

BASIC DENSITY IN NORWAY SPRUCE. PART I. A LITERATURE REVIEW

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ABSTRACT

The literature review establishes the background for a series of papers relating environmental influence to basic density of Norway spruce (*Picea abies*). The four independent theories of wood formation given indicate that crown development acts as a primary regulator of wood structure and basic density in conifers. The review focuses on variables connected to crown development and basic density. Models of basic density in *Picea abies* were based on variables dependent on crown development, such as stem taper and growth ring width. It is suggested that models accurately predicting basic density should be based on a set of variables closely related to crown development.

Keywords: *Picea abies*, crown development, stem taper, growth ring width, basic density, wood density.

INTRODUCTION AND SCOPE

Wood as a material presents variation and heterogeneity between different tree species, within species, and in the stem of an individual tree (Johansson 1940; Hildebrandt 1954; Trendelenburg and Mayer-Wegelin 1955; Larson 1969; Elliott 1970; Zobel and van Buijtenen 1989; Thörnqvist 1993; Kucera 1994). However, one gross wood characteristic, i.e., basic density, is recognized as the most significant wood property and is a function of the tracheid structure. Basic density is known to cause quality variations in wood products. For instance, basic density is correlated to the yield and characteristics of pulp and paper (Johansson 1940; Klem et al. 1945; Persson 1975), the strength and volumetric shrinkage properties of sawn wood (Panshin and De Zeeuw 1970; Bendtsen 1978; Dinwoodie 1981). Basic density has consequently been used as a measure of wood quality and a predictor of end-use properties.

For more than a century, the connection between forestry and wood formation has been studied extensively. This interest has not been limited to the influence wood structure has on

the end-use properties of pulp and paper and solid wood products, however. Interest has also been focused on how trees regulate their wood formation to comply and adapt to environmental requirements. To give a silvicultural approach to wood variation, one cannot only passively describe the variation of wood structure. There has to be an effort to determine the nature of the processes that yield the observed structure. In other words, to control wood variation by silvicultural means, it is essential to have a basic understanding of the factors that affect cambial activity in the differentiation of xylem.

This paper includes a historical perspective on some of the theoretical models used in wood formation research, with an emphasis on Norway spruce (*Picea abies*), still generally applicable to conifer trees. The four main theories reviewed focus on wood formation in relation to crown development. As a result of differing assumptions, these theories suggest that wood formation and growth allocation are results of mechanical, nutritional, water conduction, or hormonal growth regulation. Each theory includes the perspective that crown development of an individual tree causes variation in

stem taper, growth ring width, and wood structure (Schwendener 1874; Hartig 1891; Jaccard 1913; Larson 1962).

This review focuses on variables that are related to basic density, through their influence or dependence on crown development. It is the first in a series of papers relating environmental influence to wood properties and how these are associated with end-use properties.

Because of the breadth of the subject, the author used a selective approach towards the literature and acknowledges the extensive literature that it was not possible to cite.

WOOD FORMATION THEORIES

During the late 19th century, interest in the relationship among silviculture, tree growth, and wood structure was concentrated in Germany, Austria, and Switzerland. Extensive and detailed studies were carried out to determine the relationship of tree species, site quality, tree class, silviculture, and the age of the tree to wood formation and wood density. These studies provided comprehensive theories that later inspired studies of wood density development in conifers (Guttenberg and Müller 1927; Klem 1934; Spurr and Hsiung 1954; Hildebrandt 1954; Trendelenburg and Mayer-Wegelin 1955; Schniewind 1962; Larson 1969; Elliott 1970; Madsen et al. 1978, 1985; Kyrkjeeide 1990; Kucera 1994).

Stem cambial activity and wood structure in coniferous trees have been suggested to be a function of mechanical forces in terms of external wind or gravity, nutritional availability to the vascular cambium, water conductivity requirements of the tree crown, and hormonal growth regulation.

In general, the one thing these wood formation theories have in common is that they state that stem cambial activity, growth allocation, and wood structure are a function of crown development. Crown development has been reported to cause mechanical (Schwendener 1874; Metzger 1893), nutritional (Hartig 1891), water conduction (Jaccard 1913), or hormonal growth regulation (Larson 1962). Larson (1963) describes the basic concepts of

these theories. He argues that stem taper serves as an abstraction of crown development. Consequently, stem taper is recognized as a result of coniferous trees adapting to physiological and mechanical requirements, acting through the tree crown, in an ever-changing environment.

Mechanical theory

The first serious attempt to explain wood formation, the mechanical theory, is ascribed to Schwendener (1874) and later developed by Metzger (1893, 1908). Stem taper is seen as a result of wind load, where varying mechanistic bending requirements throughout the stem force the tree into a stem form that is similar to a beam of equal resistance. Metzger argues that bending of the stem by wind load will regulate stem taper, in the stem section beneath the level of the crown. Therefore, the branch-free stem becomes a beam of uniform resistance to bending. Such a beam has the form of a cubic paraboloid of equal resistance to failure at all cross sections. If a force P is applied at one end of a firmly attached beam of equal resistance, l is the distance of a given cross section from the point of application of this force, and d is the diameter of the beam at this point, then by the rules of mechanics, the bending stress is σ in kg/cm², where

$$\sigma = \frac{P \times l}{d^3} \times l \times \frac{32}{\pi}. \quad (1)$$

The force P consists of the components ω = wind pressure per area unit and F = crown area, i.e., $P = \omega \times F$. If in eq. (1), d^3 is transferred to the left-hand side,

$$d^3 = \frac{32 \times \omega \times F}{\pi \times \sigma} \times l. \quad (2)$$

As ω , F , σ can be considered constant for a given tree, the fraction can be replaced by the value c and as a result

$$d^3 = c \times l. \quad (3)$$

Thus, the diameters raised to the third power increase proportionally with the lengthening of

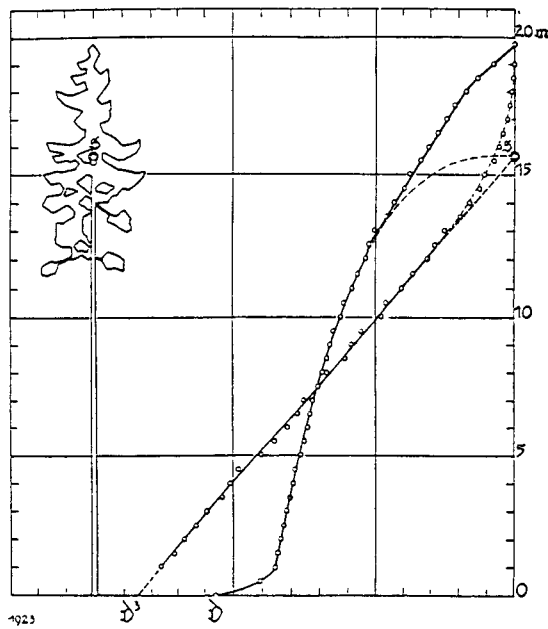


FIG. 1. Stem analysis of a 76-year-old spruce from the Tharandt Forest Garden. The branch-free part of the stem, from a height of 1 m to the beginning of the crown, forms a cubical paraboloid d (the cubes of the diameter, d^3 , lie in a straight line through the center of gravity, s , of the crown). Inside the crown, except for a short piece at the top, the stem forms a cone. The stem thus has the form of a beam of equal resistance. Scale for the height 1:200, for the diameters 1:4. From (Büsgen and Münch 1929).

the lever or with increasing distance from the central point of application of the wind force, which is assumed to be at the center of gravity of the crown (Jonson 1927; Petterson 1927; Tirén 1928; Schniewind 1962; Assmann 1961, 1970). The tree stem thereby attains the shape of a cubic paraboloid; or otherwise stated, the cubes of the stem diameters when plotted over the corresponding distances from the center of gravity of the crown must approximate to a straight line (Assmann 1961, 1970). Thus, assuming Metzger's theory D^3/l is a constant, D , being the diameter of the tree stem l meters from the application of the force, which, in a tree, is taken as the center of gravity of the crown (Fig 1).

Petterson (1927) and Tirén (1928) reported that varying tree classes will meet varying me-

chanical load; i.e., suppressed and intermediate trees with small tree crowns will experience less wind force than dominant trees. The relationship could then be used to predict the pattern of growth allocation, where long slender stems are the result of high-set small tree crowns of suppressed and intermediate trees, while dominant trees with higher mechanical requirements form strongly tapering stems (Büsgen and Münch 1929; Klein 1934; Baker 1950; Burger 1939, 1953; Assmann 1961, 1970; Mattheck 1991).

Criticism of the mechanical theory was given by Gray (1956), in that Metzger assumed that anchoring of the tree stem was totally rigid. Gray further argued that form class, as described by Jonson (1927), is a biased measurement and the original definition of stem taper by Metzger should continue to be applied in further developments of the mechanical principle. Schniewind (1962) showed that if radial increase of wood density in the stem was taken into account, a greater correlation of the general model could be obtained.

Nutritional theory

The nutritional theory deals with wood structure and stem form as a result of environmental variables (site class, tree class, and within-stand competition). In a classical study of a *Picea abies* stand near Munich, within-stand variation of wood density was found related to stem class. Hartig states that the differences in tracheid differentiation had to be found in a dynamical relationship between transpiration and assimilation requirements set by the tree crown. Moreover, nutritional availability to the vascular cambium is seen as a principal contributor to cell-wall thickness and wood density (Hartig 1892a, 1892b, 1891, 1901).

Hartig envisioned stem growth to be primarily determined by transpirational requirements. The development of shoot and needles that led to high transpiration during the spring resulted in production of conductive tissue, or earlywood. When the transpirational needs

were met for the season and the crown was fully developed, the balance shifted towards assimilation, and the tree began to produce strength tissue in the form of thick-walled latewood.

Hartig argued that changes in crown size would alter transpirational demands. Therefore, thinning and pruning were postulated to alter the proportions of "conduction tissue and strength tissue" (early- and latewood). Nutritional availability to the vascular cambium was said to be restricted during spring and early summer. The reasoning was that shoot and needle development was peaking and nutrition was diverted to this development. Therefore, the cambium only formed thin cell walls (conduction tissue) during spring and summer. Later in the growing season, when shoot and needle growth ceased, more photosynthate could be used to produce xylem, which resulted in thicker cell walls of the tracheids (strength tissue).

Consequently, dominant trees with large tree crowns formed strongly tapering stems, with a high proportion of earlywood to satisfy transpirational requirements. Suppressed trees with small crown sizes and low transpirational demands developed a narrow strip of earlywood, within the lower part of the bole. Hartig envisioned that the vascular cambium in the basal parts of suppressed trees lacked nutrition during spring and early summer, which impaired earlywood formation at the stem's base. This was said to be a consequence of a limited basipetal flow of nutrition "bildungsstoffe," where the vascular cambium was thought to gradually consume the flow of nutrition as it passed downward. He observed in very suppressed trees that a growth ring was often not formed at the base of the stem. Nutritional availability was assumed to be so scarce that the vascular cambium was unable to produce tracheids.

Hartig claimed that dominant trees with large crowns have to concentrate on the water conduction capacity and form tracheids with wider cell lumen and thinner cell walls to allow greater water conductivity. On the contrary,

suppressed trees with smaller transpirational needs would concentrate on providing mechanical support and forming a limited amount of earlywood.

In accordance with this analytical outline of physiological demands of the wood structure in an individual tree, wood structure was said to be optimized for water conduction and providing mechanical strength. Both components were seen as a result of the equilibrium of transpirational and assimilative processes within the tree crown.

Several contemporary workers (Bertog 1895; Omeis 1895; Cieslar and Janka 1902) emphasized and shared the nutritional theory on wood formation. In agreement with the theory, Bertog (1895) showed that a relationship between crown development and wood structure existed. Dominant trees exhibited a proportionally larger sapwood area and lower wood density than suppressed trees within even-aged stands of *Picea abies*. In addition, basic density was found to increase from pith and outwards, which was assumed to be the result of receding crowns following stand closure. The nutritional theory was widely accepted and greatly influenced the concepts of forestry and wood science (Hildebrandt 1954; Vorreiter 1954; Pechmann and Schaite 1955; Trendelenburg and Mayer-Wegelin 1955).

Water conduction theory

Jaccard (1913, 1915) claimed that stem taper and tracheid differentiation in conifers are regulated by water conduction. Wood formation was considered a direct response to transpirational demands of the crown. According to Jaccard, the observed variation in width of one and the same growth ring at different heights in a tree was caused by the necessity of maintaining a constant conductive area throughout the stem.

In the gradually tapering crown, the water flow decreased in proportion to living transpiring branches. As a result, stem cross-sectional area is proportional to the amount of transpirational tissue above the stem section.

Therefore, dominant trees with large branches will cause more taper than intermediate and suppressed trees.

Jaccard based his theory on measurements of a 49-year-old spruce. He found the cross-sectional area of the latest-formed growth ring in the stem near the base of the live crown to be equal to the cross-sectional area of the same growth ring at 1 m above ground. Jaccard concluded that the water conduction area has to be the same throughout the branch-free stem trunk. Furthermore, he asserted that this water conduction has to take place in the latest three to five formed growth rings.

However, he recognized that deviations from water conduction theory would occur. This recognition was based on the fact that tracheid lumen diameter varies with height within the same tree, with wider lumen diameters in the earlywood zone close to the crown and narrower lumen diameters at the stem base in the earlywood resulting in unequal water resistance within the stem. In an attempt to clarify Hartig's (1901) observation that suppressed trees sometimes lack the latest-formed growth ring in the basal part of the stem, Jaccard declared that this wood formation pattern was not due to lack of nutrition, but rather to low transpiration. The diminished transpiration caused by a poorly developed crown could therefore be satisfied by osmotic transport. His assumptions were augmented by the fact that wood formation in suppressed trees was characterized by tracheids with small diameter lumens. Dominant trees with heavily transpiring crowns would form tracheids with larger diameter lumens to improve adaptation to the presumed water mass flow. Tracheid differentiation was thereby assumed to be determined by overall turgor pressure induced by the tree crown.

Deviations from the water conduction theory were explained to be the result of compression wood, spiral grain, gravitational influence, and dead branches. These factors were argued to alter and modify cross-sectional area growth to maintain equal water flow in the branch-free bole.

Hormonal theory

It has been recognized for some time that a kind of growth regulating stimuli had to control and activate the vascular cambium in a complicated regulating system between crown and vascular cambium (Büsgen and Münch 1929; Thimann and Went 1937).

A silvicultural approach was given by Larson in 1962 when he explained cambial activity as a result of physiological crown development. The proposed concept of hormonal growth regulation perceives wood formation as a response of the vascular cambium to a basipetal flow of growth promoters produced in shoots, bud, and needle meristems within the tree crown. Consequently, distance between vascular cambium and the tree crown controls tracheid differentiation (Larson 1969; Elliott 1970). From this viewpoint, vascular cambium activity is a plastic response to the amount of hormone and carbohydrate production within the crown. The cambial activity will in turn regulate tracheid differentiation and wood structure variation (Fig. 2).

Wood formation is said to be regulated by a combination of factors: amount of carbohydrate and groups of hormonal promoters, e.g., auxin, gibberlin, cytokinin, ethylene, and abscisic acid. It was suggested that gradients of hormone and sucrose produced mainly within the needles will be basipetally transported in phloem parenchyma cells and phloem. Moreover, there seems to be a changing response of the vascular cambium to the same hormone concentration during the growing season (Woodzicki and Woodzicki 1973; Roberts et al. 1988; Raven et al. 1992). Growth hormones have been said to affect (Roberts et al. 1988; Raven et al. 1992) the following: cambial activity and division rate of cambial initials, alteration of cell wall extendability, direction of cell expansion, change of genetic expression of the individual cell, and orientation of microfibrils.

As a thoroughly conceptual generalized idea to explain general wood formation, the hormonal theory has wide acceptance (Wareing et

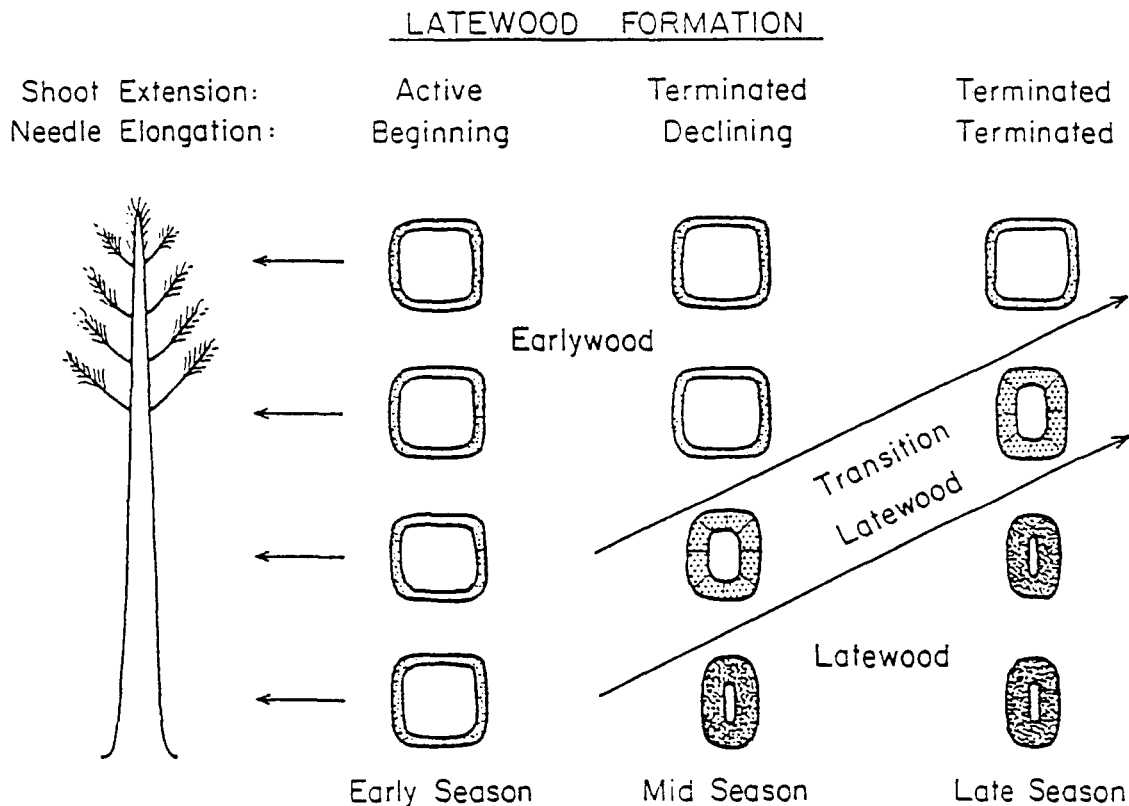


FIG. 2. The decrease in radial diameter and the increase in secondary wall thickening that characterize latewood usually begin near the stem base and progress upward as the season advances. From (Larson 1969).

al. 1964; Kramer and Kozlowski 1979; Barnett 1981; Savidge and Wareing 1981; Wilson 1984; Roberts et al. 1988; Raven et al. 1992). According to the hormonal growth concept, there is a genetically predetermined wood formation pattern for every tree species. The pattern is modified by the crown class of an individual tree. Crown class is regulated by growing conditions, such as site quality and within-stand competition, which restrict the amount of needle biomass and how it is allocated. Furthermore, if crown development in terms of size and vigor control wood formation, changes in crown size and vigor by forestry practice, such as pruning, thinning, or fertilization, will affect the wood formation. This view is shared by those in forestry, wood science, and those concerned with wood variation as a result of the environment (Larson 1969; Brazier 1977; Kra-

mer and Kozlowski 1979; Zobel and Van Buijtenen 1989; Kyrkjeeide 1990; Thörnqvist 1993; Kucera 1994).

FACTORS AFFECTING CROWN DEVELOPMENT AND BASIC DENSITY

The relationship between crown development, growth allocation, and basic density in even-aged tree stands

Crown development and stem taper have been studied in terms of crown ratio or crown percentage (Petrini 1921; Jonson 1927; Gevorkiantz and Hosley 1929; Kramer 1962, 1966).

Crown ratio, crown percentage

$$= \frac{\text{Crown length}}{\text{Tree height}} \quad (4)$$

Petrini found in even-aged mixed stands of *Pinus silvestris* and *Picea abies* that height to lowest living branch was predicted by tree height and crown ratio. Minimum crown ratio was found in trees somewhat below average stand diameter. Nonetheless, Hagberg (1942) claimed that age-related patterns influence stem taper development in even-aged stands of *Picea abies* and *Pinus silvestris*. Moreover, it was argued that the general pattern of stem taper improvement in young even-aged stands can be reversed by heavy thinning, where a more unrestricted crown development follows that deteriorates stem taper. Kramer (1962, 1966) found in even-aged stands of *Picea abies* that stand density and thinning influenced crown length, height to lowest living branch, and stem taper. These reports confirm the assumptions made in the reviewed growth theories; i.e., crown development is a determinant of vascular cambium activity and consequently the growth allocation of height and diameter at tree and stand level. Hence, tree height and stem taper of *Picea abies*, seen as a result of crown development, would be correlated to wood formation.

In general, the size of the crown strongly affects stem taper. Open-grown trees with unrestricted crown development have strongly tapering stems. Intermediate and suppressed trees in closed stands produce smaller crowns with less stem taper (Langsaeter 1941; Baker 1950; Gray 1956; Larson 1963; Kramer 1966; Kramer and Kozlowski 1979). In accordance with this view, variables that control crown development, such as stand density, growth rate, and age, also affect stem form and stem taper (Petterson 1927; Jonson 1927; Tirén 1928; Burger 1939, 1953; Langsaeter 1941; Baker 1950; Assmann 1961, 1970; Kyrkjeeide 1990; Thörnqvist 1993). Moreover, it has been argued that silvicultural alteration of crown development and stem taper would affect forest yield and net value of the yield (Schotte 1912; Petrini 1921; Petterson 1955; Langsaeter 1941; Baker 1950; Newnham 1965; Kramer 1966; Assmann 1970; Kyrkjeeide 1990).

An interpretation of the connection between

crown development and stem taper has been made in several reviews (Klem 1934; Burger 1939, 1953; Kramer 1962, 1966; Larson 1963; Assmann 1961, 1970; Kyrkjeeide 1990; Thörnqvist 1993). These reviews argue that the diversity of crown classes within a stand results in variation in taper. They suggest that the potential for growth in diameter in relation to height growth varies with crown class, with dominant trees having the lowest ratio between height and diameter. Burger (1939, 1953) found that suppressed and intermediate trees have a smaller ratio between crown length and tree height compared to dominant trees. Burger concludes that crown bases are higher in dense stands than in more open stands of the same age. These differences are also shown in the ratio between height and diameter. Several reports have compared basic density and tree class and shown that suppressed and intermediate tree classes have higher basic density than codominant and dominant tree classes within the same stand (Hartig 1892a, 1892b; Burger 1939, 1953; Schultze-Dewitz 1960; Kyrkjeeide 1990).

Average stand stem taper as an indicator of stand density

Average stem taper has been argued to be a characteristic indicating severity of lateral crown competition (Schotte 1912; Petrini 1921, Gevorkiantz and Hosley 1929; Klem 1934; Klem et al. 1945; Langsaeter 1941; Hagberg 1942; Gevorkiantz 1944; Wiksten 1960; Assmann 1961, 1970). Guttenberg and Müller (1927) showed that stem taper decreases in an even-aged stand when crown contact begins to form a continuous canopy. As crown closure continues, differentiation into crown classes takes place. Then, suppressed, intermediate, and dominant trees with corresponding slender, intermediate, and strong tapering stems develop within the stand (Gevorkiantz and Hosley 1929; Baker 1950; Kramer 1962, 1966; Newnham 1965; Assmann 1970; Kyrkjeeide 1990).

In early silvicultural studies, it was conclud-

ed that dense stands have less stem taper both at the tree level and at the stand level compared to less dense stands. Consequently, it has been argued that average stand stem taper is an indicator of stand competition (Jonson 1927; Petterson 1927; Tirén 1928, Klem 1934; Hagberg 1942). The general relationship between crown length and external tree characteristics was asserted by Jonson in 1927, when he concluded the following:

- Relative crown length decreases with increasing tree height.
- Relative crown length increases within a specific age and height class with increasing diameter.
- Relative crown length is generally greater in younger stands than in older ones.
- Relative crown length is associated with stem taper.

Jonson (1927) emphasized that increasing stand density brings about severe crown competition, with less average stem taper and reduced growth ring width. Gevorkiantz and Hosley (1929) stated that crown development was a result of growing space or lateral crown competition. Their conclusions were based on spacing experiments, where close spacing led to smaller crowns and branches, earlier natural pruning, and less stem taper. The lateral crown competition was therefore considered responsible for growth allocation and ratio of height/diameter. The first suggestion of a model to interpret competition caused by growing space of a tree at a given age was given by the following:

$$S = \frac{L}{C} \quad (5)$$

where S = growing space for the individual tree, L = branch-free stem length, and C = crown width. A high value of S was found in close spacings and suppressed trees.

The relationship was converted and further expanded by Gevorkiantz (1944) to describe stand competition at stand level:

$$C = \frac{(AH)^b}{AD} \quad (6)$$

where A = age, D = average diameter, H = average tree height; and C and b are constants that may vary between species and stand age. This means that the ratio of height to diameter varies with stand density, tree age, and tree species. If the stand is an even-aged monoculture, A and b can be canceled out, and C can be assumed to reflect stand density (Baker 1950):

$$C = \frac{H}{D} \quad (7)$$

Studies have shown that stand density has an effect on diameter distribution skewness (Ford 1975). In these studies, stand density was found to have a strong influence on diameter growth, whereas stand density was found to have minor or no influence on height development. However, as a measurement of stand density, a general H/D ratio is often restricted in that interactions between age and stem form are likely to occur (Gray 1956; Larson 1963; Newnham 1965; Assmann 1970).

Influence of crown development on growth ring width

Throughout the previously described theories, a central concept has been exerted. Size and vigor of the tree crown appear to regulate stem cambial activity of an individual tree. It has been argued that growth ring width as a result of cambial activity is dependent on crown size, vigor, and distance between tree crown and vascular cambium. Therefore, an alteration of the crown growth would be reflected in stem taper, growth ring width, and wood structure (Guttenberg and Müller 1927; Klem 1934; Klem et al. 1945; Burger 1939, 1953; Gevorkiantz 1944; Gray 1956; Schultze-De-witz 1960; Larson 1963, 1969; Kramer 1966; Elliott 1970; Brazier 1977; Kramer and Kozlowski 1979; Kyrkjeeide 1990; Kucera 1994). The basic relationship between crown devel-

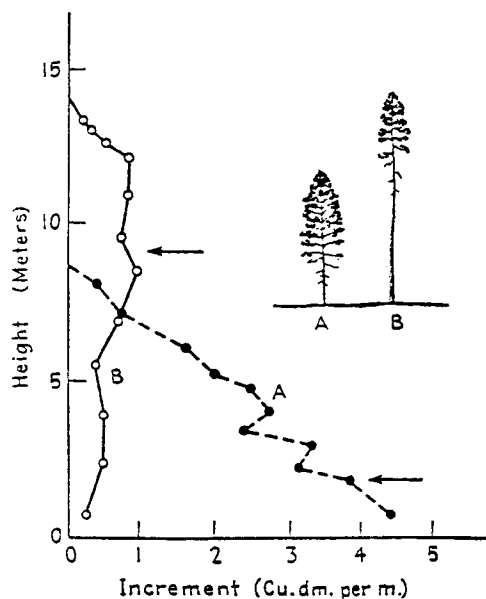


FIG. 3. Deposition of wood substance per meter of tree height in two ponderosa pine trees of equal diameter. A. open crown, 18 years old. B. Intermediate crown class, 42 years old. Arrows mark base of living crown. (Printed with permission of McGraw Hill Book company) From Baker 1950.

opment and growth ring width is illustrated by Baker (1950) in Fig. 3.

Influence of thinning and fertilization on crown development and basic density

Silvicultural treatments, such as spacing, pruning, thinning, and fertilization, have been said to affect crown development, stem taper, growth ring width, and wood structure. Regulation of crown development through silviculture has been argued to affect basic density (Larson 1969; Brazier 1977; Kramer and Kozlowski 1979; Moltesen et al. 1985; Zobel and van Buijtenen 1989; Kyrkjeeide 1990; Thörnqvist 1993; Kucera 1994).

Thinning.—Several reports have assumed that average crown length and stem taper in a stand are partly dependent on thinning procedures (Langsaeter 1941; Hagberg 1942; Wiksten 1960; Kramer 1962, 1966; Newnham 1965; Ericson 1966). Moreover, selection of thinning procedure has been held as a principal

contributor to wood quality. The arguments have been that thinning will regulate crown development and crown recession, which in turn will impact on branch volume, stem taper, and basic density (Langsaeter 1941; Ericson 1966; Larson 1963, 1969; Madsen et al. 1978; Kyrkjeeide 1990; Thörnqvist 1993).

Based on thinning procedures originally defined by Schotte (1912) and further developed by Langsaeter (1941), Wiksten (1960), and Ericson (1966), there are two ways to describe an applied thinning procedure: thinning ratio and thinning strength. The first definition is depicted by d/D , where d is average diameter of removed trees and D is average diameter of remaining trees. Thinning strength is measured as the ratio between thinned volume and total volume production within the stand. Wiksten (1960) used the thinning ratio to evaluate crown development and yield in mixed stands of *Pinus sylvestris* and *Picea abies*. He felt that thinning ratio determined crown percentage. Ericson (1966) redefined the measurement and depiction of thinning procedure when he evaluated the influence of thinning procedures on basic density at Tönnersjöhedens experimental station in southern Sweden. Ericson used a somewhat different definition of thinning ratio: dg/Dg , where dg is the stem of mean basal area and Dg is stem of mean basal area of remaining trees in the thinned stand. According to Ericson, active thinning of *Picea abies* stands lead to lower average basic density compared with non-thinned stands.

Fertilization.—Stem form is said to be altered by fertilization treatment (Madgwick and Tamm 1987; Mead and Tamm 1988). In a discussion of the logical basis, Mead and Tamm suggested that rapid crown development, following fertilization, acts as a primary contributor to stem taper. However, Madgwick and Tamm asserted that age-related patterns of stem form development are partly dependent on stand closure. Therefore, it was argued that rapid stand closure due to high stand density and site quality would result in interaction effects on stem taper.

Models predicting basic density based on stem taper and mean growth ring width

Basic density and stem taper.—The connection between basic density and stem taper has been known for a long time. Stem taper is regarded as a simple tool for wood quality assessment (Klem 1934, 1942; Klem et al. 1945; Burger 1939, 1953; Schultze-Dewitz 1960; Schniewind 1962; Hakkila 1979; Kyrkjeeide 1990).

Stem taper in *Picea abies* was found to be a predictor of wood density, with $r = 0.56$ (Klem 1934). According to Klem, this consistency prevails between stands on different quality sites, at equal ages. Hakkila (1979) found a significant but low correlation ($r^2 = 0.178$) between stem taper and basic density in stands of *Picea abies*, representing trees of unequal age, growth rate, and provenance.

Mean growth ring width and basic density.—Numerous studies show the relationship between growth ring width and basic density of *Picea abies*. These studies indicate a negative correlation between growth ring width and basic density, as a result of decreasing latewood percentage with increasing growth ring width. Linear regression of basic density on growth ring width has been found to yield a moderate correlation ($r^2 = 0.25$ – 0.60) (Klem 1942; Nylander 1953; Hildebrandt 1954; Trendelenburg and Mayer-Wegelin 1955; Ericson 1966; Persson 1975; Hakkila 1979; Kyrkjeeide 1990).

Nonlinear regression on growth ring width.—A nonlinear model was suggested by Olesen (1976, 1977) in which he used nonlinear regression that expressed decreasing latewood percentage with increasing ring width. The model expression being

$$Y = a + \frac{b}{(c + x)}, \quad (8)$$

where Y = basic density; x = mean ring width; a , b and c are positive constants, where a is said to be equal to earlywood density. The nonlinear regression model has been proved to yield a somewhat higher correlation com-

pared with linear regression of growth ring width.

DISCUSSION AND CONCLUSIONS

Despite the differences, the theories reviewed relate crown development as a main regulator of wood structure and basic density. These factors, which have been linked to basic density, are also argued to be factors that influence or seem dependent on crown development. For instance, silvicultural treatments e.g., thinning and fertilization, that affect crown development and crown competition within a stand have also been argued to impact basic density.

Basic density in *Picea abies* has been found to be significantly influenced by environmental variables. Several individual factors have been claimed to exert an influence upon basic density. However, in the search of significant factors, stem taper and growth ring width, both argued to be functions of crown development, have almost exclusively been used in models predicting basic density. As environmental variables related to crown development, such as site quality, tree age, and stand density often interact, a model for prediction of basic density would preferably include variables more directly connected to crown development. Such a model could be attained in various approaches.

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