# FIBER LENGTH, TRACHEID DIAMETER, AND LATEWOOD PERCENTAGE IN NORWAY SPRUCE: DEVELOPMENT FROM PITH OUTWARDS

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ABSTRACT

In a fertilization trial near Stråsan, central Sweden, six net parcels of Norway spruce (*Picea abies*) planted in 1957 and clear-felled in the winter of 1989/1990 were used to evaluate the influence of growth conditions on wood characteristic development. The six parcels used in the study represented two unfertilized, two medium, and two heavily fertilized treatments. Suppressed, intermediate, and dominant trees were sampled from each parcel, and wood characteristics were determined from pith outwards on every second growth ring. Dependence of wood characteristic development was evaluated in models built on a limited set of growth factors that had a high predictive capability, yet were simple.

Tracheid length was found dependent on logarithm of cambial age and growth ring width, which gave an $r^2 = 0.87$. Earlywood radial tracheid diameter was found dependent on logarithm of cambial age, growth ring width, and site quality, which gave an $r^2 = 0.67$. Earlywood tangential tracheid diameter was found dependent on logarithm of cambial age, growth ring width, and site quality, which gave an $r^2 = 0.76$. Latewood radial tracheid diameter was found dependent on logarithm of cambial age and site quality, which gave an $r^2 = 0.19$. Latewood percentage was found dependent on logarithm of cambial age and growth ring width, which gave an $r^2 = 0.53$. Basic density was found dependent on latewood percentage and the inverted value of earlywood radial tracheid diameter, which gave an $r^2 = 0.80$. Results indicate that changes in growth conditions over time, acting through crown development, will influence wood structure development of *Picea abies*.

*Keywords:* Norway spruce, *Picea abies*, *Picea abies* (L.) Karst., silviculture, crown development, tree class, wood formation, wood characteristics.

## INTRODUCTION

Within Scandinavian forestry (Kyrkjeeide 1990; Kucera 1991, 1992; Thörnqvist 1993; Lindström 1996a) and forest products research (Kärenlampi et al. 1994; Brolin et al. 1995; Kliger et al. 1995; Perstorper et al. 1995; Tyrväinen 1995), it is recognized that wood variation affects production methods and the properties and value of forest products. At present, several reports (Kyrkjeeide 1990; Kucera 1991; Thörnqvist 1993) state that increased variation in wood characteristics of *Picea abies* will occur as a result of altered forestry management methods. As an explanation of this emerging situation, Thörnqvist (1993) and Perstorper et al. (1995) argue that contacts between supposedly interacting research covering silviculture, wood science, and forest products have been insufficient.

During recent decades, Scandinavian forestry has strived to decrease costs and optimize the value of forestry. An essential part of the strategy has been to transform wood production to a smaller number of trees and to shorten rotation periods. The conversion has largely taken place through planting, thinning from below, fertilization, and clear-cutting (Kyrkjeeide 1990; Kucera 1991; Thörnqvist 1993). Although growth conditions promoted by this type of silviculture have so far mainly affected forests that are less than 40 years old, the radical change has been shown to increase tree size and individual tree growth rate, and is probably responsible for a decline in aver-

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age stand age (Elfving and Tegnhammar 1996). Therefore, it can be assumed that forestry management of this kind has been successful in its immediate goal, which is to produce a volume-based quantity of wood at a low cost. However, how this type of silviculture will change factors, such as tree form, size of branches, juvenile wood percentage, and wood characteristics, has been neglected. These factors influence the production processes in the forest industry, the properties of forest products, and consequently the value of wood as a raw material (Kyrkjeeide 1990; Thörnqvist 1993).

If the influence of growth conditions on wood characteristics of conifers could be quantified, the ability to produce, classify, and select more well-defined wood would improve (Zobel and Van Buijtenen 1989; Jozsa and Middleton 1994). As a major argument to further explore this possibility, it is said that if the forest industry could be provided with wood that has more consistent raw material properties, it would increase the value of wood (Bendtsen 1978; Jozsa et al. 1989; Thörnqvist 1993; Kennedy 1995). Such awareness is beginning to initiate a more integrated research approach, with the goal of producing wood with more consistent properties.

To do so requires insight on how environmental regulation of tree growth physiology alters not only volume production but wood structure development and consequently raw material properties of wood. Although variability in conifer wood structure is viewed as an aggregated response to environmental and genetic factors (Bannan and Bayly 1956; Klem 1957; Ericson 1960; Larson 1969; Olesen 1982; Timell 1986; Fritts et al. 1991), it is hypothesized that tracheid structure and stem growth allocation of a conifer are primarily biologically optimized outcomes to changing mechanical and water transport demands on the conifer tree stem (Larson 1963; Niklas 1992; Mattheck and Kubler 1995; Gartner 1995).

To explain how a tree is able to adapt its wood formation to varying environmental demands, the theory of hormonal regulation of wood formation developed (Larson 1969; Wareing and Phillips 1970; Roberts et al. 1988; Lachaud 1989; Aloni 1992; Raven et al. 1992; Savidge 1993; Gartner 1995). The theory states that tracheid differentiation in the vascular cambium is largely a response to the basipetal transport of carbohydrates and growth hormones, produced in actively growing needle, shoot, and apical meristems of a conifer tree crown. Availability of carbohydrates and growth hormones to the vascular cambium produced within the tree crown during the vegetation period will then act as a regulator of tracheid differentiation. Consequently, tree crown development over time as a response to growth conditions will then provide the environmental influence on wood structure development.

Wood variation in *Picea abies* caused by differences of growth physiology was noticed more than 100 years ago by Hartig (1892a,b). Later, factors such as spacing, thinning, stem taper, fertilization, cambial age, tree class, site quality, and climate were found associated with wood structure development at the stand level (Nylinder and Hägglund 1954; Klem 1957; Ericson 1966; Madsen et al. 1985; Brolin et al. 1995; Lindström 1996b), tree level (Klem 1934; Johansson 1940; Nylinder 1953; Ericson 1960; Hakkila 1968, 1979; Hakkila and Uusvaara 1968; Persson 1975; Olesen 1976; Madsen et al. 1978; Kärkkäinen 1984; Johansson 1993; Brolin et al. 1995; Lindström 1996b), and within tree variation (Lewark 1981; Atmer and Thörnqvist 1982; Olesen 1977, 1982; Kyrkjeeide 1990; Kucera 1994; Dünisch and Bauch 1994; Brolin et al. 1995; Lindström 1996c). Results from these studies suggest that wood variation of *Picea abies* to a large extent is given by environmental factors that control crown development over time. This implies, in agreement with the hormone theory, that an evaluation of environmental influence on wood structure development could be based on factors known to regulate crown development over time, e.g., growth conditions and silviculture.

This study is a limited attempt to evaluate the influence of growth conditions on wood formation, thereby possibly giving valuable insight on how variation in growth conditions influences wood characteristic development of *Picea abies.* The gradual transition of tracheid length, tracheid diameter, and latewood percentage, from pith outwards, was evaluated by models based on growth condition variables.

## OBJECTIVES

The primary objective of this study was to determine the dependency of wood characteristics in *Picea abies* on growth conditions. The study focused on the following five relationships:

1. The regression of tracheid length on growth conditions over time.

2a. The regression of earlywood radial tracheid diameter on growth conditions over time.

2b. The regression of earlywood tangential tracheid diameter on growth conditions over time.

3. The regression of latewood tracheid diameter on growth conditions over time.

4. The regression of latewood percentage on growth conditions over time.

5. The regression of basic density on wood characteristics.

## MATERIAL AND METHODS

The material was provided by a fertilizing experiment located on a glacial till at Stråsan, Gästrikland, in Central Sweden, 350 m above sea level. The treatment included different levels of fertilization intended to obtain an optimum fertility trial. The trial was established to provide information on volume production in response to altered site quality (Tamm et al. 1974). It was assumed that this material would provide biological data reflecting varying growth rates. The Stråsan fertilizing trial was established in a plantation grown stand of *Picea abies* with the same seed source. This stand had reached breast height (1.3 m above stump height) when it was chosen as suitable for the fertilizing treatment. Established in 1967, the trial consisted of a 4*3*2 factorial experiment in nitrogen (N), phosphorus (P), and other nutrients (K+) with two blocks. The K+ fertilizer consisted of K, Mg, and micronutrients. The N dressings were repeated each spring; all other nutrients were applied at less frequent intervals. The level and timing of the nutrient applications were adjusted every few years on the basis of foliar analyses to maintain constant fertility differences between treatments (Mead and Tamm 1988). Plots had a gross area of 0.09 hectare, with a central measured plot of 0.04 hectare (Tamm et al. 1974).

### *Sampling*

Six parcels, two unfertilized, two medium fertilized, and two heavily fertilized, representing a wide range of site quality, were chosen from the trial. Three suppressed, three intermediate, and three dominant trees were chosen as sample trees on the basis of relative diameter within each parcel. To enable a subsequent pulp and paper test, three additional sample trees were taken, giving a total of 57 sample trees.

A bolt approximately 0.5 m long was cut from each tree, about 1.0 m above stump height. Two knot-free discs, 2-4 cm in width, were cut from the center of each bolt. Thus, the discs were close to breast height, near 1.3 m. These discs were transported to the Norwegian Forest Research Institute, Wood Technology Section, to determine wood characteristics. Wood characteristics in every second growth ring, from pith outwards, of the 57 sampled trees were determined using methods described by Kucera (1994) for a total of 656 growth rings.

### *Growth condition variables*

*Age.*—Cambial age was recorded for all 656 growth rings.

*Temperature/precipitation.*—Daily variation in temperature and precipitation was recorded at a meteorological station, Swedish Meteorological and Hydrological Institute

TABLE 1. *Dependence of wood characteristics on growth conditions.*[a]

| Regression equation | $r^2$ | $b_{i-n}$ | $sb_{i-n}$ | $x_{i-n}$ |
|---|---|---|---|---|
| (1a) ($T_l$) | 0.87 | 593.880786*** | 41.024036 | Intercept |
| | | 810.893390*** | 13.276611 | log(*Camb*) |
| | | −28.965817*** | 6.428821 | $G_{rw}$ |
| (1b) ($Rtd_e$) | 0.67 | 0.012891*** | 0.00052810 | Intercept |
| | | 0.006054*** | 0.00017064 | log(*Camb*) |
| | | 0.000844*** | 0.00008970 | $G_{rw}$ |
| | | 0.000004196** | 0.00000131 | Site quality[b] |
| (1c) ($Ttd_e$) | 0.76 | 0.010403*** | 0.00034455 | Intercept |
| | | 0.005020*** | 0.00011133 | log(*Camb*) |
| | | 0.000388*** | 0.00005852 | $G_{rw}$ |
| | | 0.000002337** | 0.00000085 | Site quality[b] |
| (1d) ($Rtd_l$) | 0.19 | 0.01284585*** | 0.00038068 | Intercept |
| | | 0.00162043*** | 0.00013613 | log(*Camb*) |
| | | −0.00000394*** | 0.00000100 | Site quality[b] |
| (1e) ($L_p$) | 0.53 | 0.096136*** | 0.01281738 | Intercept |
| | | −0.018977*** | 0.00208261 | $G_{rw}$ |
| | | 0.070878*** | 0.00873550 | $1/G_{rw}$ |
| | | 0.016242*** | 0.00283972 | log(*Camb*) |

[a] *, **, and ***, indicate $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$, respectively (SAS Institute, 1994).
[b] $m^3$sk $ha^{-1}$ is total bole volume produced above stump height per hectare.

(SMHI), located in Falun approximately 40 km southwest of the trial during 1961-1992. From 1986-1992, weather data were recorded at a meteorological station located in Vintjärn, approximately 10 km south of the trial. Weather data from both locations were used to calculate an adjustment coefficient of the Falun data from 1961-1985. This adjustment coefficient was used to calculate the average temperature in Celsius for June–August at Vintjärn 1966-1989. Total precipitation in mm during June–August was recorded and adjusted similarly to the temperature data from 1966-1989.

*Growth ring width.*—The ring width was determined to the nearest 0.01 mm, using methods described by Kucera (1994).

*Site quality.*—Site quality of the six parcels pairs was regulated by level of fertilization: unfertilized, medium fertilized, and heavily fertilized. Site quality was defined and measured in each parcel as total stem volume production per hectare, $m^3$sk $ha^{-1}$ (Eriksson 1976; Aronsson and Tamm 1991).

*Initial stand density.*—The number of seedlings in 1966 within each parcel was recalculated to number of seedlings per hectare and used as a measurement of initial stand density.

*Tree class.*—Suppressed, intermediate, and dominant trees within each parcel were sampled based on relative diameter and given a numerical code: 1 = suppressed, 2 = intermediate, 3 = dominant.

*Thinning.*—All parcels were subject to thinning in 1982; in addition, four of the six stands were thinned in 1988. Only the thinning procedure of 1982 was included in the model because 1989 was the last vegetation period before clearfelling, which gave the thinning for 1988 a very limited tree growth response (Personal communication, February-May 1994, with Professor C. O. Tamm and Doctor of Forestry A. Aronsson, both from the Dept. of EMC, The Swedish University of Agricultural Sciences, Uppsala). Thus, in the SAS model, the variable 0 was used before 1982 and 1 after 1982.

### *Wood characteristic variables*

*Basic density $\rho_y$, Cambial age$_{Camb}$, Growth ring width $G_{rw}$.*—$\rho_y$, *Camb*, $G_{rw}$ of every second annual ring, from pith outwards, were determined using water displacement, and microscope slides; the methods are described in detail by Kucera (1994).

*Radial tracheid diameter of latewood $Rtd_l$.*—Radial tracheid diameter of latewood was determined within every second growth ring, from pith outwards, using microscope slides; the method is described in detail by Kucera (1994).

*Latewood percentage $L_p$.*—Latewood percentage was determined within every second growth ring, from pith outwards, using microscope slides; the method is described in detail by Kucera (1994).

*Tracheid length $T_l$.*—Average tracheid length within every second growth ring, from pith outwards, was made using maceration of each growth ring, where the fiber suspension was affixed to microscope slides. Then 30 undamaged fibers were determined in length; the method is described in detail by Kucera (1994).

*Radial tracheid diameter of earlywood $Rtd_e$.*—Radial tracheid diameter of earlywood was determined within every second growth ring, from pith outwards using microscope slides; the method is described in detail by Kucera (1994).

*Tangential tracheid diameter of earlywood $Ttd_e$.*—Microscope slides used to determine $G_{rw}$, $Rtd_e$, $Rtd_l$, and $L_p$, were also used to determine $Ttd_e$ within every second growth ring. Here, 5 cells were counted out from the preceding growth ring boundary; thereafter tangential distance between 20 subsequent rays was registered together with the corresponding number of tracheids. $Ttd_e$ was calculated as the total distance divided by the total number of tracheids.

### *Models predicting wood characteristics*

*Growth condition influence.*—Regression has been used to evaluate the effect of growth conditions on wood characteristics (Hakkila and Uusvaara 1968; Hakkila 1968, 1979; Fritts et al. 1991; Dünisch and Bausch 1994; Lindström 1996c). Regression is used in the following form;

$$Y = \sum_{i=0}^{n} b_i x_i + \epsilon_i \tag{1}$$

where $Y$ = wood characteristic; $b_{i\text{-}n}$ are constants; $x_{i\text{-}n}$ biological variables; and $\epsilon_i$ is a random error.

*Dependence of basic density on wood characteristics.*—Basic density has been shown to be a composite of wood characteristics (Smith 1965; Fritts et al. 1991), so the dependence of basic density on wood characters can be modeled

$$Y = \sum_{i=0}^{n} b_i x_i + \epsilon_i \tag{2}$$

where $Y$ = basic density; $b_{i\text{-}n}$ are constants; and $x_{i\text{-}n}$ wood characteristics.

Statistical analysis of the objectives using the described models was carried out using multivariate regression methods (Draper and Smith 1981) with the SAS statistical software version 6.09 (SAS Institute 1994).

## RESULTS

### *Wood characteristics*

The SAS PROC REG procedure was used to model the development of each wood characteristic on growth condition variables. Two selection techniques were used: stepwise regression and variables were chosen sequentially to add to the model (Draper and Smith 1981) that had high predictive capability and yet kept the model simple. Both yielded models of the following form:

$$Y = \sum_{i=0}^{n} b_i x_i + \epsilon_i \tag{1a-e}$$

The correlation, statistical significance, and values of $b_{i\text{-}n}$ for each model are in Table 1. See also Figs. 1, 2, and 3.

### *Basic density*

The SAS PROC REG procedure was used to determine an optimal model of basic density

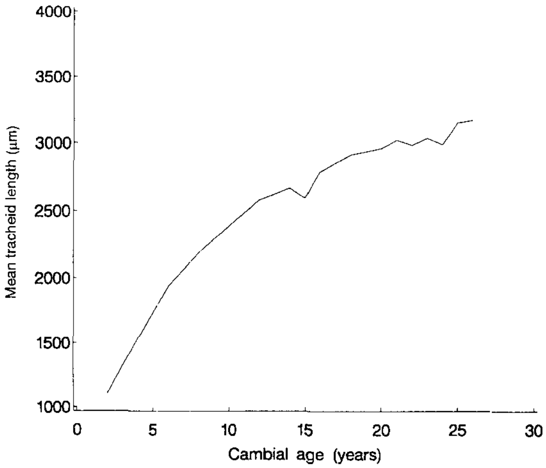


FIG. 1. Tracheid length versus cambial age.

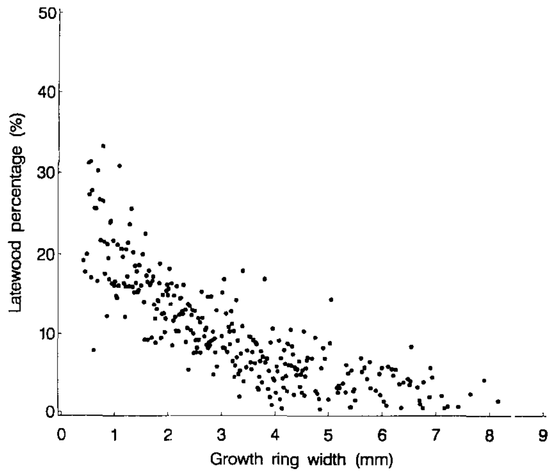


FIG. 3. Latewood percentage versus growth ring width.

based on wood characteristics. Three selection techniques were used: stepwise regression, best ADJRSQ, and best Mallow's CP (Draper and Smith 1981). All three yielded the following model:

$$Y = \sum_{i=0}^{n} b_i x_i + \epsilon_i \qquad (2)$$

Correlation, statistical significance, and values of $b_{i\text{-}n}$ for the model, are in Table 2. See also Fig. 4.

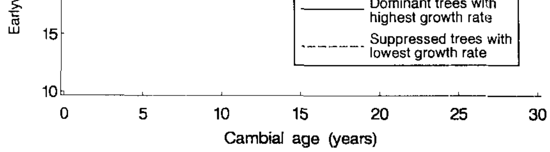


FIG. 2. Earlywood radial tracheid diameter versus cambial age.

## DISCUSSION

### *Wood variation*

In wood science, it is well recognized that wood formation is an outcome of both genetic and environmental factors. Many studies, including the present one, have concentrated on one of the two factors, so that the research study does not become too complex. However, to consider only the environmental influence becomes erratic because the genes between individual trees differ and can be assumed to partly determine vascular cambium activity and tracheid derivation. Therefore, variability of wood formation between trees will occur as a response to essentially the same external

TABLE 2. *Dependence of basic density on wood characteristics.*[a]

| Regression equation | $r^2$ | $b_{i-n}$ | $sb_{i-n}$ | $x_{i-n}$ |
|---|---|---|---|---|
| (2) ($\rho_y$) | 0.80 | 220.177638*** | 10.003866 | Intercept |
| | | 698.137307*** | 17.069543 | $L_p$ |
| | | 2.253186*** | 0.322483 | $1/Rtd_e$ |

[a] *, **, and ***, indicate p ≤ 0.05, p ≤ 0.01, and p ≤ 0.001, respectively (SAS Institute, 1994).

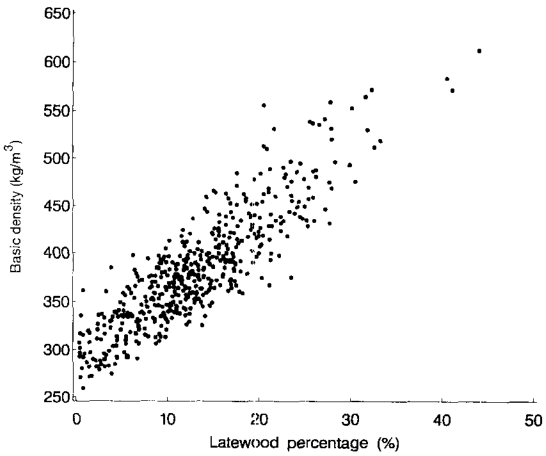


FIG. 4. Basic density versus latewood percentage.

stimuli. As a justification of the neglected genetic influence in this study, it can be argued that the trees investigated were grown from the same seed source, thereby limiting genetic effects to a near minimum.

If for a moment one disregards genetics and only considers how differences in growth conditions can alter tracheid structure, it essentially comes down to two receptors of external stimuli: root and crown development. Roots provide the water and minerals that are necessary in the photosynthesis process, and the crown development sets the limit of the carbohydrate and growth hormone production, as a function of leaf area and hormone synthesizing meristems. The concentration and ratio of carbohydrates and hormones that are basipetally transported have been assumed to be decisive for the vascular cambium activity and therefore the tracheid differentiation. So, tracheid structure development can be seen as a function of the changing environment of a tree that acts through crown development. Consequently, a model describing the environmental influence over wood formation should be based on accurately described environmental variables that affect crown development over time.

The correlation between a certain wood characteristic and a set of growth condition variables will be indicative of the relative dependency of a wood character on those growth condition variables included in the model. Nevertheless, a complete description of growth conditions is most difficult to attain; therefore this type of model often becomes limited. Moreover, as genetic influence is not included in the model, this will further add to the error term. Therefore, a crude model based on a limited set of growth condition variables will only tell us that some wood characters seem to be under more direct control of growth conditions. If it were possible to include all growth condition variables present at the time of wood formation, this would probably yield a correlation between wood variation and growth conditions that had a closer resemblance to the true dependency.

## *Material*

As noted in two previous studies (Lindström 1996b,c) the material for this study is believed to be unique, in that parcels of planted Norway spruce (*Picea abies*), of the same seed source, grown at the same geographical location were given a wide variety of site quality through fertilization. This external regulation of crown development at stand and tree level gave a wide range of tree growth physiology, yielding trees of the same age grown at varying growth rates. Therefore, the material is believed suitable for the evaluation of the environmental effect on tracheid structure development. To mirror the varying growth conditions at tree level within each parcel, a selection of suppressed, intermediate, and dominant trees was made representing the spectra of growth physiology.

## *Results*

The correlation between wood characteristics and growth conditions was found to differ between the different models ($r^2$ = 0.87–0.19). The ability of each model to explain wood characteristics development can be sought in three main areas:

1. Measurement and definition accuracy when determining a wood characteristic value.
2. Measurement and definition accuracy when determining a growth condition variable.
3. Genetic influence over wood formation.

When considering the first of these areas, it is apparent that definition and measurement of a wood character are accurate, as they will affect correlation in derived models. Note that the present study is based on limited outcuts of entire growth rings. Thus local variation in tracheid structure within growth rings, e.g., compression tracheids or tracheids derived from a frost-damaged vascular cambium can, to some degree, disproportionally affect the derived value of the determined wood characteristics.

In the same way, the quality of growth condition variables, their range, and their ability to accurately mirror differences in growth conditions, are essential for the accuracy of models based on growth conditions. For instance, model predictive capability would improve if growth condition factors that initiate compression wood formation and extractive production could be included.

Third, in the literature it is argued that some wood characteristics more strongly adhere to genetic predisposition, while others more clearly reflect differences in growth physiology induced by variability in growth conditions. Therefore, even if the requirements of data quality of areas 1, and 2 can be fulfilled, some wood characters will not be easily predicted by differences in growth conditions, as they are under considerable genetic control.

It is necessary to have these three outlined areas in mind when interpreting the variation found in tracheid structure development in order to not try to overfit a material to a specific model. However, with the perspective that crown development provides the environmental influence on wood formation (Larson 1969; Savidge 1993; Gartner 1995), it is clear that individual growth condition factors that regulate or mirror crown development will affect wood formation. So it is not surprising that the factors that repeatedly came up as significant in the models of this study seem to mirror crown development over time. With this in view, the following interpretation is given.

Cambial age was found to have a noticeable effect on tracheid structure development. It is clear that time reflects increasing crown competition between trees as stand closure sets in, which will be responsible for tree crown recession. An ever-increasing distance between the vascular cambium at breast height and a receding tree crown as a function of time will, therefore, be evident both in growth ring width and tracheid structure development at breast height.

Although growth ring width was found to have influence on tracheid structure development, it cannot be said to be a causative factor, because the growth ring width at breast height is the result of stem growth allocation of a tree, which is dependent on factors regulating crown development.

Site quality was also found to have a significant effect on tracheid structure development. Here, growth conditions altered through fertilization can again be seen to act through crown development, i.e., average crown size in a tree stand will vary with site quality and influence wood structure development of a tree.

As a brief summary of the results, it can be said that a gradual transition in tracheid size takes place from pith outwards. The revealed differences in tracheid structure development can be assumed to be created by differences in cell growth physiology created by genetic and environmental factors. For instance, close to pith wood formation is probably still under strong genetic influence. Therefore, all trees exhibit a similar nonmature tracheid size. With time, factors controlling turgor pressure and availability of carbohydrate and growth hormones to the vascular cambium and the differentiating tracheids will have a guiding effect on the final tracheid structure. Thus, it can be argued that growth conditions acting through crown development will regulate the amount of growth stimuli necessary for wood formation, which also will be evident in the final tracheid structure.

*The influence of tracheid morphology on basic density*

Basic density was found dependent on latewood percentage and earlywood radial tracheid diameter with an $r^2 = 0.80$. As basic density is a constitutive definition that reflects amount of cell-wall material per volume unit, an even higher correlation would probably have been found if cell-wall thickness had also been available for inclusion in the model.

*Forestry management–raw material properties*

Based on the present study and three preceding ones (Lindström 1996a, b, c), it can be concluded that growth conditions, acting through crown development, will influence growth rate, stem taper, and tracheid structure development of *Picea abies.* Consequently, any silvicultural practice that affects crown development of a tree will also regulate wood structure. Therefore, in a perspective concerned with the raw material properties of wood, the type of silvicultural strategy chosen becomes important, as this will form the properties of the wood produced and therefore the competitiveness and value of wood as a raw material.

Here, it can be generally argued that silvicultural procedures that promote rapid crown development and minimize crown competition (e.g., low amount of seedlings at time of stand establishment and early thinning from below) will increase growth rate of individual trees. Consequently, such procedures will shorten the time to reach a merchantable tree size and will therefore shorten the rotation periods. However, the negative effects on the quality of the wood produced by this type of silviculture are substantial in that trees on the average will have more stem taper, juvenile wood, and branch wood, while basic density decreases.

In contrast, silvicultural procedures that favor crown competition (e.g., high amount of seedlings at stand establishment and thinning from above) will increase crown recession and delay crown size development, which will lead to lower individual tree growth rate and require longer rotation periods to reach merchantable size. Nevertheless, in this scenario, several positive effects on wood quality will follow, in that trees will attain lower stem taper, less amount of juvenile wood and branch wood, while basic density increases.

In recent decades, Scandinavian forestry procedures have been aimed at transferring wood production to a few number of trees per unit area to reduce harvesting costs, attain merchantable sizes sooner, and maintain cost efficiency. Such forestry operations are now beginning to show that wood production of suppressed and intermediate trees has increasingly been transferred to more dominant and codominant trees, with higher individual tree growth rate as a result (Elfving and Tegnhammar 1996). In the same study, it was also shown that if height development is used as an indicator variable of site quality, it has increased for 40 years in Sweden. However, if one considers the fundamental silvicultural change of growth conditions that has taken place during the same time period (i.e., promotion of early rapid crown development through clear-cutting, widely spaced planting, and early thinning from below), the increase in height growth of the codominant and dominant trees does not necessarily reflect an improvement in volume production. Instead, it indicates that a shift from more extensive to more intensive methods has led to low crown competition, therefore producing large crowned, rapidly growing trees with considerable stem taper and, on the average, lower basic density of the wood produced. It is likely that when fewer trees are found per unit area, the potential for site quality is probably not fully realized, because the total amount of photosynthesizing leaf area becomes restricted within a less dense stand. So, the promise of an enhanced site quality based on more rapid height development of the dominant trees in an intensively managed forest is not necessarily associated with a greater future volume production. Moreover, even if a greater volume production is reached by more intensive methods, it is not necessarily associated with a greater monetary value, since wood properties and therefore the value of the wood produced will change with the chosen silvicultural strategy.

As a matter of fact, it could very well be that the assumption that low thinnings and short rotation periods maximize the net present value, is incorrect. Here, one has to understand that if conifer tree growth is changed by a more intensive silviculture, some negative effects will follow. These negative effects are not accounted for in the cost benefit analysis that predicts the net present value of an intensive silvicultural strategy. The seven, perhaps most important, areas of tree growth that will change the economic revenue of Swedish forestry as an outcome of more intensive silvicultural methods consist of:

- Inefficient utilization of a given site quality.
- Stem taper deterioration.
- Stem straightness deterioration.
- Branch volume increase.
- Juvenile wood percentage increase.
- Wood property changes.
- Frequency of tree injuries caused by mammals.

If these aspects of tree growth are overlooked, a serious misconception ensues, namely that the value of a volume unit of wood produced with one intensive silvicultural method should be equal to a volume unit of wood produced by more extensive methods.

For instance, if wood production is transferred to fewer trees per unit area, by wide-spaced planting, and early low thinnings, there is a high probability that the leaf area index, i.e., the total needle area in a conifer tree stand divided by the area that the tree stand occupies, will decrease. Consequently, it will mean that the potential for site quality will be less utilized compared with a tree stand where crown competition is promoted through a more extensive silvicultural strategy. Moreover, stem taper deterioration will follow in tree stands where rapid crown growth has been promoted. There are also reports indicating that stem straightness will deteriorate when using wide-spaced planting. These two factors that seem accentuated by intensive silvicultural regimes will mean that more of the wood volume in a tree stand will become pulpwood instead of saw logs at the time of clear-felling. As the value of saw logs has proved to be higher than for pulpwood, a shift in proportions towards more pulpwood and less saw logs will create a revenue decrease. Moreover, an increase in branch wood and juvenile wood, as a result of unrestricted juvenile tree growth combined with a shorter rotation period, will have a similar negative effect on the wood value. In addition, as was shown in this study, basic density as a function of wood structure will decrease if rapid crown growth is promoted in young stands of Norway spruce, which implies a further reduction in the value of wood as a raw material for forest products.

Futhermore, it is striking that the increase of the Swedish roe deer and moose population coincides with the introduction of forestry regeneration methods that used large concentrated areas of clear-cutting. In this open forest landscape, which often becomes overgrown with grass and intermixed with young conifer and broadleaf trees, grazing and browsing animals will find an excellent summer biotope. However, in winter time, when forage of grass and leafs is no longer available, young conifer trees will be more of a base forage. So, during winter time young conifers will be browsed, peeled, and broken by roe deer and moose to keep themselves alive. The tree injuries that follow result in a lower wood volume production per area unit, and the tree injuries will also lead to a change of the raw material properties and value of the conifer wood produced.

The foregoing discussion seems to indicate that the author rejects the economic concept of applying cost benefit analysis on forestry operations in order to optimize the net present value on forest land; however, this is not so. My objections concern the aspects of the given assumptions that are present in the analysis. When applying a silvicultural strategy, one has to be aware that the chosen strategy will alter the underlying components in the terms earlier indicated. For instance there has to be a correct evaluation of the value per volume unit wood produced under differing silvicultural strategies if an optimum net present value of forest land is to be reached. Here, it would be most interesting to apply net present value thinking where raw material property changes, due to the silvicultural strategy chosen, are internalized in the analysis. However, in doing so, it becomes necessary to quantify how raw material properties and the corresponding value of wood vary with growth conditions and chosen silvicultural strategy. At present, those studies await realization until a more quantitative approach is undertaken on how raw material properties of wood, and the corresponding value of wood, are regulated by growth conditions and silviculture.

### *Future studies*

As the data quality of growth conditions and wood characteristics variables will affect the ability to predict wood structure development, a more precise definition of these factors is needed to reach a greater model predictability/accuracy. However, the problem with acquiring more accurate models is substantiated by several restraints. First of all, measurement of wood characteristics is very time-consuming. Second, it is preferred that the definition of growth conditions should be general, yet individual variables must be able to precisely define growth conditions encountered. Furthermore, because wood structure is a result of complex interaction effects of genetics and environment, it is preferred that models developed for general use should be adjustable for genetic variation, e.g., provenance.

Nevertheless, it is evident that an ever-increasing accessibility to rapid and precise data acquisition will improve the possibilities of constructing relevant models. Hopefully, the ongoing progress within information technology will aid future studies in the construction of accurate nondestructive prediction models. Such models could be developed for use in forestry management decisions, which would help the prospect of enhancing the performance and value of wood as a raw material for forest products.

## CONCLUSIONS

- Logarithm of age, growth rate, and site quality were found significant in the models describing tracheid structure development.
- Correlation in the different models varied substantially ($r^2$ = 0.87–0.19), indicating that (a) definition/accuracy of wood characters and growth condition factors needs to be improved if higher correlation is to be reached; and (b) some wood characteristics are probably under strong genetic influence and will, therefore, be difficult to predict based on growth conditions.
- Basic density was found dependent on wood characteristics with an $r^2$ = 0.80.
- Growth conditions acting through crown development of a tree will influence tracheid structure development of a tree.
- Any silvicultural practice that alters crown development over time will also alter the properties and value of the wood produced.
- Future studies need to be undertaken in order to establish models that have the capability of describing wood variation as a result of differences in growth conditions. Such models will hopefully be implemented into forestry as a tool to foresee, produce, classify, and select wood with more well-defined properties and economic value.

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