GROWTH RATE EFFECTS ON TEMPORAL TRAJECTORIES OF RING WIDTH, WOOD DENSITY, AND MEAN TRACHEID LENGTH IN NORWAY SPRUCE (PICEA ABIES (L.) KARST)

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ABSTRACT

The study reported was conducted on 20 fast-grown and 20 slow-grown Norway spruces (Picea abies (L.) Karst.) from an even-aged, plantation-grown stand near Rendeux, Belgian Ardennes. The objective was to test whether increasing the growth rate of Norway spruce by heavy thinnings had an effect on the temporal trajectories (i.e., fluctuations from year to year) of ring width, wood density, and mean tracheid length, all measured yearly from pith to bark. Since the data were chronologies (i.e., time series of yearly measurements), time had to be considered as a factor (i.e., the calendar year of ring formation) in the statistical analysis of the within-tree variation (repeated measures analysis of variance).

While the effects of the growth category and its interaction with the year were highly significant after first thinning for ring width, a significant decrease in the wood density of fast-grown trees was observed in many years during that growing period; the decrease was small in magnitude, once averaged over years (−0.033 g/cm³). Tracheids were longer for the slow-grown trees after first thinning; although constant in sign and magnitude over years, the difference in mean tracheid length between growth categories was not statistically significant. In summary, increasing the growth rate in circumference of Norway spruce from 1.7 to 2.7 cm/year by heavy thinnings induced a limited decrease in wood density and mean tracheid length. These results support the statement that stand productivity might be improved without sensible loss of wood quality.

Keywords: Norway spruce (Picea abies (L.) Karst.), growth rate, ring width, wood density, mean tracheid length, chronologies, repeated measures, temporal trajectories.

INTRODUCTION

Over the last two decades, fast-grown plantations have steadily spread worldwide, and their number, for both softwood and hardwood, will continue to increase until they become predominant (Zobel 1980). Management uses large-space planting, heavy thinnings, fertilization of forest stands, and genetics, in order to speed up the tree growth. As a result, the raw material base of forest products and
paper mills is shifting from old-growth to short-rotation plantation stocks with trees having grown more rapidly.

By acting on the growth process, stimulation of the tree growth rate affects the formation of wood and hence its technological and anatomical properties (Senft et al. 1985; Bendtsen and Senft 1986; Keith and Chauret 1988; de Kort et al. 1991). The use of wood in the construction and paper industry is thus potentially subject to significant changes. A crucial question then arises: "What are the effects of accelerated tree growth on the main technological properties of wood?" A better knowledge of the quality of wood from fast-grown plantations will help make the use of this wood more effective, as value of a product goes together with satisfaction at the end-user's level (Perstopper et al. 1995).

Among the variables used to select wood for the industry and paper mills, wood density, fiber length, and ring width are the most important. Wood density influences both the quantity and the quality of pulp, and has a close relationship with most of the anatomical and physical properties of wood (Dinwoodie 1965; Dorn 1969; Bendtsen and Senft 1986; Frimpong-Mensah 1987). This variable can thus be used as an indicator for other wood properties (Kucera 1994). Fiber length has been shown to be important for paper strength properties such as tensile, bursting, tearing, and folding (Dinwoodie 1965; Zobel and van Buijtenen 1989; Kibblewhite et al. 1996). Ring width is a readily measurable variable. It has been found to be negatively correlated with wood density and fiber length (Dinwoodie 1965; Olesen 1976; Chalupka et al. 1977). Ring width is related, but not equivalent, to the concept of growth rate defined below.

Variation of wood structure within a tree species follows from a complex system of interacting environmental and genetic factors that determine the physiological processes involved in the production of xylem (Zobel and van Buijtenen 1989). Patterns of variation within individual trees (Taylor and Burton 1982) are equally important because the long-term growth effects, which are associated with height and radial position from the pith, can create major variation in wood quality (Frimpong-Mensah 1987). As a result, failure to account for the inherent variation with age or distance from the pith is likely to lead to false conclusions concerning the effects of growth rate on wood density and tracheid length, for instance.

From a perspective of data analysis, sequences of yearly measurements of ring width, wood density, and fiber length are time series (Diggle 1990), called here "chronologies." They are also repeated measures made of the same characteristic on the same observational unit (the tree) on more than one occasion (the year) (Crowder and Hand 1990). Such data generally present temporal autocorrelation (e.g., the ring width on a given year is dependent on the ring width of the previous year), heteroscedasticity (e.g., the variance of wood density is not constant over years), and non-stationarity of the mean (e.g., the mean fiber length is not constant over years) (Moser et al. 1990; Dutilleul 1998a). These temporal characteristics, when not adequately taken into account, result in biased statistical tests with inflated type I error risk; that is, the null hypothesis of absence of year effects is rejected erroneously more often than theoretically expected at the significance level fixed by the experimenter (Potvin et al. 1990; Dutilleul 1998b). Moreover, representing chronologies graphically in a time plot (Diggle 1990) helps visualize the fluctuations over years or "temporal trajectory" of each variable, and whether the trajectories change depending on the growth rate. The comparison of two trajectories of the same variable for two different growth categories will be based on the overall mean level (i.e., growth category main effects in terms of analysis of variance) and the increments from year to year (i.e., interaction between growth category and year).

Therefore, the study reported here was designed to test whether increasing the growth rate of Norway spruce by heavy thinnings has an effect on the overall mean and the fluctu-
ations from year to year of ring width, wood density, and mean tracheid length, through the analysis of their temporal trajectories. A within-tree approach incorporating time explicitly as a factor (the year) has been followed to take the temporal characteristics of chronologies adequately into account. Forty Norway spruce trees (*Picea abies* (L.) Karst.) from an even-aged, plantation-grown stand in the Belgian Ardennes were used. Twenty trees were randomly sampled from each of two growth categories: a fast-growth category made of trees whose growth rate in circumference is above 2.2 cm/year and a slow-growth category composed of trees that do not reach such a rate. The growth rate effects observed on wood (i.e., final product of the growth process), from fast-grown vs. slow-grown trees, are discussed from the perspectives of forest management and paper production.

**PRELIMINARY DEFINITIONS**

*The concept of growth rate*

In the present study, “growth rate” does not refer to the number of rings counted per cm on a radial piece of wood or to the average ring width of a tree along a given radius. It refers instead to the average annual increment in circumference, calculated within a given time period. In fact, silvicultural (e.g., thinning, soil fertilization), environmental (e.g., soil properties, climate, topography), and genetic (e.g., provenance, social status of the tree within the stand) factors are all likely to modify the physiological equilibrium of the secondary growth process and hence, the amount of radial annual deposit of woody tissues (Zobel and van Buijtenen 1989). Isolating one of these factors, while maintaining the others fixed, to study the specific influence of that factor on the growth increment, both technologically and anatomically, is not practically feasible. All these factors act together on the tree growth process or even interact with each other, with the increase in circumference as an outcome.

Accordingly, the hypothesis to be tested had to be simplified by integrating all the factors into a single concept of growth rate. Whatever combination of factors governs the secondary increment of the tree, the result is that the tree has grown in circumference within a given time period. The increase in circumference to time period ratio then provides an expression of the average growth speed of the tree: its growth rate in circumference.

If all environmental factors cannot be controlled, at least some can, by working with trees sampled from the same stand characterized by homogenous climatic and edaphic (i.e., related to the soil properties) conditions. This restricts, to some degree, the range of our results, but the interest of such a study lies in the integration of all factors into the growth rate in circumference. Our study thus primarily aims to assess the impact of accelerated growth in circumference on wood density and mean tracheid length in Norway spruce trees from the same stand.

*The fast-growth and slow-growth categories*

In Belgium, it is acknowledged (Anonymous 1981) that Norway spruce stands managed as even-aged high forest by the Forestry Services are characterized by an average growth rate in circumference of 2.2 cm/year at the end of the rotation period. Using this figure as reference under Belgian conditions, a fast-grown Norway spruce is defined here as a tree whose growth rate in circumference is above 2.2 cm/year, while a slow-grown Norway spruce is a tree that does not reach such a rate.

From a silvicultural point of view, the above definition of growth rate clearly indicates that in a normal tree population, the fast-growth category may include dominant or codominant trees (i.e., individuals with better genetic potential) as well as trees that benefited from a favorable treatment (e.g., heavy thinning). The slow-growth category may include dominant trees from weakly thinned plantations or dominated trees that are suppressed when managing heavy thinnings. However, both growth categories included only dominant and codominant trees in our study (Herman et al. 1998).
Hermun et al.—GROWTH RATE AND TEMPORAL TRAJECTORIES


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MATERIALS AND METHODS

Experimental design and tree sampling

The material comes from trees harvested in an experimental even-aged high forest located at Rendeux (50°13’15” N latitude, 05°27’05” E longitude), Belgian Ardennes, 390 m above sea level. The mean annual precipitation is about 1,078 mm/year, and the yearly average temperature, 7.05°C. In 1949, Norway spruce was planted in this old agricultural soil of the acid-brown soil category. A broad research project on the influence of five thinning intensities on both the ecology and the wood productivity of the stand was started in 1969; treatments A (low intensities) to E (heavy intensities) were assigned according to a randomized complete block design with three blocks (André 1976; André et al. 1994).

An average annual increment of circumference at breast height (1.5 m) was computed for each individual tree of the stand over the growing period from 1970 (year after first thinning) to 1987. In December 1987, twenty trees were then randomly sampled within each growth category (fast versus slow), provided they showed no technological defects such as injuries, twisted grain, or noncylindrical shape. The individual coordinates of the 40 trees sampled are reported in Table 1.

Technological variables

For each tree sampled, a 15-cm-thick slice was cut from the trunk at 2.3 m height because the lower base of the log was used for another study. Along the north radius of each cross-sectional disc, three 2-cm-thick wedges of wood were sawn from pith to bark. This direction was chosen in order to minimize the occurrence of compression wood since the prevailing winds were westerly.

After a drying period in laboratory conditions, ring width (mm) was measured on one wedge from each tree, using a graduated scale under a binocular lens. For the measurements of
wood density (g/cm³) and mean tracheid length (mm), the growth rings of the other two wedges were separated individually, using a chisel.

Wood density has been calculated for each wood sample per yearly growth ring, following Walker (1993). After conditioning at 12% MC in drying oven, the weight of each sample was measured to the nearest 0.0001 g on a precision balance (Sartorius type 2492), and its volume was measured by immersion, using mercury.

For fiber length measurement, each growth ring was macerated in a boiling solution of acetic acid (½) and hydrogen peroxide 27% (½) for two hours. Tracheid lengths were measured with a Kajaani-FS 200 (Kajaani Electronics Ltd, Kajaani, Finland). The number of tracheids measured per growth ring ranged between 12,500 to 15,000. The weighted average tracheid length (Clark 1985) was retained for further analysis.

For all trees sampled, thirty-three annual growth rings were observed, from 1955 to 1987. Fifteen of them belong to the growing period before first thinning (1955–1969), and the eighteen others, to the period of thinnings (1970–1987).

In the following, the annual radial increment measured is referred to as the “ring width” variable, and the mean tracheid length, as the “fiber length” variable. Three 40 X 33 data tables resulted from the measurement process, one for each of the three variables (ring width, wood density, fiber length). In each data table, there is one row per tree sampled and one column per year; a tree is a “subject” and a row defines an individual “profile” in the jargon of repeated measures analysis of variance (Crowder and Hand 1990; Dutilleul 1998a, b). For each variable, a mean profile has been calculated from the 20 individual profiles of each growth category.

Statistical analyses

The wood density data were log-transformed because of the presence of outliers on many years for this variable (i.e., an outlier is a value out of range, atypically high in the present case); the log-transformation is known to be normalizing and variance-stabilizing (Sokal and Rohlf 1995, p. 413). Classical t-tests for difference between two means and classical F-tests of homogeneity of two variances (Sokal and Rohlf 1995) were carried out between growth categories for each variable (ring width, wood density, fiber length), year by year; the SAS procedure used was PROC TTEST (SAS Institute Inc. 1989).

For each variable, a repeated measures analysis of variance or ANOVAR (Crowder and Hand 1990; Dutilleul 1998b) was performed on the 40 individual chronologies from the two growth categories, to assess 1) the main effects of the growth category, averaged over years (between-subjects effects), and 2) the main effects of the year and its interaction with the growth category (within-subject effects), over the growing period before and after first thinning. The SAS procedure used was PROC GLM (for General Linear Model), with the REPEATED statement (SAS Institute Inc. 1989).

RESULTS AND DISCUSSION

Ring width

Both growth categories show the same pattern of temporal trajectory for ring width (Fig. 1a). Ring widths are wide in the first years of tree life and then decrease slowly to reach a plateau after 15 years of growth. The pattern of radial variation of ring width is well documented for softwoods (Panshin and de Zeeuw 1980; Seth 1981) and the Norway spruce (Petty et al. 1990; Blouin et al. 1994; Kucera 1994; Perstopper et al. 1995). Compared to the age of cambium (i.e., the number of rings) and the distance from the pith that were used in other studies, the calendar year of ring formation (i.e., our choice) has the advantage of facilitating the comparison among trees and the analysis of tree response to external factors (e.g., climate).

Before first thinning, the two growth categories significantly differ in the mean values of ring width for three years; concerning the vari-
Fig. 1. Mean profiles of a) ring width, b) wood density (12% MC weight and volume), and c) fiber length, over the 1955–1987 growing period for the two growth categories. Bounds of vertical intervals = sample mean ± standard error, for each combination of growth category and growing year (sample size: 20). The stars and crosses indicate the years where the growth categories differ, either in the mean (stars) or in the variance (crosses) of the variables: *, + = the difference is significant at the 0.05 level; **, ++ = the difference is significant at 0.01. For wood density, the comparison of means and that of variances were performed on the log-transformed data (see text).
TABLE 2. Repeated measures analysis of variance (ANOVAR): Results in terms of significance probabilities $P > F$

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1 ANOVA = univariate analysis of variance. This testing procedure is restricted to the between-subjects effects (i.e., growth category main effects); a tree is a "subject."  
2 The within-subject effects (i.e., year main effects, growth category-by-year interaction) are tested in the modified ANOVA. In this modified testing procedure, the probabilities of significance $P > F$ are adjusted by using Greenhouse and Geisser's (1959) and Huynh and Feldt's (1976) estimates of Box's (1954a, b) epsilon correction factor. The correction is applied to the number of degrees of freedom of the ANOVA $F$ test statistic in order to take into account the autocorrelation and heteroscedasticity of the variables over years, the lower the epsilon value, the stronger the required correction due to autocorrelation and heteroscedasticity. The corresponding adjusted probabilities are denoted G-G and H-F, respectively.  
3 GC = growth category main effects.  
4 GC * Year = growth category-by-year interaction.  
5 The log-transformed data were analyzed for wood density (see text).

...
width (e.g., in response to climatic changes) depends on the growth dynamics of the tree. As an illustration, all the trees studied here showed a narrower ring increment in 1976, owing to severe drought conditions in the summer (Fig. 1a), but the subsequent increase in ring width was greater for the fast-grown trees than for the slow-grown ones.

Wood density

The pattern that we found for the temporal trajectory of wood density (weight and volume at 12% MC) (Fig. 1b) is similar to that reported in other studies (e.g., Taylor et al. 1982; Savill and Sandels 1983; Wang and Micko 1984; Petty et al. 1990; Blouin et al. 1994; Kucera 1994; Kennedy 1995; Lindström 1996): in the juvenile wood, density is slightly higher in rings near the pith, then decreases over a few years and reaches a minimum before increasing and stabilizing while fluctuating over the following years. However, the trees of both categories show a higher wood density in 1959, compared to 1958 and 1960. This disturbance, which affects the general pattern of the temporal trajectory, is due to a false ring. The latewood tracheids associated with it are characterized by thick cell wall and small lumen; these tracheids are thus of higher density on that year.

Before first thinning, the only significant differences between growth categories were found in the variance of wood density, whose homogeneity was rejected on two years (Fig. 1b). This lack of growth category effects is in accordance with the growing conditions (e.g., stand density) prevailing during this period; the same argument applied to ring width. The year main effects are highly significant (Table 2), so the temporal trajectory of wood density is effective (i.e., there are fluctuations from year to year) and does not differ between growth categories over the 1955–1969 period in the absence of significant interaction between growth category and year.

After first thinning, significant differences between growth categories appear on some years in the mean value of wood density; these differences are numerous (Fig. 1b), though less frequent (11 years out of 18) than for ring width. On the other hand, homoscedasticity seems to be the rule with the exception of 1985 (Fig. 1b). The growth category main effects are significant (Table 2). The nonsignificant GC-by-year interaction reflects the similar response of fast-grown and slow-grown spruces to the same variation of environmental growing conditions, in direction and magnitude. The year main effects are highly significant (Table 2), as illustrated by the high temporal variation of wood density (Fig. 1b). Any further analysis should thus take these time effects adequately into account.

Assuming that increased growth rate results in growth rings with higher proportion of earlywood, which is considered as a wood of lower density than latewood, wood density should be negatively influenced by the tree growth rate in softwoods (e.g., Zobel and van Buijtenen 1989). Some studies showed that wood density was not significantly affected by thinning, even though the individual tree growth was considerably improved (e.g., Moschler et al. 1989). In our study, increasing the growth rate of Norway spruce resulted in a significantly (P = 0.005) lower wood density overall, as revealed by the ANOVA (Table 2). The overall mean value of wood density after first thinning is 0.402 g/cm³ for the fast-grown spruces, and 0.435 g/cm³ for the slow-grown ones. Under our Belgian conditions, and according to our definition of growth categories, wood density is thus, on average, about 7.6% lower for the fast-grown spruces than for the slow-grown ones. Though significant, this decrease in wood density is of low magnitude (0.033 g/cm³), compared to the within-tree variations and the variations between dominant and suppressed trees that can occur within a stand (e.g., Petty et al. 1990; Lindström 1996).

During the 1955–1969 period (juvenile wood), the overall mean value of wood density here was 0.409 g/cm³ for the fast-growth category and 0.417 g/cm³ for the slow-growth
category, which represents a difference of 
\(-0.007 \text{ g/cm}^3\) between juvenile and mature 
wood for the former category and of \(+0.018 \text{ g/cm}^3\) for the latter. Accordingly, increasing 
the growth rate of Norway spruce may be seen 
as a way to maintain wood density at an even 
mean level overall, which is a key objective 
in forestry (e.g., Zobel and van Buijtenen 
1989).

Fiber length

Our results (Fig. 1c) show a logarithmic 
pattern for the temporal trajectory of this vari-
able from pith to bark. Such a pattern is well 
known, especially for the softwoods, and has 
been reported in other studies (Dinwoodie 
1961; Seth 1981; Taylor and Burton 1982; 
Frimpong-Mensah 1987).

Before first thinning, the mean value of fi-
ber length is significantly different between 
the two growth categories for three years (Fig. 
1c). The year main effects are highly signifi-
cant (Table 2). In fact, tracheids are short near 
the pith and then increase in length very rap-
idly and nonlinearly (Fig. 1c), which is a main 
characteristic of the juvenile wood (Seth 1981; 
Shiokura 1984; Kucera 1994). Moreover, the 
two mean profiles are crossing in 1963-1964 
(Fig. 1c), which illustrates the GC-by-year in-
teraction declared significant by the ANOVAR 
after modification for temporal autocorrelation 
and heteroscedasticity (Table 2). It follows 
that the trees classified into the fast-growth 
category on the basis of their increment in cir-
cumference between 1970 and 1987 are trees 
that originally developed tracheids a little lon-
ger on average, before the tendency was re-
versed in 1963. A similar pattern has been re-
ported for the Norway spruces studied by 
Stairs et al. (1966). It remains to be confirmed 
by further studies.

After first thinning, the overall mean value 
of fiber length is 3.14 mm for the fast-grown 
spruces, and 3.22 mm for the slow-grown 
one. On average, fibers from fast-grown 
spruces are thus 2.5% shorter than those from 
slow-grown spruces. Accordingly, the mean 
profile of the fast-growth category is system-
atically below that of the slow-growth cate-
ogy (Fig. 1c), except in 1985 and 1986. In 
spite of that, the difference between the 
growth categories is nonsignificant, except in 
1979 (Fig. 1c), and there is no evidence of 
growth rate effects on the temporal trajectory 
of fiber length because both the GC main ef-
teffects and the GC-by-year interaction are non-
significant (Table 2). On the other hand, the 
year main effects are highly significant (Table 
2), which leads to the same recommendation 
as for the other two variables concerning any 
eventual correlation analyses: time must be in-
corporated in these.

It is well established that the tracheids of 
earlywood are shorter than those of latewood 
in conifers (Bisset and Dadswell 1949; Mer-
gen et al. 1964; Seth and Jain 1976; Zobel and 
v Buijtenen 1989). Assuming that increased 
tree growth rate results in an increased per-
centage of earlywood with shortened fibers in 
growth rings, an increased growth rate should 
encourage earlier pseudo-tranverse division. 
Therefore, the earlier the fusiform initials are 
transversely divided in their cycle of elonga-
tion and division, the shorter the derived tra-
cheids should be (Bannan 1954, 1957). This 
expected change in the pattern of the temporal 
trajectory of fiber length over the 1970–1987 
growing period was not statistically significant 
in our study, despite sample sizes of 20 trees 
per growth category.

The difference between growth categories 
in the temporal trajectory of fiber length over 
the 1955–1969 period and the absence of ef-
fects due to the acceleration process of the 
Norway spruce growth emphasize the impor-
tance of the primary growing period for fiber 
length. To produce Norway spruce with high 
yield and optimum tracheid length, foresters 
could maintain trees at a high competition lev-
el in the stand for 15 or 20 years and then 
increase their growth rate by heavy thinnings. 
Practically, the resulting decrease in mean fi-
er length by about 2.5% for the fast-grown 
spruces should have very little effect on the 
quality of paper produced with such raw ma-
material. Indeed, if the average tracheid length is already about 3.0 mm, a variation of up to 0.5 mm will have little impact on the quality of the final product (Dadswell and Wardrop 1960; Zobel and van Buijtenen 1989). In addition, such a silvicultural practice would have the effect of limiting the percentage of juvenile wood in the stem, that is, the portion of wood of poorest quality for solidwood products due to its low wood density and with the shortest tracheids that diminish the tear strength properties of the paper.

CONCLUSIONS

We have studied the effects of increased tree growth rate on variables of primary technological interest such as ring width, wood density, and fiber length, using chronologies of yearly measurements made on 40 Norway spruces grown under Belgian conditions and classified as 20 fast-grown and 20 slow-grown. In our study, we have followed a within-tree approach that incorporates the calendar year of ring formation as a factor. This approach based on the analysis of temporal trajectories is particularly designed for wood technologists who want to follow up the tree response to a given silvicultural treatment over time. It merely requires the data to be collected according to a repeated measures design, so that statistical analysis can be performed with due allowance for temporal autocorrelation, heteroscedasticity, and nonstationarity of the mean.

As expected, increased growth rate had a highly significant effect on the radial variation of the annual ring width overall (+56%). The temporal trajectory of ring width not only changed in its mean level, but also showed uneven increments from year to year depending on the growth category. Growth rate effects on the overall mean level of wood density were significant but of lower magnitude (−7.6%) than for ring width, while mean fiber length was not really modified (−2.5%) by the acceleration of Norway spruce growth. On the other hand, the fiber length of trees in the first growing years (i.e., during the juvenile period) seemed to predetermine the further temporal variation of this variable. Time effects are highly significant for the three variables, even before application of the first thinning to the stand in 1969. This result underlines the importance of taking the temporal characteristics of such data adequately into account, especially when assessing the correlations among these variables (Dutilleul et al. 1998).

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