BASIC DENSITY IN NORWAY SPRUCE. PART III. DEVELOPMENT FROM PITH OUTWARDS

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ABSTRACT

A change in forest management using intensive silviculture is gradually transforming the conifer raw material base of the Swedish forest industry. As the end-use properties of forest products greatly depend on wood characteristics, such as tracheid length, tracheid diameter, microfibril angle, and basic density, there is increasing concern to foresee how silvicultural regulation of growth conditions alters wood properties.

In this study, 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 varying growth conditions on basic density. Growth rate of each parcel had been regulated by annual dressings of nitrogen, phosphorus, potassium, and micronutrients.

The basic density, kg/m^3, of individual growth rings at breast height, from pith outwards, using suppressed, intermediate, and dominant trees sampled from each parcel, was evaluated in different modeling approaches. In a modeling attempt based on growth conditions, site quality, initial stand density, thinning, tree class, climate, and cambial age were, separately or in interaction, found significant for basic density development with r^2 = 0.46–0.63. These results suggest that crown development at stand and tree level over time will affect basic density.

Keywords: *Picea abies,* tree class, silviculture, wood formation, basic density, wood density, wood characteristics, crown development, models.

INTRODUCTION

This study contains a background on how environmental and genetic factors relate to basic density development in conifers, with an emphasis on Norway spruce (*Picea abies*). Separate models are used to determine impact of growth conditions on basic density development. The material consists of suppressed, intermediate, and dominant trees, sampled from even-aged planted parcels with varying site quality, in a fertilization trial located at Stråsan, central Sweden.

Basic density, seen as a descriptive composite of wood structure, has become the most used quality indicator of conifer wood (Zobel and Van Buijtenen 1989). This feature is also reflected in the end-use properties of forest products. For instance, basic density has been found to correlate with pulp yield, paper properties (opacity, tensile-, tear- and burst strength) (Nylinder and Hägglund 1954; Persson 1975; Kärenlampi et al. 1994; Brolin et al. 1995), and structural lumber properties (dimensional stability, bending stiffness, and strength) (Bendtsen 1978; Barrett and Kellogg 1989; Kliger et al. 1995).

In recent decades, the forest industry has increasingly received a material that is characterized with a higher content of juvenile wood and a higher degree of wood variation. Basic density is believed to be only one wood feature that is gradually changing as an outcome of altered forestry management methods (Zobel and Van Buijtenen 1989; Thörnqvist 1993; Kennedy 1995). This has created an increasing need to predict how silvicultural regulation of growth conditions regulates wood structure and thus properties and value of wood as a raw material for forest products.

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In general, growth conditions acting through crown development of a conifer regulate wood structure. Here, it is understood that within the foliar organs, growing meristems produce hormones that, together with produced photosynthate, are basipetally transported to the vascular cambium. The ratio and amount of growth promoters that reach the vascular cambium regulate the wood formation (Larson 1969; Elliott 1970; Savidge 1993). As a result, variation occurs in tracheid diameter, cell-wall thickness, and latewood percentage, factors that are reflected in basic density (Larson 1969; Megraw 1985; Kennedy 1995).

Although genetic and latent factors are viewed as sources of wood variation affecting conifer wood formation, this study is concerned with the environmental influence on basic density development of Norway spruce (*Picea abies*).

BACKGROUND

In the following, a short background is given regarding how basic density in *Picea abies* is regulated.

Genetic factors

Genetic influence on wood formation in *Picea abies* is mainly divided into two terms:

- Provenance
- Cyclophysis

In the geographical range of a tree species, genetic adaptation of growth rhythm and wood formation results in a differentiation of provenances of the species. Each provenance possesses a growth physiology well-adapted to a certain geographical region (Zobel and Van Buijtenen 1989). It is assumed that a provenance poorly adapted to its growing climate results in wood formation characterized by incomplete lignification, less latewood production, and stemcracks (Dietrichson 1963, 1964; Malmqvist 1994). Recent studies have also shown that provenance modifies basic density of *Picea abies* (Ilstedt and Eriksson 1986; Blouin et al. 1994).

Cyclophysis is a genetic feature describing the maturing of the vascular cambium that is responsible for a more rapid tracheid diameter transition from pith outwards at 5- and 10-m stem height compared with the transition time required at stem height of 1.3 m. Therefore, cyclophysis is said to cause variation of basic density along the tree stem (Olesen 1982).

Environmental factors

Environmental factors that have an effect on wood formation are as follow:

- Climate variation
- Silvicultural treatment
- Site quality

Climate is regarded as a factor that determines tracheid development and the ratio between early- and latewood of individual growth rings in *Picea abies* (Eklund 1957; Kienast et al. 1987; Dünisch and Bauch 1994).

Silvicultural treatment in terms of spacing (Klem 1942; Persson 1975; Moltesen et al. 1985), thinning (Hildebrandt 1954; Ericson 1966; Madsen et al. 1978), and fertilization (Madsen et al. 1985) alters growing conditions and the basic density of the wood produced. It is argued that treatments promoting excessive crown development of *Picea abies* yield trees with more stem taper and lower basic density (Kyrkjeeide 1990; Thörnqvist 1993; Lindström 1996a, b).

Although it is not a high growth rate per se that will have an effect on wood formation, unrestrained crown development that follows on a good site quality will have a governing influence over the vascular cambium activity until stand closure when crown competition begins (Larson 1963, 1969; Elliott 1970). Hence, site quality can be seen as a regulator of cambial activity, tracheid differentiation, and consequently basic density.

Latent factors

The following features disclose the interaction between genetics and environment:

- Crown development
- Cambial age

- Compression wood
- Extractive production

During the successional stand phases of *Picea abies*, individual trees will attain variability in height and stem diameter as a function of crown vigor and crown competition. Crown competition within an even-aged *Picea abies* stand can be visualized as the transition of trees into suppressed, intermediate, codominant, and dominant trees. The initially attained crown class is usually maintained throughout the lifespan of a stand. For *Picea abies*, studies have shown that dominant and codominant trees acquire a lower basic density than intermediate and suppressed tree classes (Burger 1953; Kärkkäinen 1984; Kyrkjeeide 1990; Johansson 1993; Lindström 1996b).

Gradual transformation in tracheid diameter and cell-wall thickness is considered to be a combined effect of a maturing process of the vascular cambium and an ever-increasing distance between the vascular cambium and a receding tree crown (Larson 1969; Elliott 1970; Olesen 1982; Megraw 1985; Zobel and Van Buijtenen 1989). As an illustration, for *Picea abies*, Olesen (1982), Kyrkjeeide (1990), and Kucera (1994) reported a seemingly age-dependent pattern of basic density from pith towards bark where basic density initially decreases to reach a minimum, followed by a gradual increase of basic density.

Conifers that have leaning or crooked stems form compression wood, i.e. tracheids with large fibrillar angle, a thick cell wall, and short length. Here, interaction between genetic predetermination and outer mechanical forces on the tree causes vascular cambium differentiation of compression wood (Timell 1986). Kyrkjeeide and Thörnqvist (1993) argue that trees with large crown areas, caused by rapid branch growth, are most likely to be exposed to mechanical force. The authors concluded that there is a gradient in the amount of compression wood being formed in differing stem classes.

Extractive content is another source of basic density variation. The extractives are deposited in the inner cell walls of tracheids, thereby reducing void lumen volume, consequently causing a greater basic density (Trendelenburg and Mayer-Wegelin 1955). Frequently, traumatic production of extractives can take place as a result of tree injury, caused by severe climate or mammals and insects (Timell 1986; Zobel and Van Buijtenen 1989).

OBJECTIVES

In this study, basic density development, kg/m^3, from pith outwards, of Norway spruce (*Picea abies*) is evaluated using different models. Interest is restricted to the following six relationships:

1. Relationship between basic density and height-diameter development,
2. Linear and logarithmic relationship of basic density and growth ring width,
3. Olesen's relationship of basic density and growth ring width,
4. Regression of basic density on cambial age and growth ring width,
5. Regression of growth ring width on growth conditions, and
6. Regression of basic density on growth conditions.

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. It was assumed that this material would provide biological data reflecting varying growth rates (Tamm et al. 1974; Mead and Tamm 1988). The Stråsan fertilizing trial was established in a plantation-grown stand of *Picea abies* with the same seed source. This stand had roughly 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

TABLE 1. *Stand characteristics of each parcel.*

Parcel	Treatment	Site quality (m^3sk ha^{-1})[a]	Initial stand density (number of seedlings ha^{-1})	Average diameter[b] suppressed tree class (mm)	Average diameter[b] intermediate tree class (mm)	Average diameter[b] dominant tree class (mm)
P34	Unfertilized	39.5	2,525	59	84	114
P51	Unfertilized	87.2	1,750	71	126	177
P10	N1P1	218.8	3,025	114	153	178
P36	N1P1	249.5	2,775	100	160	195
P18	N3P2	321.3	2,625	131	200	244
P41	N3P2	227.5	2,625	130	184	213

[a] m^3sk ha^{-1} is total bole volume above stump height per hectare.
[b] Based on diameter close to breast height (1.3 m) outside bark, at the time of clearcutting.

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 and basic density determination

Six parcels, two unfertilized, two medium fertilized, and two heavily fertilized, representing a wide range of site quality (Table 1), were chosen from the trial. Stand characteristics and tree diameter distribution of each chosen parcel are given in Lindström (1996b). Three suppressed, three intermediate, and three dominant trees were chosen as sample trees on the basis of relative diameter within each parcel (Table 1). To obtain enough material for 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 thickness, 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. Basic density, kg/m^3, every second annual ring, from pith outwards, for a total of 656 growth rings were determined using methods described by Kucera (1994).

Variables

Age.—Cambial age was recorded for all basic density determined growth rings.

Average temperature June–August/Total precipitation June–August.—Daily variation in temperature and precipitation was recorded at a meteorological station, Swedish Meteorological and Hydrological Institute (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 similar to the temperature data from 1966–1989.

Growth ring width.—The ring width of the basic density determined growth rings was determined to the nearest 0.01 mm, using methods described by Kucera (1994).

Site quality.—Site quality of the three parcel 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^3sk ha^{-1} (Eriksson 1976; Aronsson and Tamm 1991) (Table 1).

Initial stand density.—The numbers of seedlings in 1966 within each parcel were recalculated to numbers of seedlings per hectare and used as a measurement of initial stand density (Table 1).

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

Height-diameter development.—About half the trees within each parcel were measured in 1975, 1978, 1982, 1986, 1988, 1989 for height in dm and breast height diameter outside bark in mm (Aronsson and Tamm 1991). Height-diameter development of these trees was calculated as Tree height in dm/Breast height diameter, o.b., in mm for each year yielding 95 observations.

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 clear-felling, 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 Department of EMC, The Swedish University of Agricultural Sciences, Uppsala). Thus thinning in the SAS model was an indicator variable with the value 0 before 1982 and 1 afterward.

Models predicting basic density

Models that indirectly seem to represent crown development at stand or tree level have frequently been used to predict basic density of *Picea abies* (Lindström 1996a, b). These models are used in the statistical analysis of the objectives. The models were applied on the data in this study with the SAS statistical software version 6.09 (SAS Institute 1994).

Regression of basic density on stem taper.—Klem (1934) found a relationship between average basic density and stem taper for *Picea abies* at 1.3 m. The relationship is thought primarily applicable for even-aged trees (Hakkila 1979; Lindström 1996b).

$$Y = a + bx + \epsilon \qquad (1)$$

where Y = average basic density; a and b constants; x = stem taper; and ϵ is a random error.

Regression of basic density on growth ring width.—The negative relationship between average basic density and mean growth ring width for *Picea abies* is explained as decreasing latewood percentage with increasing growth ring width (Nylinder and Hägglund 1954; Hildebrandt 1954; Trendelenburg and Mayer-Wegelin 1955; Hakkila 1968, 1979; Persson 1975). Decreasing latewood percentage with increasing growth ring width is, however, not entirely linear. A logarithmic relationship was indicated by Hakkila (1968), and an exponential model based on growth ring width was developed by Grammel (1990).

$$Y = a_i + b_i x + \epsilon \qquad (2a)$$

$$Y = a_i + b_i \log(x) + \epsilon \qquad (2b)$$

$$Y = a_i \times \exp(b_i \times x) + \epsilon \qquad (2c)$$

where Y = average basic density of a tree or basic density of sectioned growth rings, a_i is a positive constant, b_i is a negative constant, and x is mean growth ring width of a tree or mean growth ring width of sectioned growth rings.

Another basic density model, showing the nonlinear relationship, was suggested by Olesen (1976, 1977);

$$Y = a + \frac{b}{(c + x)} + \epsilon \qquad (3)$$

where Y = average basic density of sectioned growth ring samples; x is mean ring width of sectioned samples; a, b and c are positive constants, where a is said to be earlywood density (Olesen 1976, 1977, 1982).

Multivariate regression of basic density based on growth variables.—Multivariate regression has been used to evaluate the effect of growth conditions on average basic density of trees at 1.3 m (Hakkila and Uusvaara 1968; Hakkila 1979; Kärkkäinen 1984; Lindström 1996b). Multivariate regression here is used in the form.

TABLE 2. *Relationship of basic density, kg/m³, of an individual growth ring and height-diameter development, (Tree height in dm)/(Breast height diameter, o.b., in mm), for the years 1975, 1978, 1982, 1988, and 1988.*[a]

Regression equation	r^2	a	s_a	b	s_b
(1) $Y = a + bx$	0.28	193.04***	29.86	227.92***	37.36

[a] *, **, and ***, indicate $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively.

$$Y = \sum_{i=0}^{n} b_i x_i + \epsilon_i \quad (4)$$

where Y = average basic density, b_{i-n} are constants, and x_{i-n} are growth condition variables. It seems evident that Eq. (4) can be applied to evaluate the effect of growth conditions on basic density development from pith and outwards.

RESULTS

Basic density of individual growth rings and height-diameter development.—Linear regression was used to determine the relationship between basic density of individual growth rings and height-diameter development. SAS PROC REG was used to build a linear model in the following form:

$$Y = a + bx + \epsilon \quad (1)$$

where Y = basic density, kg/m³, of an individual growth ring at breast height; x = Tree height in dm/Breast height diameter, o.b., in mm of the tree when the growth ring is formed. Correlation, statistical significance, and values of a and b are in Table 2.

Basic density of individual growth rings and growth ring width.—Regression was used to determine the relationship between basic density of individual growth rings and growth ring width. SAS PROC REG was used to build models in the following form:

$$Y = a_i + b_i x + \epsilon \quad (2a)$$

$$Y = a_i + b_i \log(x) + \epsilon \quad (2b)$$

where Y = basic density, kg/m³, of an individual growth ring at breast height; a_i is a positive constant; b_i is a negative constant; x is mean growth ring width or mean growth ring width of sectioned samples. Correlation, statistical significance, and values of a_i and b_i are in Table 3. Models (2a) and (2b) are here fitted to both a complete and a reduced data set, where growth rings 2 and 4 were omitted.

A program written in SAS using PROC NLIN was used to fit Olesen's model to the reduced data set.

TABLE 3. *Relationship of basic density development based on growth ring width.*[a]

Regression equation	r^2	a	s_a	b_1	s_{b1}	b_2	s_{b2}	c	s_c
(2a) $Y = a + b_1x_1 + \epsilon$ based on nonreduced data set	0.33	458.84***	4.33	−25.02***	1.39				
(2b) $Y = a + b_1\log(x_1) + \epsilon$ based on nonreduced data set	0.41	452.55***	3.47	−72.82***	3.37				
(2a) $Y = a + b_1x_1 + \epsilon$ based on reduced data set	0.43	455.12***	4.14	−28.21***	1.39				
(2b) $Y = a + b_1\log(x_1) + \epsilon$ based on reduced data set	0.52	455.39***	3.19	−78.33***	3.22				
(3) $Y = a + \frac{b_1}{(c + x)} + \epsilon$ based on reduced data set	0.50	227.27	21.93	604.59	165.33			1.75	0.49
(4) $Y = a + b_1x_1 + b_2x_2 + \epsilon$ based on reduced data set	0.53	467.11***	6.66	−1.23***	0.33	−82.66***	3.39		

[a] *, **, and ***, indicate $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively.

$$Y = a + \frac{b}{(c + x)} + \epsilon \qquad (3)$$

where Y = basic density, kg/m^3, of an individual growth ring at breast height; a, b, and c positive constants; x is growth ring width. Standard tests of significance of the parameters were not given by SAS. However, the standard deviation, an asymptotic standard deviation, can be used to approximate significance intervals of the values of a, b, c, and x in Table 3.

Basic density of individual growth rings on cambial age and growth ring width

The SAS PROC REG procedure was used to examine several potential models based on the reduced data set. The simplest model that explained a significant part of the variation was:

$$Y = a + b_1x_1 + b_2x_2 + \epsilon \qquad (4)$$

where Y = basic density, kg/m^3, of an individual growth ring at breast height; x_1 = log (growth ring width); x_2 = cambial age. Correlation, statistical significance, and values of a, b_1, and b_2 are in Table 3.

Growth ring width on growth conditions

The SAS PROC REG procedure using the reduced data set (growth rings 2 and 4 omitted) was used to determine the following model based on growth condition variables via stepwise regression.

$$Y = \sum_{i=1}^{n} b_ix_i + \epsilon_i \qquad (5a)$$

A simpler model, denoted as "(5b)", was derived based on factors significant at $P \leq 0.001$. Correlation, statistical significance, and values of b_{i-n} for each model, are in Table 4.

Basic density on growth conditions

Stepwise regression, based on the reduced data set, was used to determine the following model based on growth condition variables.

$$Y = \sum_{i=0}^{n} b_ix_i + \epsilon_i \qquad (6a)$$

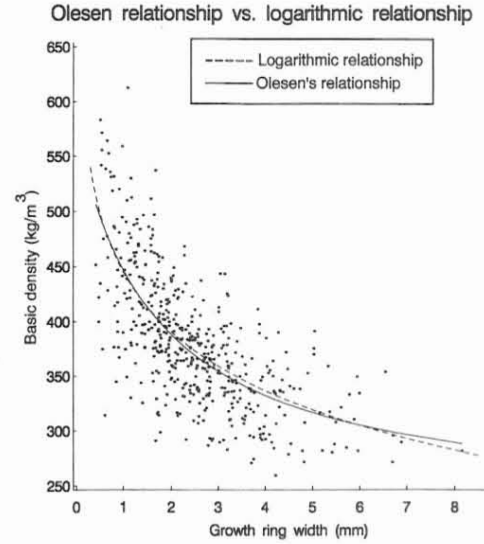

FIG. 1. The fit of Olesen's relationship (3) and the logarithmic relationship (2b) to the material.

A simpler model, denoted as "(6b)", was derived based on factors significant at $P \leq 0.001$. Correlation, statistical significance, and values of b_{i-n} for each model are in Table 5.

DISCUSSION

Literature

In previous studies dealing with wood formation of conifers, both environmental and genetic factors were found to influence vascular cambium activity and therefore xylem structure. Consequently, basic density has been reported as a combined effect of genetics and environment, likely to be optimized to the demands of a geographically restricted region. In this paper, crown development at stand and tree level is seen as a continuous adaptation to long- and short-term variation of growth conditions. Variables such as site quality, climate, and silvicultural treatment acting through crown development are said to assert control over vascular cambial activity and tracheid derivation. As a result, basic density models used for *Picea abies* have been based on variables regulating or dependent on vascular cambium activity.

TABLE 4. *Dependence of growth ring width on growth conditions.*[a]

Regression equation	r^2	b_{i-n}	sb_{i-n}	x_{i-n}
(5a) $Y = \Sigma_{i=0}^{n} b_i x_i + \epsilon_i$	0.76	1.793260***	0.185852	Intercept
(All significant factors)		−0.151872***	0.030341	Cambial age • Treeclass 1
		0.015702***	0.001032	Site quality
		0.018830***	0.003892	Site quality • Treeclass 3
		−0.000353***	0.000071	Cambial age • Site quality • Tree class 3
		−0.000682***	0.000061	Cambial age • Site quality
		−0.003243***	0.000736	Site quality • Tree class 1
		−0.000038***	0.000008	Cambial age • Initial stand density
		0.005726***	0.000842	Cambial age • Cambial age
		0.000041***	0.000013	Cambial age • Initial stand density • Tree class 1
		−0.000004**	0.000001	Site quality • Initial stand density • Tree class 3
		−0.070771***	0.015215	Thinning • Cambial age
		0.004118***	0.000734	Thinning • Total precipitation Jun-Aug
		0.027041*	0.011304	Thinning • Cambial age • Tree class 1
		0.001787*	0.000733	Thinning • Initial stand density • Tree class 3
(5b) $Y = \Sigma_{i=0}^{n} + \epsilon_i$	0.71	1.982840***	0.282021	Intercept
(Based on *** factors)		0.070079***	0.012790	Cambial age
		−0.033462***	0.008021	Cambial age • Tree class 1
		0.016143***	0.001141	Site quality
		0.008405***	0.001007	Site quality • Tree class 3
		−0.000302***	0.000058	Cambial age • Site quality • Tree class 3
		−0.000721***	0.000064	Cambial age • Site quality
		−0.000548***	0.000092	Initial stand density
		−0.002718***	0.000623	Site quality • Tree class 1

[a] *, **, and ***, indicate $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively.

Material

This first modern Swedish fertilization trial of *Picea abies* was initialized with the primary aim on volume production studies. Although the genetic variation is by no means eliminated, it should be kept low by using the same seed source. Therefore, this study provides a somewhat unique opportunity to discern the effect of growth conditions on basic density development. The material used in this study consisted of individual growth rings taken every second growth ring, from pith outwards, from suppressed, intermediate, and dominant trees within each parcel. This ensured that the effect on basic density caused by variation in growth conditions over time could be evaluated.

Some factors that inadvertently influence basic density development and model validity/accuracy should be mentioned. The first is that although wood formation is laid down into growth rings circumferentially, determination of the basic density of individual growth rings was based on a limited outcut of the entire growth ring. To base measurements on the entire growth ring, instead of a limited outcut, would restrict impact due to local variation of basic density in the growth ring. However, such measurements would be very time-consuming and have seldom or ever been completed. Two other factors that influence basic density development, extractive and compression wood content, were not registered in this study. Here, the extractive content was assumed negligible in that the trees were so young that heartwood formation had not begun. Still, it is possible that parenchyma cells and resin ducts became activated in a response to the clear-felling, thereby starting a traumatic extractive production. Compression wood was chosen not to be quantified, in that compression wood only seemed present to a minor extent.

Results

Stem taper, as a result of tree crown development, has been linked to average basic density at breast height. Variation in crown development is the suggested reason why even-aged trees within a stand differ in height-diameter development. It is assumed that dominant trees with wide and deep crowns will develop more stem taper than suppressed and intermediate trees. Objective (1), based on a restricted number of observations, was found to have correlation with basic density development (r^2 = 0.28). These results and those from an earlier study in this series (Lindström 1996b), where average basic density at breast height and stem taper was found to have a higher correlation (r^2 = 0.34–0.61), are an indication that basic density of the wood produced in a tree stand can be improved by selectively thinning strongly tapering trees.

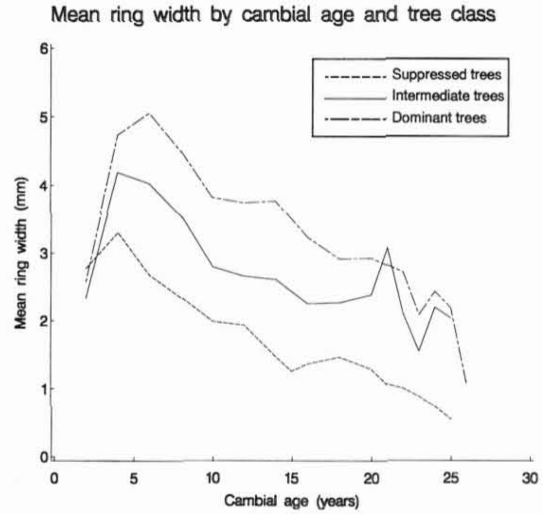

FIG. 2. Growth ring development, from pith outwards, for suppressed, intermediate, and dominant trees.

The high values of basic density in growth rings 2–4 of the material for this study appear to be an indicator of immature tracheid diameter combined with a high compression wood content. To avoid this effect, a statistical curve-fitting method led to a reduction of growth rings 2–4. In evaluation of objectives (2)–(6), this reasoning was used to build alternate models.

For objective (2) using a nonreduced data set, a negative correlation was found between basic density of individual growth rings and growth ring width with r^2 = 0.33–0.41, using the reduced data set improved correlation to

TABLE 5. *Dependence of basic density on growth conditions.*[a]

Regression equation	r^2	b_{i-n}	sb_{i-n}	x_{i-n}
(6a) $Y = \Sigma_{i=0}^{n} + \epsilon_i$	0.63	390.493665***	21.377320	Intercept
(All significant factors)		−0.721846***	0.063145	Site quality
		0.027016***	0.004007	Cambial age • Site quality
		0.212983***	0.023759	Cambial age • Cambial age • Tree class 1
		0.013273*	0.005312	Initial stand density • Tree class 3
		−0.265897**	0.096472	Cambial age • Average temperature Jun–Aug
		0.002779***	0.000584	Average temperature Jun–Aug • Initial stand density
		−0.392567***	0.092360	Cambial age • Average temperature Jun–Aug • Tree class 3
		0.136813***	0.035034	Thinning • Cambial age • Cambial age
		−0.425012***	0.045180	Thinning • Total precipitation Jun–Aug of each year
		0.019915**	0.006155	Thinning • Initial stand density
		0.000070*	0.000035	Thinning • Initial stand density • Tree class 1
		69.756096***	20.810762	Thinning • Tree class 3
		−0.113753*	0.0599116	Thinning • Site quality • Tree class 3
		289.858720***	81.499189	Thinning lagged • Tree class 1
		0.113125*	0.057539	Thinning lagged • Site quality • Tree class 1
		−24.446440***	5.992430	Thinning lagged • Average temperature Jun–Aug • Tree class 1
(6b) $Y = \Sigma_{i=0}^{n} + \epsilon_i$	0.46	317.388286***	16.411582	Intercept
(Based on *** factors)		−0.431348***	0.031920	Site quality
		0.040072***	0.006156	Initial stand density
		−58.902680***	10.484143	Thinning
		2.748718***	0.313240	Cambial age • Tree class 1
		0.286580***	0.040526	Site quality • Thinning
		−1.681592***	0.286430	Cambial age • Tree class 3
		2.705067***	0.728411	Cambial age

[a] *, **, and ***, indicate $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively.

$r^2 = 0.42–0.52$. It has to be mentioned, however, that a further examination of the material revealed that there were significantly different slopes and intercepts for each tree class.

In objective (3), Olesen's nonlinear model was fitted to the reduced data set and had a correlation of $r^2 = 0.50$. Three constants (a, b, and c) had to be determined via iteration to reach the highest possible correlation. Of the constants, a is supposed to be equal to the basic density of earlywood; b and c are said to possibly be related to provenience and cambial age. In this study, a, b, and c were found highly correlated, indicating that an iteration process can yield a wide range of estimates and still reach almost the same correlation. In this perspective, it would be preferable to use the more accurate model derived in objective (2) using the logarithmic value of growth ring width to predict the value of basic density.

Objective (4) was to add age effect to the most accurate model derived in objectives (2)–(3). This led to the use of a model based on the logarithmic value of growth ring width and cambial age. Using the reduced data set, the model had a correlation of $r^2 = 0.53$. Here, the negative effect of growth ring width was expected, but the negative effect of cambial age was not, as the literature suggests a positive effect of cambial age on basic density. However, as cambial age and growth ring width are correlated, i.e., growth ring width is negatively correlated with age, their isolated effect is probably different from their combined effect. The negative effect of cambial age found in this bivariate regression can possibly be seen in the perspective that the result depicted declining compression wood content from pith outwards. A second reason, partly evaluated in objective (6), is that the seemingly age-dependent pattern of xylem structure development possibly differs between suppressed, intermediate, and dominant trees.

Objective (5) evaluates the assumption that growth ring width is dependent on growth conditions. The best fit of the reduced data set of growth ring width based on growth conditions had a correlation of $r^2 = 0.76$, where 14 variables and interaction effects were found significant. If only factors significant at $P \leq 0.001$ were included, 8 variables and interaction effects gave a model with a correlation of $r^2 = 0.71$. Both models indicated that long- and short-term variation in growth conditions will regulate crown development, hence growth ring width. Therefore, it can be assumed that the negative relationship between basic density and growth ring width found in objectives (2)–(3) was indirect.

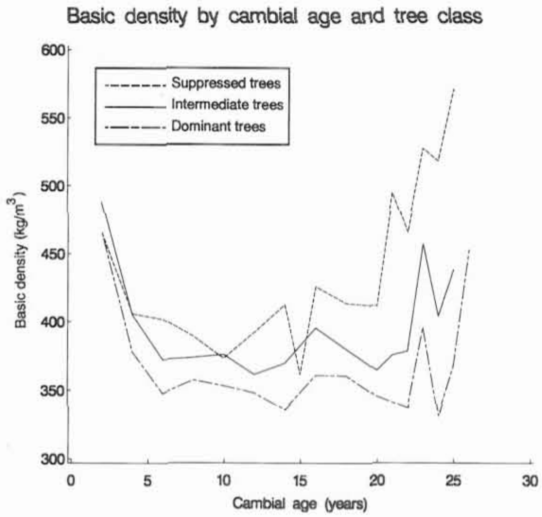

FIG. 3. Basic density development, from pith outwards, for suppressed, intermediate, and dominant trees.

Objective (6) follows the assumption that growth conditions, acting through regulation of crown development, will influence wood formation. Based on all available variables and interaction effects, a model was developed with $r^2 = 0.63$, where 15 variables and interaction effects were found significant. The interpretation is that growth condition factors, such as climate, site quality, silviculture, tree class, and cambial age, separately and in interaction, will affect basic density on a yearly basis. However, to clarify the effect of factors related to silviculture, a simpler model was constructed. This second model, based on 7 variables and interaction effects, each significant at $P \leq 0.001$, had a correlation of $r^2 = 0.46$.

Based on the hypothesis that crown development at stand and tree level will have a guiding influence over basic density of conifers (Larson 1969; Elliott 1970; Lindström 1996a), the following interpretations are given.

The negative effect of site quality on basic density can be seen as a result of the amount of foliage created in a stand and at what rate it is produced, thereby governing overall crown development of the trees within a stand. Rapid crown development as a result of high site quality, until a stand closure, seems to be a factor that lowers basic density of all tree classes within a stand.

The positive correlation between basic density and initial stand density of a stand is possibly descriptive of crown competition regulation, which starts earlier in a dense stand compared with a more open stand.

The negative effect of thinning on basic density is believed to be a result of decreasing crown competition following thinning of a stand. The result can be seen within the hypothesis of crown development as a regulator of basic density, where relative crown size and crown length of a conifer will affect wood formation of the vascular cambium.

The positive interaction effect of thinning procedure and site quality indicates that if, at the time of the thinning, a high amount of foliage is already present on most trees, the negative effect of thinning is lessened. Following thinning, the relative change in crown size is probably less on a high site quality than on a low site quality. Therefore, the lesser reduction in crown competition found on a high site quality after thinning will yield less reduction in basic density.

This study, showing the effect of cambial age to vary with tree class, supports an assumption that age has divergent effect on suppressed, intermediate, and dominant trees. Possibly, cambial age mirrors the successive fading activity of the vascular cambium at lower stem height of suppressed and intermediate trees caused by increasing distance to a small amount of foliage. Meanwhile, the age effect on basic density of a dominant tree is less pronounced, in that crown size counteracts the effect of crown recession.

Comments on the models

The effect of growth conditions on wood formation has earlier been conceptualized as hormonal regulation of vascular cambium activity through the influence of crown development, at stand and tree level (Larson 1969; Elliott 1970). In this study, growth ring width and basic density were found dependent on growth conditions. If growth ring width is taken as a response to growth conditions, acting through crown development at tree and stand level, then the negative correlation found between basic density and growth ring width must be viewed as indirect.

Thus it would make sense to consider regulation of crown development at the tree and stand level as the primary path to assert direct control over basic density. Here, the ability to control wood formation via alteration of growth conditions, i.e., silviculture, requires the construction of reliant models that have nondestructive potential. Attempts to develop such models have historically been very restrained by quantification and measurement procedures. These restraints are still existent, especially when determination of a wood feature is actualized.

Moreover, the prospect of increasing model accuracy will be dependent on which type of basic density we are predicting. For instance, the results of this study and the ones found in this series (Lindström 1996b) suggest that it will be much easier to predict between-stand variation than between-tree variation, which is still easier to predict than within-tree variation of basic density. One possible explanation of this phenomenon is that genetic variation when averaged, as for a tree stand, is considerably less than the actual genetic variation between trees. The same argument can be raised for the environmental influence. Averaged values at stand level will have less variation than those encountered by individual trees. Therefore, the results of this study may only reflect the complexity of nature, where "normal" averaged values of populations are based on the much wider range of variation found between individuals. In that case, average wood characteristics at stand level should be more easily predicted than wood characteristics at tree and within-tree level.

Nevertheless, it is conceivable that the ever-increasing data processing accessibility will open new possibilities to gather descriptive field data necessary in nondestructive models of basic density. In combination with emerging methods of basic density determination, the possibility to construct more accurate nondestructive models based on well-defined growth condition factors exists. Here, prediction accuracy and model construction will depend on differentiation ability and data quality of growth condition factors. For instance, model accuracy and validity would presumably be gained by including causative factors of compression wood and extractive production.

If the outlined construction of more sophisticated nondestructive models of wood formation takes place, it would provide us with a valuable forest management tool to control wood variation, and thus raw material quality. Hopefully, such nondestructive models could be included in the framework of economical evaluation of forest management decisions.

CONCLUSIONS

The following conclusions can be drawn from this study:

- Height-diameter development, a depiction of crown development, has an influence on basic density development.
- Basic density is negatively correlated with growth ring width.
- Olesen's model prediction of basic density is less accurate than prediction based on the logarithmic value of growth ring width.
- Growth ring width is dependent on crown development; thus alteration of crown development through silviculture will influence growth ring width.
- Basic density is dependent on crown development; thus alteration of crown development through silviculture will influence basic density development.
- This study indicates that accurate nondestructive models of basic density development are possible if improved quantification of causative effects can be undertaken. Until then, this study indicates that crown development over time is the best nondestructive predictor of basic density for *Picea abies*.

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