Tree age was evaluated at stem base while sample disks were taken at 2.5 m. The number of rings used in the study is therefore not expected to match the measured number of rings from the pith.

the natural stand and 20.6 ± 2.8 cm in the plantation. Mean crown base height was 10.7 ± 1.5 m in the natural stand and 7.6 ± 0.6 m in the plantation. Ring counts at trunk base were used to estimate the age of the trees. At the time of felling, the mean tree age was 46 years in the natural forest and 22 years in the plantation (Table 1). A 2.5-m log was cut from each sample tree (branch free portion), and a 2-cm thick transverse disk was taken from the top of each log and transported to Laval University's Wood Research Center for further testing.

Wood density measurements

Following the methodology described by,[23] pith-to-bark radial segments (approx. 2.0 cm longitudinal × 1.0 cm tangential × disk radius) were cut from each disk in the southernmost direction. From these, radial strips measuring 1.6 mm (longitudinal) × 10 mm (tangential) were sawn with a specially designed precision twin-blade saw, and then conditioned to approx. 12% moisture content in a room maintained at 21°C and 65% relative humidity. Finally, the samples were scanned at right angles to the fibre direction in a Quintek QTRS-01X scanning X-ray micro-densitometer and tree ring analyser (Quintek Measurement Systems, Knoxville, TN). Density profiles were obtained using the image analysis software QMS Tree Ring System (QTRS, version 2.03).

Profile analysis

Early-, latewood and full ring (hereafter referred to as wood types) width and density were measured for each cross-section. The criteria used to (1) separate annual growth rings and (2) find the position of the earlywood–latewood transition were of primary importance in this analysis. We therefore decided to work from the raw data to identify density thresholds within each density profile. To achieve this, we developed a specific algorithm using the tcltk library in the R statistical programming environment.[24] First, density data were normalized to zero mean and unit variance in order to increase the robustness of calculations. The limit between two consecutive annual rings was defined as the point where the maximum change in density was reached.[25] The same method was used to determine the limit between early- and latewood within each annual ring. Data were smoothed to eliminate noise and detect significant changes between adjacent data. A moving average filter was used, i.e. each data point was replaced with the average of the neighbouring data points defined within the span. In this case, a five-point average was used. In most trees, the first two rings (near the pith) were removed from the analysis because the strips were not perfectly aligned with the pith. Early-, late- and ring average density and width are henceforth referred Q2 to as EWD, LWD, RD and EWW, LWW and RW, respectively. The number of rings analysed per tree varied from 31 to 40 for the trees from the natural stand and from 9 to 14 for the plantation-grown trees. The difference between the age of the trees and the number of rings analysed is due to the fact that tree age was evaluated at the base of the stem while sample disks were taken at 2.5 m.

Statistical analyses

Model development

Correlations between EWD, LWD and RD, and EWW, LWW, RW, ring number from the pith (hereafter 'ring number' in the text or RNP in tables and equations) and their mathematical transformations were assessed using Pearson correlation coefficients for each study site. Variables with the highest values were selected as independent variables for the models. Time series of growth measurements within each tree produced auto-correlation that induced heterogeneous error variances. Graphical techniques were first used to provide diagnostic information on the covariance structure of the errors. As recommended by,[26] the data were fitted with an unstructured covariance matrix. The resulting auto-correlated covariances were then plotted against the distance between two measurements (lag), which highlighted any general trends. At this stage many different types of error covariance structure can potentially represent the behaviour of the within-subject residuals over time. Goodness-of-fit statistics (Akaike's[27] and Bayesian information criteria,[28] henceforth referred to as AIC and BIC) for different pre-selected error structures were then compared in order to determine the best fit to the observed structure.

Mixed-effects modelling techniques were used in this analysis since they efficiently accommodate between-subject variations in longitudinal series and have previously been used successfully for wood density analysis.[29,30] Linear mixed models were specified using the MIXED procedure of the SAS software.[31] Independent variables were centred on the mean (i.e. for each independent variable, the mean was subtracted from each individual value). In multiple regression analysis, this procedure is used to reduce multicollinearity among covariates,[32] and helps reduce convergence errors during parameter estimation. In addition, the coefficients of centred models are easier to interpret because they represent the response to a unit change in the independent variable when the other predictors are at their mean values.[33]

Models parameters were estimated using restricted maximum likelihood (REML). As with maximum likelihood estimation (ML), REML accommodates data in unbalanced designs (i.e. the data set contains missing values),[34] but it is less numerically intensive and its estimates tend to be less biased.[26] Models were fitted separately to data from each study site (stand type), with the general aim of expressing the density of each wood type as a function of its width and ring number. The following independent variables were introduced sequentially into each model: EWW, LWW or RW, RNP and an interaction term between width and RNP. The interaction term accounted for the change in the strength of the relationship between wood type density and width that occurs with an increasing ring number. The models were fitted in four stages. First, the fixed effects variables were assessed (stage 1) before tree-level random effects were introduced, first on the intercept alone (stage 2), and then on the selected independent variables (stage 3). Finally, a correlation structure was introduced to account for the autoregressive correlation of the errors (stage 4).

Evaluation of model performance

At each stage of the fitting process, model selection was based on AIC and BIC, and the evaluation of model performance was based on visual observations of plots of observed *vs* predicted values, and selected of goodness-of-fit statistics. The root mean square error (RMSE) was used to represent the standard error of the estimate, and model precision or mean absolute error (MAE)[35] was used to assess the average error associated with a single prediction. Both RMSE and MAE were calculated in the same units as the original data. They are usually similar in magnitude, but the RMSE is more sensitive to occasional large errors and is therefore generally slightly higher than MAE.[36] Mean absolute percentage error (MAPE) is also often useful because it is an expression of MAE in generic percentage terms of the observed values. It therefore gives a better idea of the relative importance of the error. Average model bias was used to indicate whether predictions tended to be disproportionately positive or negative.[37] The modelling efficiency (EF)[38] was used as a dimensionless statistic analogous to R^2. It is, however, more powerful to compare simulated and observed data since information is obtained on both the degree of correlation between the variables and the magnitude of the model errors. A perfect model is characterized by EF = 1 while EF = 0 indicates that the model is no better than a simple average. EF < 0 indicates a poor model. The simultaneous *F*-test of bias (close to 1 when variances of the two distributions compared are not significantly different) for slope = 1 and intercept = 0 provides information about the statistical significance of the deviation of the fitted line between predicted and measured values. The level of statistical significance was set to 5% and simultaneous *F*-tests were performed using the REG procedure in SAS. Only independent variables that improved model performance were retained.

Results

Tree characteristics

Trees from the natural stand (Havelock) were older than those from the plantation (Saint-Anicet) (Table 1), although neither stand had reached commercial maturity. Between-tree variability in density was equivalent (SD = 5%) between stand types. Mean RW in the plantation (5 mm) was significantly larger than that in the natural stand (1.9 mm) ($F\ (1, 30) = 150.3$, ms = 75.7, $P < 0.0001$) whereas RD did not differ significantly between the two stand types (734 kg m^{-3} and 760 kg m^{-3} in the plantation and in the natural forest, respectively) ($F\ (1, 30) = 7.41$, ms = 7442.4, $P = 0.0807$).

Incorporating radial growth criteria into the wood density models

Identifying predictor variables from Pearson correlation coefficients

The inverse of EWW and the square root of RNP were selected as predictor variables in the EWD models as they were associated with the best Pearson correlation coefficients. An analysis of the residuals, however, suggested a remaining effect of RNP and EWW that was alleviated by including an additional linear effect of the untransformed variables. Using the same selection criteria, LWW and RNP were chosen as independent variables in the LWD models. Finally, for the RD models, the inverse of RW and the square-root of RNP were selected as predictor variables.

Tests of parallelism (two-way Analysis of covariance (ANCOVA)) were performed on the density data. These are intended to determine the significance of a group effect by testing whether two non-parallel straight lines are a better fit to the data than two parallel lines. Significant deviation from parallelism implies that responses differ between groups. Wood type width and stand type were first introduced as covariance factors to test for the effect of stand types on the relationship between the density and width of each wood type. The significant interaction indicated that regression lines had different slopes for EWD ($F_{\mathrm{EW}}\ (3, 729) = 27.8$, ms = 95, 138.9, $P < 0.0001$) and RD ($F_{\mathrm{RT}}\ (3, 729) = 17.5$, ms = 47395.5, $P < 0.0001$). In latewood data, a significant effect of stand type ($F_{\mathrm{LW}}\ (3, 729) = 12.45$, ms = 35775.8, $P = 0.0004$), but with no significant interaction ($F_{\mathrm{LW}}\ (3, 729) = 0.01$, ms = 37.0, $P = 0.91$), indicated that LWW had a similar relationship with LWD in both stand types. The stand type effect is, however, important as although the regression lines were parallel, they had different intercepts. RW and RNP were hence introduced as covariance factors. This highlighted the fact that the slope of the relationship between wood density and width changed with ring number only in the natural stand for LWD and RD.

Model form

Final models were of the general form:

$$\begin{aligned} WD_{ij} = {} & (a + \alpha_i) + (b + \beta_i) \bullet \sqrt{RNP_{ij}} + (c + \chi_i) \bullet RNP_{ij} \\ & + (d + \delta_i) \bullet \frac{1}{EWW_{ij}} + (e + \zeta_i) \bullet EWW_{ij} \\ & + (f + \Phi_i) \bullet \frac{1}{LWW_{ij}} \\ & + (g + \gamma_i) \bullet LWW_{ij} + (h + \eta_i) \bullet \frac{1}{RW_{ij}} \\ & + (i + \theta_i) \bullet RW_{ij} + (j + \kappa_i) \bullet Int_{ij} + \varepsilon_{ij} \end{aligned} \tag{1}$$

where WD$_{ij}$ denotes wood density (either EWD, LWD or RD) of ring *j* in tree *i* (kg m^{-3}); EWW$_{ij}$ is earlywood width centered to its mean (mm); LWW$_{ij}$ is latewood width centered to its mean (mm); RW$_{ij}$ is ring width centered to its mean (mm); RNP$_{ij}$ is the ring number from the pith centered to its mean; Int$_{ij}$ is the interaction term formed by multiplying both centered predictors; *a*, *b*, *c*, *d*, *e*, *f*, *g* and *h* are the fixed part of the parameters associated with the predictor variables; α_i, β_i, χ_i, δ_i, ζ_i, ϕ_i, γ_i, η_i, θ_i and κ_i are the random tree-level parameters, and $\varepsilon_{\mathrm{ij}}$ is the residual error term.

Although fitting models using centered variables as predictors has been shown to alleviate multicollinearity,[32] the existence of multicollinearity between the main terms and any variable derived from them (i.e. the multiplicative interaction term in equation (1)) was nonetheless assessed. In equations where the introduction of an interaction between variables was necessary (see Table 3), appropriate diagnostic statistics i.e. Variance Inflation Factor (VIF), condition number and variance proportions were computed as recommended by Belsley *et al.*[39] and these indicated no multicollinearity problems among the predictors.

Evaluation of model performance

The successive addition, at the tree level, of a random intercept term, followed by a random slope for each variable, improved the EF estimate of the mean ring density models (Table 2). Between stage 1 and stage 3, modelling efficiency was improved by more than 30% in the natural stand and by almost 50% in the plantation-grown trees. The specific inclusion of a correlation structure in the models resulted in a slight increase in both AIC and BIC (stage 4). The final models were hence systematically fitted according to stage 3 specifications. Model residuals

Table 2 Performance statistics of models at different stages of fit

Stage of fit	RMSE (kg m^{-3})	MAE (kg m^{-3})	MAPE (%)	Av. bias (kg m^{-3})	EF	Sim. F-test	AIC	BIC
Natural stand								
EWD								
1	57.5	45.6	7.8	0.0	0.11	0.0ns	5619	5649
2	44.0	34.2	5.9	0.0	0.48	0.19ns	5395	5396
3	40.3	32.1	5.5	0.0	0.56	0.84ns	5361	5364
4	40.3	32.1	5.5	0.0	0.56	0.84ns	5363	5366
LWD								
1	52.1	40.9	4.6	0.0	0.15	0.0ns	5540	5557
2	42.9	32.9	3.7	0.0	0.43	0.23ns	5387	5388
3	41.3	31.6	3.6	0.0	0.47	0.61ns	5375	5377
4	41.3	31.6	3.6	0.0	0.47	0.61ns	5377	5380
RD								
1	49.8	39.1	5.14	0.0	0.2	0.0ns	5484	5500
2	40.8	31.9	4.2	0.0	0.46	0.22ns	5327	5329
3	39.7	31.1	4.09	0.0	0.49	0.54ns	5320	5321
4	39.7	31.1	4.09	0.0	0.49	0.54ns	5322	5324
Plantation								
EWD								
1	50.9	40.9	7.5	0.0	0.17	0.0ns	2314	2334
2	38.0	30.2	5.6	0.0	0.54	0.62ns	2235	2237
3	34.4	27.5	5.1	0.0	0.62	1.59ns	2227	2229
4	34.4	27.5	5.1	0.0	0.62	1.59ns	2229	2232
LWD								
1	48.5	37.8	4.7	0.0	0.15	0.0ns	2309	2319
2	36.0	27.6	3.4	0.0	0.53	0.63ns	2232	2234
3	33.0	25.6	3.2	0.0	0.61	1.49ns	2225	2228
4	33.0	25.6	3.2	0.0	0.61	1.49ns	2227	2231
RD								
1	42.5	33.3	4.54	0.0	0.14	0.0ns	2237	2257
2	31.1	23.8	3.24	0.0	0.54	0.64ns	2150	2152
3	22.4	18.1	2.47	0.0	0.76	1.70ns	2092	2096
4	22.4	18.1	2.47	0.0	0.76	1.70ns	2094	2099

Stage 1: fixed effects only; stage 2: fixed effects and random tree effect on the intercept only; stage 3: fixed effects and random intercept and slope; stage 4: fixed and random tree effects and autoregressive correlation of the errors accounted for.

Explanation of abbreviations: RMSE = root mean square error; MAE = mean absolute error; MAPE = mean absolute percentage error; EF = modelling efficiency; Av. Bias = average bias; Sim. F-test = simultaneous F-test for intercept = 0 and slope = 1 and statistical significance established at the 5% rejection level.

$^{**}P$-value < 0.05.

^{ns}P-value > 0.05.

were examined, and were found to be evenly distributed around zero for all models from both stand types. At the 5% significance level, goodness-of-fit tests supported the assumption of normally distributed model residuals in every case. In addition, visual inspection of distribution histograms, probability plots and qq-plots confirmed no departure from normality. Simultaneous F-tests of bias showed that predictions were unbiased. The average percentage error associated with a single prediction was also very low (MAPE $< 5.5\%$). Graphs of observed *vs* predicted values show regressions very close to the 1:1 line in all models (Figure 1).

Interpreting the model parameters

Because the models were fitted using centered variables, the intercept values obtained (Table 3) correspond to the mean density values for each wood type given in Table 1. As expected from the analysis of covariance, the introduction of an interaction term between width and ring number in the models improved the LWD and RD models for the natural stand. The inclusion of the multiplicative interaction term in these models implies that the relationship between density and width depends on the specific values of ring number.[32]

The interaction is symmetrical and wood density could equivalently be expressed as a function of ring number conditional on width. In the context of this study, however, expressing the regression of density on width as a function of ring number is more coherent. Estimates of the standard deviation of the random effects represent the estimated between-tree variation around the population-level parameter estimates, and were generally higher for the random intercept than for the random slope terms (Table 3). Tree-level variation in the model intercepts was equivalent among stand types, whereas tree-specific variation

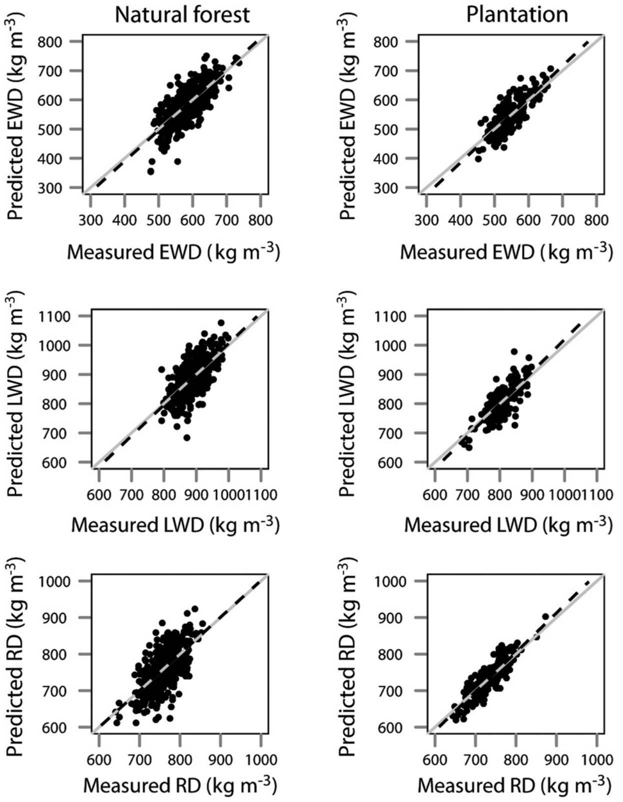

Figure 1 Measured density values plotted against values predicted with the models developed in this study. The dotted line represents the regression line and the solid grey line represents the line $y = x$.

in wood density associated with increasing ring number was of greater significance in the natural stand. Conversely, tree-specific variability associated with ring width was greater in the plantation, particularly for the RD model (Table 3).

Comparing the effects of ring number and radial growth rate on wood density between stand types

Wood density trends associated with variation in ring number and radial growth are presented graphically in Figures 2 and 3, respectively. For each stand type, predictions of wood density variation with ring number were calculated across the range of data using the mean width of each wood type at each ring number, while the variation with radial growth rate was predicted at fixed ring numbers (rings numbers 5, 15 and 40 for the natural stand model; rings numbers 5 and 15 for the plantation model). Density trends were discernible in both stand types, although the interaction term was not significant in the models fitted to the plantation dataset. Trends for specific wood types are presented in the following sections.

Earlywood density

Earlywood density generally decreased with ring number in both stand types, although the decline was more gradual in

Table 3 Estimation of fixed effects, standard error of random effects and residuals of models for early wood, late wood and ring wood density. Int: interaction term between ring width and ring number; a: intercept of the model fitted using centred values; σ_{tree}: random tree-level parameters associated with the variable indicated between parentheses; ε_i is the residual error term. Standard errors are given in parentheses. Non-significant random effects were omitted

	Int	a	Fixed effects parameters									Random effects parameters						Residuals
			$\sqrt{RNP}$	RNP	1/EWW	EWW	1/LWW	LWW	1/RW	RW	Int_{jk}	σ_{tree} (a)	σ_{tree} $\left(\frac{\sigma_{\text{tree}}}{\sqrt{RNP}}\right)$	σ_{tree} (RNP)	σ_{tree} (1/EWW)	σ_{tree} (LWW)	σ_{tree} (1/RW)	σ (ε_i)
Natural stand																		
EWD	–	583.5** (10.4)	−42.5** (11.6)	3.7** (1.3)	70.4** (16.4)	94.6** (26.5)	–	–	–	–	–	38.4	–	10.3	26.3	–	–	41.8
LWD	LWW × RNP	887.8** (8.5)	–	1.6** (0.3)	–	–	–	–	–	–	1.3** (0.3)	30.9	–	1.0	–	–	–	42.3
RD	(1/RW) × RNP	761.9** (8.0)	–	–	–	–	–	–	−78.0** (15.7)	–	−5.3** (0.8)	29.9	–	–	–	–	52.3	41.3
Plantation																		
EWD	–	542.4** (8.2)	−155.1** (35.1)	24.2** (6.4)	89.6** (18.9)	76.4** (13.1)	–	–	–	–	–	33	4.3	–	–	–	–	37.1
LWD	–	807.3** (7.7)	–	–	–	–	–	−15.5** (3.2)	–	–	–	31.2	–	–	–	10.4	–	35.3
RD	–	734** (7.0)	−113.2** (28.2)	16.6** (5.3)	–	–	–	–	−338.1** (82.3)	−18.6** (3.6)	–	28.7	–	–	–	–	139.3	24.8

**P-value < 0.05.
*P-value < 0.1.
^{ns}P-value > 0.1.

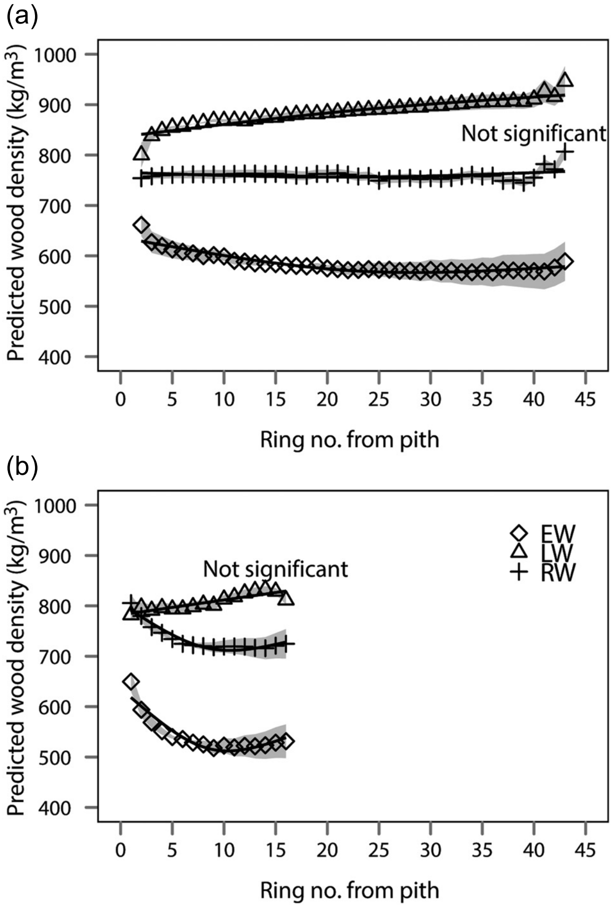

Figure 2 Comparison of the evolution of wood density with ring number (a) in the natural forest and (b) in the plantation (ring width not fixed). Symbols are simulated values, splines were fitted to the simulated values and greyed areas are 95% confidence intervals of simulated values. 'Not significant' denotes the non-significance of the slope parameter associated with the predictor.

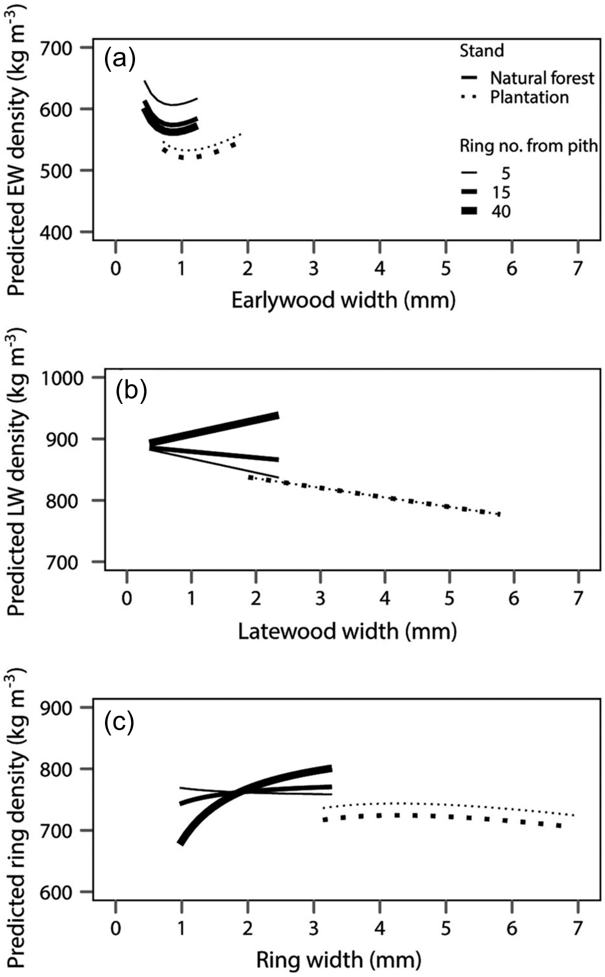

Figure 3 Comparison of the evolution of wood density with ring width for (a) earlywood, (b) latewood and (c) the overall ring at fixed values of ring number in the natural forest and the plantation. Latewood density in the plantation (b) is not age-dependent. Lines are simulated values.

the natural stand (Figure 2a). In the plantation, however, predicted EWD increased slightly after around 10 years of growth (Figure 2b). In both stand types, EWD showed a decreasing curvilinear trend with EWW, although the initial decrease was steeper in the natural stand (Figure 3a). Values of EWD decreased with increasing EWW to a minimum value, before increasing again in the widest earlywood bands (Figure 3a). In the plantation, EWD was higher at the maximum value of EWW than at the minimum value, while the opposite was the case in the natural stand. Overall, EWD was lower in the plantation than in the natural stand.

Latewood density

The overall trend with ring number was positive in the natural stand (Figure 2a), while the radial trend with age in the plantation-grown trees, although slightly positive, was not significant (Figure 2b). The relationship between LWD and LWW was modified by ring number in the natural stand, with the direction of the effect evolving from negative to positive values at higher ring number (Figure 3b). In the plantation, however, LWD decreased with increasing LWW (Figure 3b), although the main effect of ring number and the interaction between the explanatory variables were not significant.

Overall ring density

The overall effect of ring number in the natural stand was non-significant (Figure 2a), while in the plantation, RD declined in the first 10 years before reaching more stable values (Figure 2b). In the natural stand, the effect of RW on RD was modified by ring number, changing from a slightly negative relationship at a ring number 5 to a strongly positive effect at ring number 40 (Figure 3c). In the plantation, RD decreased with increasing ring width, with slightly lower values at a ring number 15 than at ring number 5 (Figure 3c). Figure 4a shows that the proportion of latewood within annual rings increased with enhanced growth rate in both the natural forest (from 50% to 85% for rings ranging

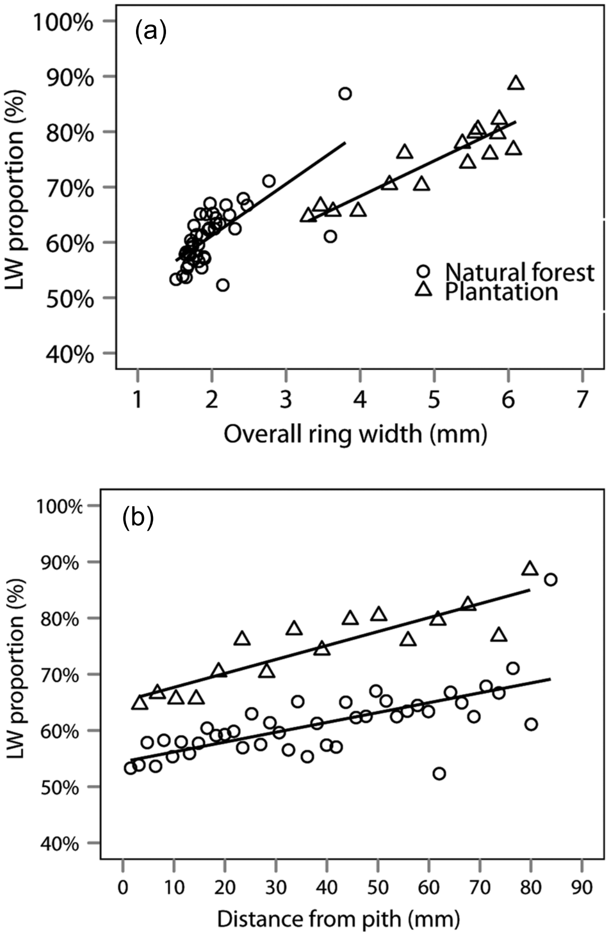

Figure 4 Evolution of the proportion of latewood within annual growth rings (a) as a function of ring width, and (b) as a function of distance from the pith, in the sampled trees of the natural forest and of the plantation. Straight regression lines were fitted through the points.

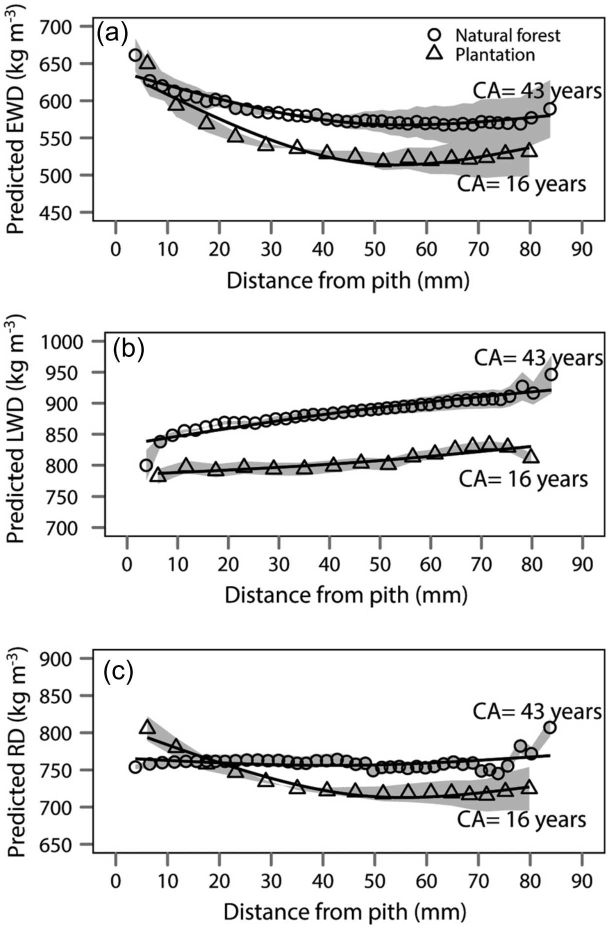

Figure 5 Evolution of wood density with ring radial position in the stem (distance from pith) for (a) earlywood, (b) latewood and (c) the overall ring in the natural forest and the plantation (ring number not fixed). Symbols are simulated values, splines were fitted to the simulated values and greyed areas are 95% confidence intervals of simulated values.

between 1.5 and 4 mm) and the plantation trees (from 60% to 85% for rings ranging between 3.2 and 6.5 mm). The proportion of latewood increased with increasing distance from the pith at both sites, but was consistently higher in the plantation-grown trees (Figure 4b).

Comparing variations in density between stand types for a given distance from the pith

Because intensive silvicultural practices aim to improve radial growth rate and shorten rotation age, we examined the variations in density with distance from the pith for trees grown under natural and intensive management conditions (Figure 5). Although the plantation-grown trees were on average 2.5 times younger than those from the natural stand, they had reached equivalent diameters (16.0 cm and 16.8 cm in the plantation and in the natural stand, respectively) by the time of sampling. Differences in RD and EWD between the stands tended to increase in the first 5 cm from the pith, with values generally lower in the plantation, although at distances greater than 6 cm the differences became smaller. Differences in LWD, however, remained constant between the natural stand and the plantation (Figure 5). The influence of stand type on the evolution of the relative proportions of early- and latewood within the annual growth rings was evaluated on the sample trees. A two-way ANCOVA was performed to compare the slopes of the linear regression lines in Figure 4 using ring width and stand type as covariance factors. *F*-tests indicated no significant differences between the slopes for both wood types and both stand types (F_{EW} (3, 54) = 1.56, ms = 0.003, $P = 0.2170$; F_{LW} (3, 54) = 1.74, ms = 0.003, $P = 0.1927$).

Discussion

Age-related characteristics of the wood samples

The transition between juvenile and mature xylem is estimated to occur at around 25–30 years in European oak.[19,40] However, the transition age could be higher in plantation-grown trees, since management practices that stimulate crown development have been shown to prolong the formation of wood with juvenile properties in the stem.[41] Considering the age of the trees sampled in this study, it is highly probable that our samples were composed mainly of juvenile wood, a fact that was taken into consideration when interpreting the results.

Tree-to-tree variation in wood density

The large between-tree random variation in the model intercepts has also been found in other studies relating wood density in various oak species to growth variables.[7,14,15,18,42,43] This effect is thought to reflect intrinsic genetic differences among trees.[5,7] Tree-to-tree variation in wood density was mainly independent of growth variables, although in some models there were significant tree-level random slopes for the ring number or ring width parameters. This indicates that trees respond differently to equivalent changes in radial growth and ring number, as previously observed by Guilley *et al.*[7] However, the greater relative importance of the random slope for ring number in the natural stand and of the random slope for ring width in the plantation might simply reflect the greater range of ages in the natural stand and of ring widths in the plantation, respectively.

The influence of stand type on the relationship between wood density and ring number

Earlywood density

Decreasing earlywood density with increasing ring number under the different stand types in this study is consistent with observations on other oak species.[7,18] From the work of Gasson,[40] we know that an increase in mean earlywood vessel diameter with ring number is typical of juvenile xylem. When xylem maturation processes begin, earlywood vessel diameter fluctuates across growing seasons, but other associated anatomical changes, such as enlargement of vessel and fibre lumens, decreasing proportion of high density fibres and lower density of axial parenchyma, imply a persistent reduction of earlywood density over time.[19,43,44] The parabolic trend in EWD with ring number observed in the plantation might therefore be an artefact of the modelling process, when in fact the overall direction of change over time remains negative. Possibly as a result of the positive effect of thinning on earlywood vessel diameter,[45] earlywood density of the plantation trees in this study remained lower than that of the natural forest trees.

Latewood density

In the natural forest stand, there was a positive linear overall effect of ring number on LWD. This result is in accordance with previous work, which reported an increase in the latewood density of oak juvenile wood with ring number.[19,46] These authors highlighted the fact that, whereas in mature xylem vessel diameters abruptly decrease at the transition point between early- and latewood, in juvenile xylem the reduction in vessel diameter is more gradual. During the first years of growth, the diameter of latewood vessels therefore progressively decreases, leading to increased latewood density. Both studies, indicated that the relationship was parabolic and that the relationship of latewood density to ring number is likely to become negative after around 30 years of growth. Other studies on mature wood in oak species have confirmed this observation.[7,15,18,19,43,46–48] In addition to the linear relationship found in the current study, ring number appeared to modify the relationship between LWW and LWD in the natural stand. In the first years of growth there was a negative correlation between latewood density and latewood width, but this relationship became positive from ring number 20 to 30. This means that for a given ring width, the latewood produced by older cambium will have higher density, with the difference being more apparent in wider growth rings. As far as we are aware, no other studies exist that have reported on the effect of the interaction between ring width and ring number on latewood density. The lack of a significant relationship between latewood density and ring number in the plantation could be due to the lower range of ring numbers in those samples.

Overall ring density

Overall ring density showed no significant relationship with ring number in the natural forest stand. However, ring number modified the relationship between ring density and ring width such that the direction of the relationship became positive in older annual rings. The unbalanced nature of each data set with respect to the range of tree ages in each stand makes differences associated with ring number more difficult to interpret.

Since growth rings are composed mostly of latewood, the increase in overall ring density with increased growth rate can be related to an equivalent trend in latewood density with latewood width at higher ring numbers. In a study on East-Liaoning oak (*Quercus liaotungensis*), Zhang and Zhong[46] reported similar results. For a given width, they found that wood density increased until approximately ring 30, before decreasing again thereafter.

In the plantation, overall ring density decreased with increasing ring number, reaching stable values after an initial decline in the first few growth rings. Since latewood density in the plantation trees was not influenced by ring number, decreasing overall ring density with ring number is likely to be associated with the observed decrease in earlywood density as the cambium matures.

The influence of stand type on the relationship between wood density and growth rate

Earlywood density

The curvilinear relationship between earlywood density and earlywood width was observed in both stand types, but with an overall trend of increasing EWD with increasing EWW in the plantation. We are not aware of any studies specifically relating juvenile earlywood density to ring width, but results reported for mature European oak indicated a positive relationship between earlywood density and width.[7,10] In the latter studies, the observed relationship was associated with anatomical changes in the earlywood, such as an increased proportion of lignified rays and a slight decrease in the proportion of axial parenchyma.[44] These contrasting results, therefore, could be attributable to differences in the internal anatomy of juvenile and mature xylem. In the current study, enhanced growth during the period of juvenile wood formation initially resulted in the production of less dense earlywood cells, although the density of earlywood began to increase at higher values of EWW. In addition, EWD was generally lower in the plantation-grown trees than in the natural stand. Lower earlywood density in trees from intensively-managed stands is in agreement with the work of Phelps and Workman,[45] who observed a positive effect of commercial thinning on the percentage area of earlywood vessels in white oak (*Quercus alba* L.) trees before cambial maturity. Our results suggest that the effect of enhanced radial growth on the anatomical properties of juvenile earlywood would be stronger in plantation-grown trees than in trees from natural stands.

Latewood density

Although the relationship between LWD and LWW in the natural forest varied with ring number, the overall effect of LWW was non-significant. This is consistent with the findings of previous studies on the juvenile wood of various oak species.[19,46] Rao *et al.*[19] did not find any significant variation in juvenile latewood anatomy due to increased ring width. Conversely, in the plantation-grown trees in the current study, latewood density decreased linearly with increasing growth rate. This result suggests that silvicultural treatments dedicated to radial growth enhancement could have some influence on the anatomical structure of red oak latewood over the period of juvenile wood formation. This finding is consistent with the work of Phelps and Workman,[45] who also reported a higher proportion of latewood vessels in commercially-thinned white oak trees. An increase in the porosity of the early- or latewood, which would improve water transport to the more vigorous crowns, could explain this result.

Overall ring density

A slight decrease in ring density with enhanced radial growth rate was observed at ring number 5 both in the natural stand and in the plantation, but in the natural stand the relationship became positive at higher ring numbers. This seems to support our initial hypothesis that the positive relationship between ring density and ring width described in the literature would not hold in plantation-grown trees. However, the higher ring numbers at which this positive relationship was observed were not attainted in the plantation trees. For the range of ring number that was common to both stand types, i.e. from 0 to 15, the relationship was almost equivalent.

The results observed in the natural stand are consistent with previous findings on mature wood density in various oak species.[7,15,18,43,46] Conversely, in studies of juvenile wood density in *Quercus liaotungens* and *Q. robur* L., respectively, Zhang and Zhong[46] and Rao *et al.*[19] found no significant correlation between average ring density and growth rate.

Future studies should test the same hypothesis with older plantation trees. However, for wood quality considerations, the consequences of faster growth do not depend only on the relationship between ring width and wood density at a given ring number, but also on the range of ring number that will be included within a log at the end of the rotation.

The influence of stand types on the relationship between wood density and distance from the pith: implications for silvicultural practices

The relationships between growth variables and wood density in the different stand types should be compared with caution, due to the possible confounding influence of site conditions. However, in the course of normal forest operations, trees are harvested at a specified target diameter rather than at a fixed age. The implications for wood quality of different forest management systems should therefore be discussed in terms of stem diameter at harvest. In northern red oak this is typically up to 50cm. After 22 years of simulated growth, the plantation trees in this study reached a mean DBH of 16 cm (Figure 5c). If the current growth rate is maintained, these trees should reach commercial maturity just after 60 years of age, while natural forest trees would require a further 100 years to reach harvestable size.

Studies conducted on mature oak species concluded that wood properties would be enhanced in fast-grown oak because slower growth resulted in a higher proportion of earlywood in the annual rings.[15,46,49] The present study supports these findings, since the proportion of earlywood in the plantation trees was consistently lower than in the natural stand, for a given distance from the pith. However, wood density averaged over the radial profile of the mean tree from each stand was observed to be slightly lower (3.4%) in the plantation than in the natural stand. This was mainly attributable to differences in earlywood and latewood densities, which could also have been influenced by site conditions. However, the uncertainty surrounding these differences does not alter the conclusions of this study since the expected wood density of red oak for wood processing is 705 kg m^{-3}.[50] Based on the results of this study, silvicultural interventions designed to improve growth rate in red oak would not be detrimental to overall wood density, even though trees would most likely contain a higher proportion of juvenile wood at harvest.[41] However, a comprehensive financial analysis will be necessary in order to determine whether the increased costs associated with intensive silvicultural treatments (e.g. establishment, thinning, pruning) will have a significant impact on the profitability of fast grown red oak stands.

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