Influence of wood density in tree-ring based annual productivity assessments and its errors in Norway spruce.

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Abstract

Estimations of tree annual biomass increments are used by a variety of studies related to forest productivity or carbon fluxes. Biomass increment estimations can be easily obtained from diameter surveys or historical diameter reconstructions based on tree rings records. However, the biomass models rely on the assumption of a constant wood density. Converting volume increment into biomass also requires assumptions on the wood density. Wood density has been largely reported to vary both in time and between trees. In Norway spruce, wood density is known to increase with decreasing ring width. This could lead to underestimating the biomass or carbon deposition in bad years. The variations between trees of wood density has never been discussed but could also contribute to deviations. A modelling approach could attenuate these effects but will also generate errors.

Here were developed a model of wood density variations in Norway spruce, and an allometric model of volume growth. We accounted for variations in wood density both between years and between trees, based on specific measurements. We compared the effects of neglecting each variation source on the estimations of annual biomass increment. We also assessed the errors of the biomass increment predictions at tree level, and of the annual productivity at plot level.

Our results showed a partial compensation of the decrease in ring width in bad years by the increase in wood density. The underestimation of the biomass increment in those years reached 15%. The errors related to the use of an allometric model of volume growth were modest, around ±15%. The errors related to variations in wood density were much larger, the biggest component being the inter-tree variability. The errors in plot-level annual biomass productivity reached up to 40%, with a full account of all the error sources.

Key words: Forest biomass, Uncertainty propagation, Bayesian framework, Wood density, Norway spruce, tree-ring

1 Introduction

Predicting trees biomass increment is a key step in quantifying and understanding forest productivity. Considerable efforts have been spent to evaluate forest productivity and carbon sink strength (Ciais et al., 2008). While productivity has long referred to volume growth, amply used in the forest management and displayed in yield tables, the focus recently switched to biomass, for its relationships with energy or carbon storage. Field-based estimations of biomass growth have a wide variety of applications, from forestry to carbon fluxes estimation, for example in comparison against eddy covariance (Barford et al., 2001; Rocha et al., 2006; Gough et al., 2008; Curtis et al., 2011; Ilvesniemi et al., 2011). Considerable efforts have been spent to estimate annual forest productivity in relation to climate fluctuations and forests carbon sink strength (Richardson et al., 2010; Wu et al., 2013). The importance of having both annual resolution and high spatial coverage has been illustrated by numerous studies (e.g. Reichstein et al., 2003; Ciais et al., 2005; Beer et al., 2010). Several methods are used to estimate forest productivity and carbon sink: eddy covariance, modelling, or field-based estimations such as inventories or tree-ring studies. Tree-ring based studies have the advantage of offering a large spatial covering, a potentially long time scale and also an annual resolution. They are therefore amply used to produce reference annual biomass production estimations, to compare against other methods (Beck et al., 2011; Babst et al., 2014a) or to bring complementary information (Babst et al., 2013). However several issues are associated to the use of tree-ring based estimations and the estimation of their error remains a critical poorly documented (Nickless et al., 2011).

In the reconstruction of the annual productivity or of the above-ground carbon uptake from field-based studies, one limiting element is the estimation of the wood density variations (Babst et al., 2014a). Indeed, volume increment time series can be produced by a variety of methods, such as the reconstruction of the diameter growth based on tree rings (Wirth et al., 2004; Rocha et al., 2006) or inventory reconstruction (Ohtsuka et al., 2007), but none of these methods bring information on the variation of wood density. Converting volume into biomass requires an estimation of the wood density, which is most likely based on literature and therefore neither related to site conditions, nor to trees growth rate, as for example in Vila et al., (2013). In the same manner, biomass equations implicitly rely on the use of an average and constant wood density despite the many evidences of substantial wood density variations. In both cases, wood density is considered constant in time, and equal between trees.

Wood density has however been acknowledged as a highly variable characteristic and several major sources of annual density variations have been identified. Very high precision in the description of the wood density variations with new techniques (e.g. SilviScan, Evans, 1994) are possible but not widely available, while other techniques based on X-ray are rather time consuming and thus not applied to forest productivity studies. Within-tree variations occur at distinct time scales (Jyske et al., 2007). Over medium or long scales, annual wood density was proved to be related to ring age or to tree diameter, with higher values close to the pith in many species (Schweingruber, 1988). At inter-annual scale, wood density variations can be substantial. There were several reports that (annual) ring density decreases with increasing ring width, for instance in Norway spruce (Bergqvist, 1998; Dutilleul et al., 1998; Lundgren, 2004; Bouriaud et al., 2005; Franceschini et al., 2010; 2013). Wood density was also proved to vary between trees (Wilhelmsson et al., 2002; Guilley et al., 2004), a fact which is never accounted for in studies using diameter surveys to produce biomass increment estimations.

The variations of wood density between trees and between years could compensate the variations in annual volume increment, or at least soften them. Recent studies brought evidences of such compensation, proving that neglecting annual wood density fluctuations could lead to substantial errors or bias in estimating the biomass (Molto et al., 2013; Babst et al., 2014a). The errors generated by neglecting the variations in wood density have been considered as small compared to those resulting from that of the volume increment estimation, but to our knowledge, such assumptions were never tested and the consequences not documented.

To be properly quantified, the consequences of neglecting wood density fluctuations between years and between trees had to be tested using an integrated approach, whereby the errors of the density model are propagated and combined with those of the model for volume growth. Such chain can be decomposed, and the impact of each step studied by modelling the steps into a single Monte Carlo Markov Chain (MCMC) process (e.g. Molto et al., 2013). Analytical solutions to estimate the biomass estimation error, based e.g. on Taylor expansion can sometimes be determined, depending on the model's complexity. But the errors of biomass increment, obtained by subtracting subsequent estimations, are anyhow less predictable and particularly challenging at the plot level, when summing tree-level estimations (Nickless et al., 2011). The MCMC approach therefore appears as the most suitable to estimate the biomass increment, where such estimations and the propagation of the errors from one model to another is done without assumptions.

Our study aimed at quantifying the impact of density variations, both between years and between trees, on the estimations of annual biomass increment in Norway spruce (*Picea abies*), and compare it with the impact of volume increment estimation errors. The objectives were: (i) to quantify and model the influence of annual radial growth variations on wood density, (ii) to quantify the consequences of annual and between tree variations of wood density on biomass increment estimations and (iii) to compare the errors related to wood density estimations to those of volume increment.

2 Material and methods

2.1 Site, sampling and data

All samples analysed for this study were taken from the Wetzstein site near the village of Lehesten in Thüringia, Central Germany (50º45'N, 11º46'E, ~ 760 m a.s.l.), which was amply used for eddy covariance measurements (e.g. Anthoni et al., 2004) or biomass modeling (Wirth et al., 2004). The site is characterised by mono-specific Norway spruce (*Picea abies* L.) stands. The climate is typical for the mid-elevation montane sites with an annual mean temperature of 6ºC and a mean annual precipitation sum of ~1000 mm. Soils have a sandy loam texture. The footprint of the eddy covariance tower is dominated by an extensive 80 (±2.1 SD) year old stand. This stand is mostly even-aged but also contains pockets of regeneration and scattered emergent trees. The footprint stand is surrounded by three even-aged stands with a mean age of 15 (±0.86), 38 (±7.9) and 116 (±1.3) years. The four stands representing the site are referred as W15, W38, W72 and W116

This study combines data from three successive samplings realized in this site: (i) Stem analysis performed to quantify the relationship between breast-height radial growth and stem volume increment. This was achieved in connection with a biomass harvest of the four stands (see below). (ii) Wood density measurements were done for selected harvest trees to establish a relation between ring-width and wood density variations, and (iii) a dendro-chronological analysis of inter-annual growth variation of many trees using micro-cores for scaling up to the plot-scale. The volume increment and wood density and volume increment measurements are used exclusively to develop models, while the micro-cores sampling is used as an application to quantify and compare the errors of each model on this representative case study.

2.1.1 Stem analysis for volume increment

The stem volume increment model was fit based on a stem analysis realized on 22 trees – seven samples in the footprint stand W72 and five in each of the additional stands (W15, W33, W116). Trees were selected to represent seven/five dbh (diameter at breast height) classes defined based on the population of all inventoried trees (W15: n = 144, W38: n = 59, W72: n = 133, W116: n = 68). Jointly, the 22 trees represented the size range (dbh between 7.3 and 59.5 cm) and age range (between 14 and 117 years) of Norway spruce trees at the Wetzstein site. This comprehensiveness ensures applicability of the models for all trees in the inventories of the test site. Trees were felled in the context of a full biomass harvest. The circumference was measured every meter along the bole where a 3-8 cm thick disc was cut in order to determine annual increment along the entire stem. All discs were dried and sanded with a belt grinder. The ring width series was measured along four radii on each disc. The average diameter increment measured on the lower and upper disc of each 1 to 2 m segment was used to calculate the increment of under bark volume in successive years using the formula for a truncated cone. The difference in volumes of all segments per tree of successive annual time steps yielded stem dry wood production of individual trees. The dendrochronological analysis was carried out using a digital tree ring measurement device (LINTAB III Digital Linear Table; 410-1/100-HF-130, Frank Rinn Distribution, Heidelberg, Germany) in combination with the software TSAP (Time Series Analysis Program, Frank Rinn Distribution, Heidelberg, Germany).

2.1.2 Wood density measurements

For the annual wood density (WD) measurements wood discs were sampled at breast height from trees representing the lowest, the central and the highest diameter class in each of the four stands. This yielded a total of 12 sample trees, again representing the size and age range of Norway spruce tree at the site. Two 1-2 cm-wide slices from opposite radii were sawn from the wood discs, for which wood density was measured by X-ray densitometry in the densitometric Laboratory of Krasnoyarsk, Russia (Walesch Electronics, Switzerland) using the standard procedure described by Schweingruber (1988). Longitudinal strips with a constant thickness of 1.2 mm were sawn, air dried, and exposed to X-ray radiations for 1 h on a Kodak TL film using standard exposure conditions: acceleration tension of 8.5 kV, flux intensity of 15.0 mA, distance to the source of 3.5 m. Annual wood density (WD, kg m^{-3}) values were obtained from density profiles of single tree-rings as the total mass of earlywood and latewood divided by tree-ring width. X-ray derived densities represent dry wood. Rescaling to fresh wood dimensions was not done as all ring-width series (stem analysis and micro-cores) were measured on dry wood.

2.1.3 Application dataset

The volume increment and WD models were applied together on an independent set of trees sampled in 13 randomly placed inventory plots inside the footprint stand W72. The plots were established within the context of the project FORCAST (Rey and Jarvis, 2006). From 31 to 62 trees per plots (551 in total) with diameter varying from 8 to 51 cm (thus well within the range of the sample trees) were sampled for historical diameter reconstruction based on micro-cores. The micro-cores enabled the reconstruction of the past growth over the last 10 years only, since these short cores are ~2 cm long. The diameter was reconstructed based on the simple assumption of proportionality of the bark thickness to the diameter using the external diameter of the trees at sampling.

2.2 Wood density and annual volume increment modelling

Models of WD or annual volume increment were fit using both maximum likelihood methods and MCMC approach. The structure of the two models was first determined using likelihood fits before being implemented in a Bayesian MCMC framework using WinBUGS 1.4 (Spiegelhalter et al., 2003), based on the same datasets exactly, using non-informative flat priors. The maximum-likelihood estimations were realized using the nlme package (version 3.1-102, Pinheiro et al., 2011) of R (R version 3.0.1, R Development Team, 2014).

2.2.1 The wood density model

Following recent publications on Norway spruce wood density (Franceschini et al., 2010; 2013), the diameter and the ring cambial age (as counted from the pith) were used as independent variables. The selection of the model was based both on the AIC (Akaike Information Criterion) and the examination of the residual distribution. Fixed and random tree-level effects were considered. The principle of parsimony was also followed in the model building process, and random effect parameters were considered only if improvements were observed based on the likelihood ratio test.

Several candidate models were tested, as follows

$$WD_{ij} = a_0 + a_1 RW_{ij} + a_2 RW_{ij}^2 + \frac{a_3}{X_{ij}} + \varepsilon_{ij} \quad (1)$$

$$WD_{ij} = a_0 + \frac{a_1}{1 + RW_{ij}} + \frac{a_2}{X_{ij}^{a_3}} + \varepsilon_{ij} \quad (2)$$

$$WD_{ij} = a_0 + a_1 RW_{ij}^{a_2} + \frac{a_3}{X_{ij}^{a_4}} + \varepsilon_{ij} \quad (3)$$

where i denotes the tree and j the year, $a_0 \ldots a_4$ are fixed effects and potentially random tree-level effects, X is either DBH or cambial age, $\varepsilon \approx N(0, \sigma^2)$. Random effects are assumed to be normally distributed.

2.2.2 The annual volume increment model

The annual volume increment was modelled as a non-linear function of ring width and tree diameter, based on the annual estimations of volume growth resulting from the detailed stem analysis. The model reflects the fact that, for a given ring width, volume increment depends strongly on the current size of the tree, here its diameter, mostly for geometrical reasons. The taper was therefore not supposed to be constant in time, and the trends in tree growth with age were directly absorbed in the model since the volume increments resulted directly from the stem analysis measurements, not from using models. Another specificity of this model was the specification of a variance function in order to cope with the heteroscedasticity in the errors. The resulting model is given in equation 4 and includes random coefficients for the exponent b_3:

$$\Delta Vol_{ij} = b_0 + b_1 DBH_{ij}^{b_2} RW_{ij}^{b_3} + \varepsilon_{ij} \quad (4)$$

where $b_{3,i} = c_3 + d_{3,i}$ is the sum of a fixed parameter c_3 and a random tree-level term $d_{3,i} \sim N(0, \sigma_{d3})$ that varied for each tree *i*.

The residual ε_{ij} was modeled as a power function of the diameter:

$$\varepsilon_{ij} = b_4 + DBH^{b_5} \quad (5)$$

2.3 Application to a case study, scenarios of biomass increment

The micro-cores dataset was used as a concrete case study for estimating the consequences of wood density variations and comparing the errors resulting from the wood density and from the volume increment model. Both models were fit based on their specific datasets within the MCMC framework, then the parameters and the variance terms estimated were applied to compute the biomass increment of the micro-cores trees, which represents an external set. The models were therefore fit using the same structure as that used in the likelihood method, the parameters estimated being further used to produce estimations of WD or annual volume increment on the micro-core trees. Having both the fitting and the application run in a single MCMC loop enables the propagation of the errors of each model.

The tree-level biomass increment estimations were the product of the WD and the volume increment, then summed up to obtain stand-level per-ha biomass estimations based also on the plot size. But according to the way the errors could be accounted for, four different scenarios were distinguished:

1) The baseline scenario was using a constant wood density set to be equal to the average observed value across the dataset (475 kg m^{-3}). The volume increment is estimated based on the model fitted but without considering random tree-level variations (using the fixed part of the model only) and without residual error (ε_{ij} =0). Thus, for tree *i* and year *j*, the biomass increment was computed as

$$\Delta B_{ij} = \quad 0.475 \cdot \Delta Vol_{ij} \quad \text{where } \Delta Vol_{ij} = b_0 + b_1 DBH_{ij}^{b_2} RW_{ij}^{b_3}$$

Only the fixed part of the parameters b_0 to b_3 was used.

2) In the second scenario, the annual wood density was held constant but the volume increment included both the random tree-level variation and the residual error.

For tree *i* and year *j*, the biomass increment was computed as:

$$\Delta B_{ij} = \quad 0.475 \cdot \Delta Vol_{ij} \quad \text{with } \Delta Vol_{ij} = b_0 + b_1 DBH_{ij}^{b_2} RW_{ij}^{b_{3,i}} + \varepsilon_{ij} \quad (6)$$

where $b_{3,i} = c_3 + d_{3,i}$ is the sum of a fixed parameter c_3 and a random tree-level term that varied for each tree *i* and sampled as: $d_{3,i} \sim N(0, \sigma_{d3})$, σ_{d3} being estimated from the volume increment fit dataset. Thus, the parameter d_3 for the application varies from tree to tree and is being sampled from within the variability observed in the fit set. ε (the residual variation) is computed as a function of the diameter as presented in Eq. 5. All the parameters and the variance estimations were made by the Bayesian model within the MCMC loop.

3) In the third scenario, the biomass increment was defined as the product of the parametric estimations of both the WD and the annual volume increment: here only the fixed part of the models was used to produce both the WD and the volume increment estimations, while not accounting for random effects or residual variance. This represents the most common and probable use of such models, when no data are available for a calibration.

$$\Delta B_{ij} = \quad WD_{ij} \cdot \Delta Vol_{ij} \quad \text{where}$$

$$WD_{ij} = a_0 + a_1 RW_{ij}^{a_2} + \frac{a_2}{DBH_{ij}^{a_3}} \text{ and } \Delta Vol_{ij} = b_0 + b_1 DBH_{ij}^{b_2} RW_{ij}^{b_3}.$$

Only the fixed part of the parameters are used.

4) In the last scenario, a full error propagation was conducted: the random and the residual errors of both the WD and the volume increment models were used to produce the biomass increment estimation.

$$\Delta B_{ij} = \quad WD_{ij} \cdot \Delta Vol_{ij} \quad \text{with } WD_{ij} = a_{0,i} + a_{1,i} RW_{ij}^{a_2} + \frac{a_{3,i}}{DBH_{ij}^{a_4}} + \varepsilon_{ij}$$

having $\forall k \in (0,1,3)$, $a_{k,i} = \alpha_k + a_{k,i}$ where α_k is the fixed part of the parameter, a_k the random component, $a_{k,i} \sim N(0,\sigma_{ak})$ and $\varepsilon_{ii} \sim N(0,\sigma_{WD})$ where σ_{WD} is the residual variance, estimated on the WD fit set.

$\Delta Vol_{ij} = b_0 + b_1 DBH_{ij}^{b_2} RW_{ij}^{b_{3,i}} + \varepsilon_{ij}$ with $b_{3,i} = c_3 + d_{3,i}$ and $d_{3,i} \sim N(0,\sigma_{d3})$ as in scenario 2, and $\varepsilon_{ii} \sim N(0,\sigma_{\Delta Vol})$ where $\sigma_{\Delta Vol}$ is the residual variance, estimated on the volume increment fit set.

Thus, four different biomass increment estimations were produced, according to the density estimation and the error propagation, and their difference summed at plot level. In all the scenarios, volume increment was estimated based on measured ring width series and the historical diameter of the trees.

The MCMC process generated posterior distributions of the model parameter estimates, with their associated errors, and the estimations of the variance of the random effects based on the Metropolis-Hastings algorithm over 10^4 iterations. It also produced estimations of wood density, a volume increment computed from the fitted model and applied to new data, along with a prediction uncertainty interval, here represented by the range between 2.5 and 97.5% of the estimates distribution density. The first 4000 iterations were used as pre-convergence and thus were excluded from estimations, which were based on subsequent iterations only.

3 Results

3.1 Describing wood density variability

The (annual) ring wood density (WD) varied from 287 to 787 kg m^{-3} with within-trees variations as considerable as variations between trees. Individual tree-ring series showed a reduced WD in the first 5-10 years, followed by a linear increase up to 60 years and then fluctuated around a tree-specific sill (Fig. 1a). Variations difference between two successive years reached 200 kg m^{-3}.

Figure 1.

Variations in WD were mostly related to ring width with a linear correlation of -0.75 ($t = -39.23$, $df = 1199$, p-value $< 10^{-4}$) when pooling the data from all cores (Fig. 1b). As shown in figure 1, WD series with very distinct average density values were seemingly following the same linear pattern. The correlation with age was not as high ($R_{Pearson} = 0.38$, $t = 14.25$, $df = 1199$, p-value $< 10^{-4}$).

3.2 Modelling annual wood density variability

The selection of the WD model resulted from the comparison of several models based on independent variables such as ring width, cambial age and diameter. The models offered very comparable results (Table 1) although model 2 had a greater Root Mean Square Root (RMSE) and bias. Using cambial age or diameter as second independent variable did not lead to significant differences in the fit according to the Likelihood Ratio Test (LRT). Nevertheless, models differed in the ease of the convergence or on the sensitivity to initial parameters provided. The exponent parameters a_2 and a_4 of the independent variables (RW and X) being close to 0.5 in model 3, a simplification was tested which enabled to reduce the number of parameters and considerably eased the fitting, whereby both exponents were fixed to 0.5. This simplification did not lead to a significant change in the AIC. The model retained was therefore the model 4 derived from Eq. 3 with exponent parameters set to 0.5, and with the DBH as second independent variable, which is also a variable easier to measure than the cambial age.

Table 1.

3.3 Modelling the annual volume increment

The volume increment model was fit as a function of diameter and ring width, with fixed and random tree-level effects, to a set of 22 trees. The intercept was kept free after testing its significance using the LRT by comparing models with intercept held constant or forced to 0. It appeared that a free intercept increases the likelihood, while the estimated value of the intercept was very realistic. The use of a weight function (constant plus power) was also amply confirmed by the LRT (L.ratio=1368, $p<0.0001$). Thus, the final model consisted in a function of diameter and ring width, with fixed and random (tree level) parameters weighting (Table 2). The adequacy of the model was confirmed by the standardized residuals plot (Fig. 2).

Figure 2.

Table 2.

3.4 The compensation problem: WD buffers annual volume increment variations

Provided that there was an overall decrease in wood density with increasing ring width, a compensation of ring width annual variability by wood density was also probable. The ring width series showed peak years of growth (e.g. 1967, 1989) or depressions (1976, 1983). In these years, the radial growth was much more affected than the wood density, as suggested by the deviations relative to the mean value calculated over the entire series length. The deviations peaked in 1967 at +30±12% (±standard error), which means a radial growth greater than average by 30%, while the reduction of density was only -5±2%. In 1976, the growth reduction was -30±6% but the density did not significantly increase: +1±2%. The consequences for biomass increment of neglecting the annual WD variations is further shown in Fig 3 where the biomass increment was estimated for the trees used for WD measurements. The annual volume increment was estimated by applying the model fitted (Eq. 4), multiplied by either the annual WD values or by the mean WD for each tree and radius. The deviation between the two estimates are expressed as a percentage of the annual biomass increment using annual WD values. Although the deviations seemed random (Fig. 3a), their ordination in time proved that they were not, and that they exceeded 15% on average among all trees during extreme years (Fig. 3b).

Figure 3.

3.5 Application to an independent data set

The two models presented and fitted above were introduced in the Bayesian framework, with the same structure exactly and on the same data, and further re-fitted using the MCMC method. A comparison of the parameters estimated by both methods is presented in table 2. Expectedly, the parameters were not exactly the same but very close, and the correlation between the predictions was very high.

When applied on the independent application set, the estimated wood density varied from 278 to 541 kg m^{-3}, with a mean of 425 (±35) kg m^{-3} as a result of the variable ring-width and diameter input values. The model reproduced large between-tree differences for a given year, up to 225 kg m^{-3}. Including random effects did not affect the prediction mean (Fig. 4). The overall (pooling trees from all plots together) average difference between the two predictions was only 0.1 kg m^{-3}. The inclusion of the random effects changed the predictions only very marginally but increased the prediction interval five times: it jumped from ±20-40 kg m^{-3} to ±160 kg m^{-3}. Accounting for the residual variation (the epsilon term in Eq. 3) increased only slightly the prediction interval: it added an extra ±10 kg m^{-3}.

Comparable results were obtained with the volume increment model: the contribution of the random effects and the inclusion of the residual variance inflated substantially the prediction interval (Fig. 4). Nevertheless, the relative prediction interval were substantially lower than that of the wood density: typically less than 40% of the predicted value, against 60% for WD.

Figure 4.

3.6 Consequences of WD variations and error sources for the biomass increment estimations

3.6.1 At tree level

The annual variations of the predicted biomass increment resulting from considering a dynamic wood density were always smaller than predictions based on a constant density (Fig. 5). The prediction uncertainty was considerably higher when accounting for random effects on either the WD or the volume increment. The full error propagation (sc4) had a relative prediction uncertainty up to 60% of the predicted value on average, occasionally reaching or overcoming 100%. Constant density predictions had logically the lowest uncertainties (less than 10%) since they include only the error from the volume increment estimation. Wood density had the greatest contribution to the prediction uncertainty, and mainly through the between-tree variations. The parametric estimation (sc3) had a prediction interval four times lower than the full error propagation prediction (sc4), showing an underestimation of the error made by considering the uncertainty related to the regression coefficients only.

Figure 5.

3.6.2 At plot level

At plot level, which is the aggregation of the tree-level predictions and errors, the prediction errors tended to compensate each other since the relative prediction intervals of the annual biomass production were smaller than at tree-level (Fig. 6). Thus the interval of biomass production estimates varied from ~7% (sc1: no random effect, no residual error) to 10-30% (sc4: full error accounting) at stand level. It is noticeable that the relative prediction interval at 95% was never greater than 40% despite the combined errors of the two models (wood density and volume increment) plus the errors related to the random tree-level variations.

Figure 6.

The variation between years in the prediction error was also very low (Fig. 6) despite contrasted ring widths. The error of the predictions based on regression errors only (sc1 and sc3) did not vary with increasing number of trees in the plot (Fig. 6). In contrast, the predictions error decreased slightly with increasing number of trees for the scenarios that used a (tree-level) random-effect term (sc2 and sc4).

4 Discussion

4.1 Overestimations of the variations in annual biomass increment under constant density

Wood density was found to decrease when ring width increased, in agreement with previous studies on Norway spruce (e.g. Olesen, 1976; Lindström, 1996; Dutilleul et al., 1998). Despite the seemingly high correlation between ring width and WD, the decrease of WD was not enough to compensate the increase in ring width but contributed to attenuate its effects. The order of magnitude of the WD variability was not -and by far- as large as that of ring width. Hence, it is logical to find a moderate compensation between radial growth and wood density variations even in extreme years such as 1976: 15% at plot level. Nevertheless, when the focus is put on key years, such as years of climatic extremes, the measurements of WD is necessary to avoid a systematic underestimation of the biomass increment or carbon uptake. Climate is indeed probably the most important driver of WD variations with influences at both inter- and intra-annual time steps (e.g. Gindl et al. 2000, Bouriaud et al. 2015). These results are consistent with those reported in Babst et al. (2014a) showing that accounting for the variations in WD strongly improved the match between the tree-ring based above-ground wood biomass increment estimations and the seasonal CO_2 fluxes measured by eddy covariance.

A constant value of wood density, such as implicitly used in a biomass equations, can generate systematic deviations because it has only few chances to be equal to the mean density of the trees to which the model is applied. Even if using a site-specific WD value, neglecting the radial increment of WD (i.e. the age-related trend) will also lead to under-estimating the biomass increment. This source of error can unfortunately not be compensated by a larger sampling since it affects all the trees simultaneously. This has consequences not only for the annual productivity estimations but also for periodical productivity assessments, such as those conducted on permanent sample plots over a 5 or 10-years period.

Compensations of increased growth rate by a decrease in wood density was documented for Norway spruce but over a long time scale (Bontemps et al., 2013). The trends in radial growth and in WD reported for many species could lead to such deviations between the actual WD and the modelled or implicit WD. In this context, a local calibration would reduce such errors but cannot solve the problem of the variations between years and between trees.

The anticorrelation between ring width and wood density seems to be a general feature in Norway spruce according to the literature (e.g. Olesen, 1976; Lindström, 1996; Dutilleul et al., 1998) but the phenomenon is not limited to this species (Babst et al., 2014). The attenuation therefore probably occurs at a large scale. The between-tree variability in the relationship has also been reported in several studies and probably is a widespread feature with potentially large consequences on the error of annual biomass increment predictions, as demonstrated by this study. The fact that the trees used to assess both the wood density variations and to model the volume increment came from the same site as those used for the error estimations has ruled out the issues of using locally inappropriate models. Additional errors should be considered in practice when using models that may not be locally valid.

4.2 Predictions uncertainty

The inventory-based or tree-ring-based estimations of annual biomass production or carbon uptake are often used for comparisons against other methods such as remote sensing, vegetation models or eddy covariance (Beck et al., 2011; Bunn et al. 2013; Babst et al., 2014a). To be conclusive, the benchmarking however supposes that prediction errors are known or can be estimated. High prediction errors would invalidate the biometric approaches but the errors are not always accounted for. Analytical solutions are indeed not always available to estimate the errors of the allometric models, and their estimation remains very complex or based on assumptions. In the case of the biomass increment, the error results from the combination of several models, and the estimation is even more challenging. The use of the MCMC framework here avoids the cumbersome analytical approximations for prediction variances (e.g. Wutzler et al., 2008).

The prediction interval at plot level was on average between 20 and 40% of the predicted biomass increment value. The uncertainty related to the regression parameters were about 10% only for both models. Reduced variance may be inherent to the use of local trees and the Bayesian modelling (Zapata-Cuartas et al., 2012) but these values are similar to those found by Nickless et al. (2011) for biomass estimations following a parametric approach -as opposed to the MCMC method used here. Unlike our results, this study did however not include the random tree-level variations, which appeared to be quite an important source of uncertainty. Indeed, accounting for random tree-level variations in the relation between wood density and ring width increased the prediction interval of the tree-level biomass increment drastically (i.e. decreased the prediction confidence), by a factor of 5. Further errors related to the residual non-explained variance, were, in comparison, very small. Consequently, the prediction interval of the biomass annual increment at plot level increased twofold by accounting for the random-tree effects. Hence, the contribution of WD to the prediction error of the biomass increment was much larger than that of the volume increment model.

The tree-level prediction error (in percentage of the prediction value) was found to be greater than those at plot level. Thus, the compensations occurred at plot level when summing up trees predictions. We speculate that these compensations happen because the variations are centred by construction around zero and have both negative and positive values. This explains also why the mean prediction values were always unaffected by accounting for random effects. Hence, neglecting random effects affected more the prediction interval than the predictions themselves.

4.3 Variations between trees

The relation between wood density, ring width and cambial age were proven to fluctuate between trees sampled within a same stand for many species: oak (Guilley et al., 2004; Bergès et al., 2008), common beech (Bouriaud et al., 2004), Norway spruce (Mäkinen et al., 2002; Jaakola et al., 2005; Franceschini et al., 2010). For a given radial growth rate, the trees are building more or less biomass and so storing more or less carbon, according to the density of the wood.

This fluctuation is considered random because it cannot be attributed to a measurable factor. Random tree-level variations were nevertheless reported as a major source of wood density variations in a population (Zhang et al., 1994; Guilley et al., 2004; Bouriaud et al., 2004; Jaakola et al., 2005). It is often hypothesized to be related to the genetics, although not proven. Provenience studies brought some insight on it (Hylen, 1999; Rozenberg et al., 2004), but much of the determinism remains unknown. Other factors, such as crown development (Lindström, 1996), could also be invoked to explain this variation source in wood density.

The changes in silvicultural practices, whereby the focus is put on targeted individuals, further stress the importance of errors in tree-level estimations of biomass and biomass increments. The tree-level variations were the largest error source and showed that the inter-tree variations can be seen as a limitation to the tree-level biomass prediction. Despite the many evidences of tree-level random effects, this variation source was largely ignored. Our study proved that the between-tree variations in the relation between ring width and wood density -although within the same species- contributed the most to the uncertainty in the biomass increment predictions. The variations are hypothesized to follow a normal distribution (Lindström and Bates, 1990). Thus, at plot level, a compensation is likely to occur. But this situation may not be true for all samplings, and certain designs could generate additional biases in the biomass production estimations. In this study, all the trees in a plot were sampled. Other samplings, for instance the selection of the biggest trees in a plot as classically done in dendrochronology, could lead to serious deviations as it could involve sampling faster-growing trees. Apart from the bias in productivity caused by a sampling focusing on faster-growing trees (Nehrbass-Ahles et al., 2014), the productivity at stand level would probably generate an over-estimation related to a decreased wood density as trees producing larger rings would be sampled. Another issue in using the tree-ring parameters (width and density) to produce annual productivity estimations is the presence of autocorrelation or carry-over effects in the series, which are reflected in the derived productivity estimations but are generally not observed in the carbon fluxes measured or modeled (Babst et al. 2014a, b, Ramming et al. 2015).

4.4 Modelling wood density for biomass increment

Apart from the climate, the two foremost used variables used to model annual WD variations are ring width and ring (cambial) age. The relation between WD and radial growth was strong in our study and probably dominant in Norway spruce but may not be so for other species. In beech, for example, the relation between ring width and WD was shown to be weak (Bouriaud et al., 2004) and there was no clear trend in WD related to the age neither. Several studies reported a lack of significant correlations between ring width and WD for Norway spruce (e.g. Dutilleul et al., 1998). The relative stability in annual WD values is not calling for a correction of the biomass increment in such situation. It is probable that variations in WD would affect the estimation of biomass increment in species for which a relationship with ring width was already observed such oaks (Zhang et al., 1993; Bergès et al., 2008) or larch (Karlman et al., 2005). The contribution to the error in the prediction of biomass production is however likely to be important.

Conversely to ring width, ring age was found to be only slightly influent on the annual wood density in Norway spruce. Ring age is often considered in density models for representing the age trend or for the variations observed near the pith –the juvenile versus mature wood transition (e.g. Franceschini et al., 2010). WD in Norway spruce has been shown to present an age-dependent trend from pith to bark (Dutilleul et al., 1998; Hylen, 1999; Mäkinen et al., 2002), apart from the juvenile wood effect. In our study, the juvenile effect was not included for simplicity (series were pruned to exclude the first 3 years) but also because rings near pith anyway are often missing when working with increment cores. Part of the age effect can be absorbed by the irregular ring width variations exhibited by trees growing in stands where thinnings induce successive episodes of growth surge.

Wood density should not be mistaken for stem specific gravity (Williamson et al., 2010). Bark has a different mass to volume ratio than wood. The contribution of bark to the annual increment is however negligible. The approximation made consist in stating that the variations in specific gravity are proportional to that of wood density. Variations in ring width and WD at upper stem positions were however documented for different species (Bouriaud et al., 2005; Repola, 2006; Van der Maaten-

Theunissen and Bouriaud, 2012). These variations were mostly in the sense of a lesser reduction in growth of upper stem parts during years of limited growth. Altogether with the WD density effect, these effects show that the reaction of trees to unfavourable climate conditions are exacerbated or over-estimated by the breast-height radial growth.

5 Conclusion

Annual variations in wood density were proved to compensate partially (up to 15%) the variations in radial growth. Ignoring the relation between ring width and wood density would result in an underestimation of the biomass production in bad years. The use of allometric equations generated estimations with large prediction intervals at tree level, up to 60%, but the prediction errors at plot level compensated each other. Most of the error in the prediction of a tree's annual biomass increment comes from the great between tree variability in wood density. Plot-level errors were found to range between 10 and 20% only. This study validates the approach based on historical diameter records for estimating tree annual biomass increment and stand annual biomass production, but a local calibration of the allometric models reduces considerably the prediction errors.

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Tables and figure captions

Table 1. Fit statistics and parameters for the wood density models.

Table 2. Comparison of the fixed parameters estimated for the wood density and the volume models, obtained by maximum likelihood and MCMC. Standard deviations are provided in brackets.

Figure 1. Relation between annual wood density and cambial age (left) or ring width (right) at tree level. Two trees with very distinct average wood density were highlighted (dark gray/black colors).

Figure 2. Observed and fitted annual volume increment model and standardized residuals of the volume increment model fit.

Figure 3. Left, Comparison of biomass increment estimations for Norway spruce trees growing in Wetzstein, based on constant density hypothesis vs actual wood density measurements; Right, time-course of the average ratio of biomass increment estimations (actual over constant density) and time-course of the detrended mean ring width (spline smoothing, for illustration purposes).

The ±2sd interval for the average biomass ratio is displayed as a gray band.

Figure 4. Left, variations of the MCMC annual predictions and prediction intervals (95%) of wood density and volume increment for one given tree randomly chosen while accounting for different error sources: regression only/regression and random effects/regression, random effects and residual variance; Right, distribution density of the relative prediction interval (expressed in percentage of the prediction) for all trees used for the simulation, according to the error sources included.

Figure 5. Annual biomass increment (posterior MCMC distribution) for one given tree chosen as representative with its associated prediction error for scenario 1 and 2 (a) or

scenario 3 and 4 (b); c) distribution density of relative prediction interval (expressed in percent of the prediction) for all trees used for the simulation, according to the scenario. Scenario 1 is based on constant WD and no random or residual error from the volume increment model, Scenario 2 is based on constant WD and random error in the volume increment model, Scenario 3 is based on modelled WD but without random and residual error accounting, Scenario 4 is based on modelled WD and volume increment with a full error accounting (see section 2.3 for more details).

Figure 6. Plot-level annual relative prediction intervals of the biomass increment as a function of the number of trees sampled in the plot for the 4 scenarios (a). Distribution density of the relative prediction interval of the biomass increment at plot level, all plots pooled, (b).

Table 1

Eq.	Model	Fixed effect	df	AIC	RMSE	Bias
					kg m^{-3}	kg m^{-3}
1	WD = $a_0+a_1.RW+a_2.RW^2+a_3/X^{0.5}$	RW, CBA	12	12549	44.62	0.135
		RW, DBH	12	12567	44.90	0.135
2	WD = $a_0+a_1/(1+RW)+a_2/X^{0.5}$	RW, CBA	11	12770	60.24	0.874
		RW, DBH	11	12802	64.70	0.674
3	WD = $a_0+a_1.RW^{a2}+a_3/X^{a4}$	RW, CBA	12	12554	44.90	0.018
		RW, DBH	12	12569	45.15	-0.046
4	WD = $a_0+a_1RW^{0.5}+a_2/X^{0.5}$	RW, CBA	11	12552	44.92	-0.019
		RW, DBH	11	12567	45.20	-0.073

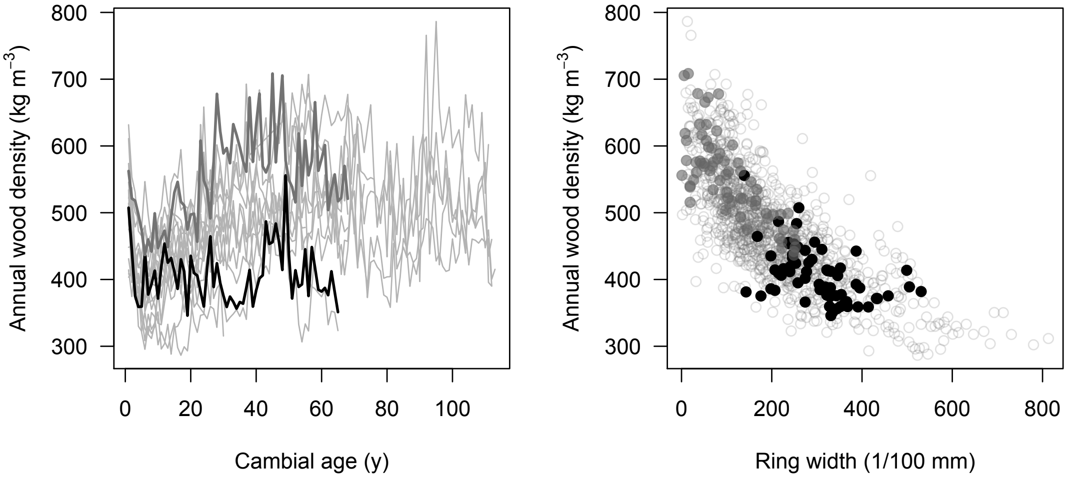
WD: (annual) wood density, RW: (annual) ring width, X: either cambial age (CBA) or diameter (DBH).
Models 1 to 3 correspond to equations 1-3 presented in the section 2.2.1, and model 4 corresponds to equation 3 with parameter a_2 and a_4 set to 0.5.
They were 1201 observations, 10 groups.

Table 2

Model	Parameters	Likelihood fit	MCMC fit
WD = $a_0+a_1RW^{0.5}+a_2/DBH^{0.5}+e$	a_0	594.33 (16.11)	555.10 (20.04)
	a_1	-10.09 (0.43)	-9.23 (0.70)
	a_2	13.93 (41.21)	17.13 (29.00)
	e	2054	2083 (93)
$\Delta V = b_0+b_1DBH^{b2}RW^{b3}+e$	b_0	0.284 (0.041)	0.047 (0.005)
	b_1	0.161 (0.012)	0.009 (0.001)
	b_2	1.820 (0.034)	1.733 (0.011)
	b_3	0.645 (0.019)	0.649 (0.019)
	$e = b_4+ DBH^{b5}$	9.316e-03	0.283 (0.136)
	b_4	15.505	-0.093 (0.009)
	b_5	1.871	0.225 (0.005)

WD: (annual) wood density, RW: (annual) ring width, DBH: (annual) breast-height diameter, e: residual error.

Figure 1



Annual wood density (kg m^{-3})
800
700
600
500
400
300
0
20
40
60
80
100
Cambial age (y)
Annual wood density (kg m^{-3})
800
700
600
500
400
300
0
200
400
600
800
Ring width (1/100 mm)

Figure 2

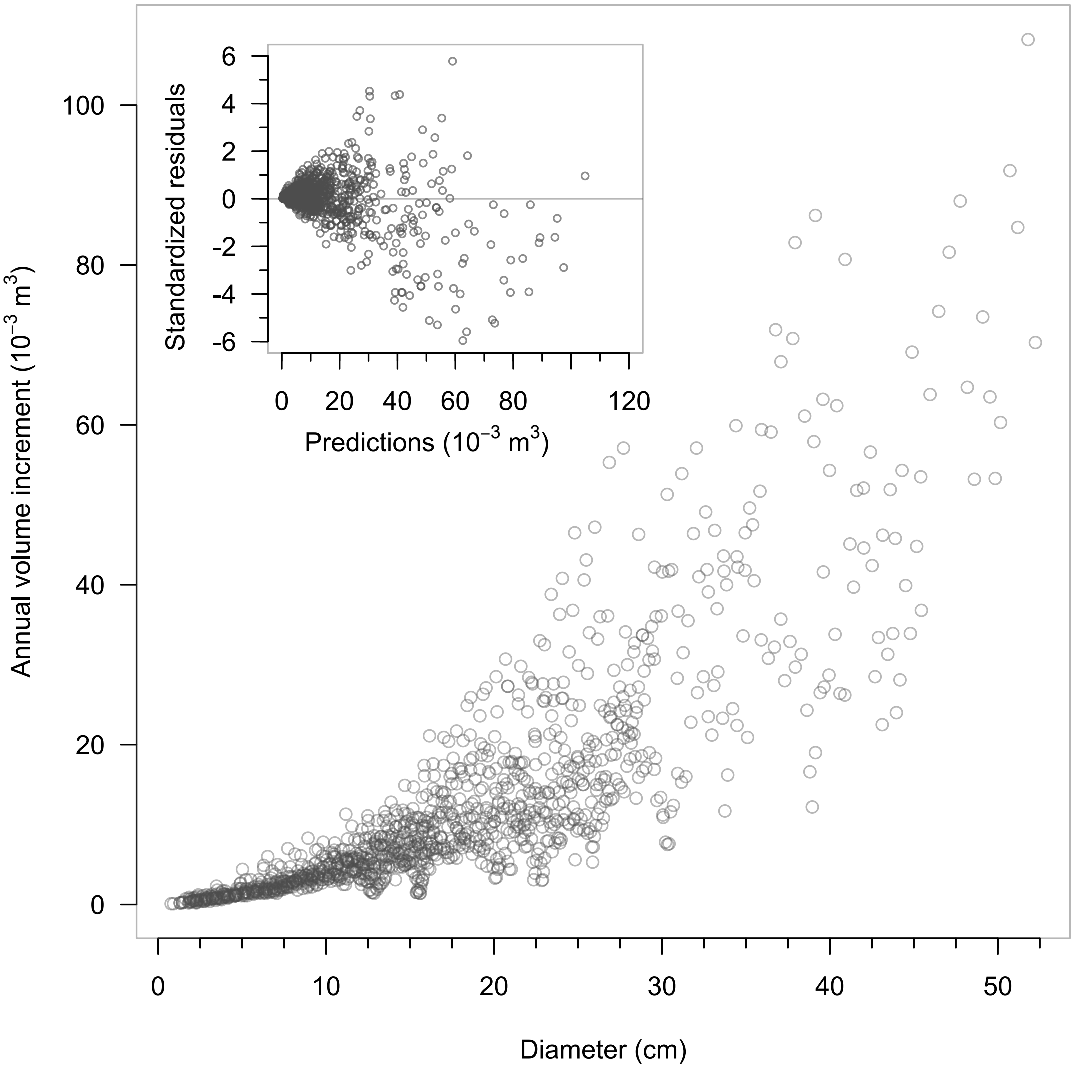

Annual volume increment (10^{-3} m^3)
Diameter (cm)
Standardized residuals
Predictions (10^{-3} m^3)
0
20
40
60
80
100
0
10
20
30
40
50
6
4
2
0
-2
-4
-6
0
20
40
60
80
120

Figure 3

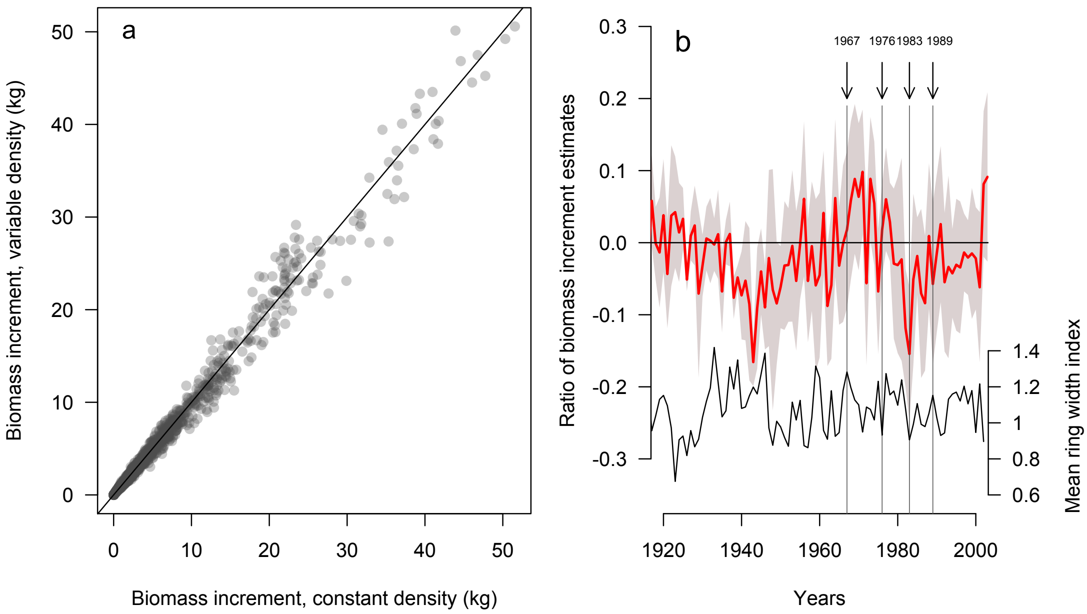

a
Biomass increment, variable density (kg)
Biomass increment, constant density (kg)
b
1967
1976
1983
1989
Ratio of biomass increment estimates
Mean ring width index
Years

Figure 4

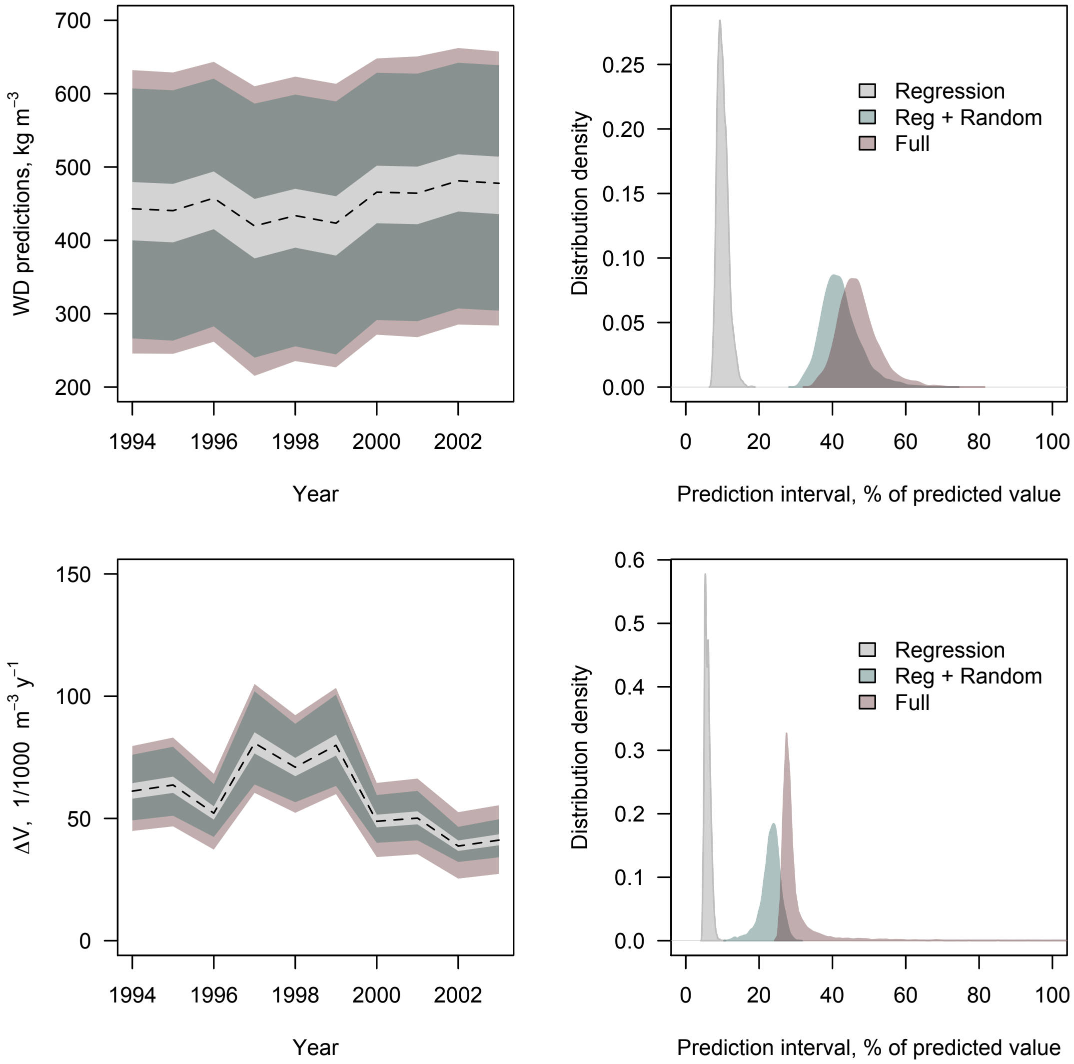
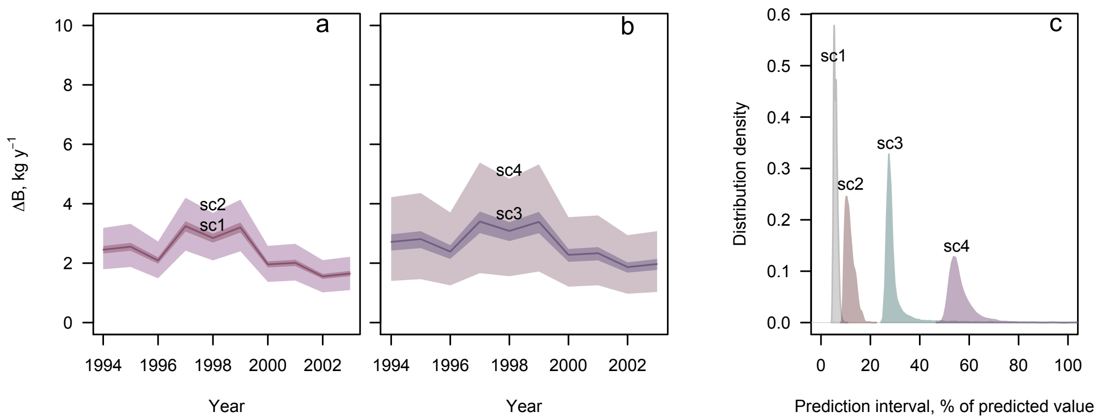
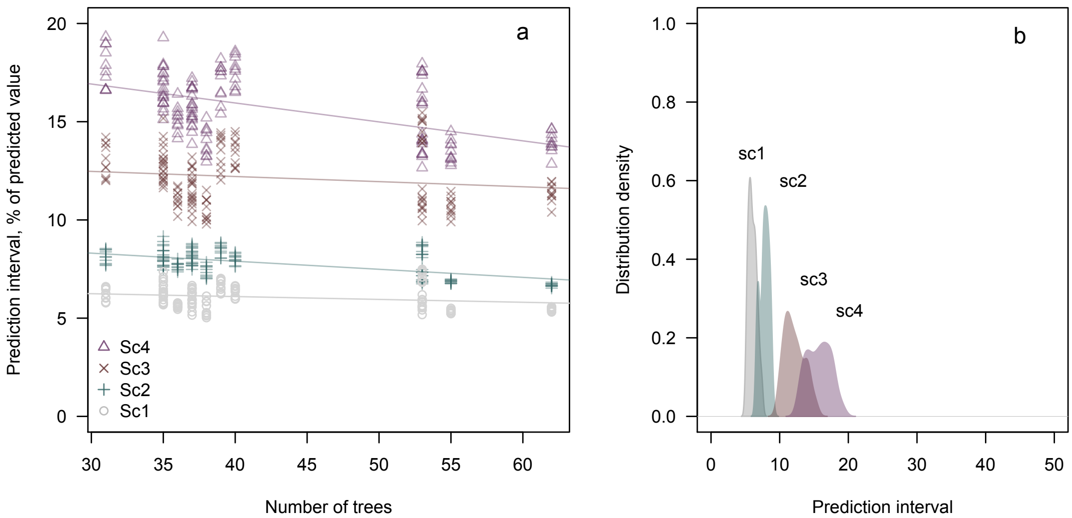

WD predictions, kg m^{-3}
700
600
500
400
300
200
1994
1996
1998
2000
2002
Year
Distribution density
0.25
0.20
0.15
0.10
0.05
0.00
Regression
Reg + Random
Full
0
20
40
60
80
100
Prediction interval, % of predicted value
ΔV, 1/1000 m^{-3} y^{-1}
150
100
50
0
1994
1996
1998
2000
2002
Year
Distribution density
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Regression
Reg + Random
Full
0
20
40
60
80
100
Prediction interval, % of predicted value

Figure 5


a
b
c
ΔB, kg y^{-1}
Year
Year
sc1
sc2
sc3
sc4
Distribution density
Prediction interval, % of predicted value

886 Figure 6



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