*SILVA FENNICA VOL.* 13, 1979, *N:o* 4: 304–315

# THE EFFECT OF SOLAR RADIATION AND AIR TEMPERATURE ON BASIC DENSITY OF SCOTS PINE WOOD

SEPPO KELLOMÄKI

*SELOSTE:*

*SÄTEILYN JA LÄMPÖTILAN VAIKUTUS MÄNNYN PUUAINEEN TIHEYTEEN*

Saapunut toimitukselle 1979-04-20

The effect of solar radiation and air temperature on the basic density of Scots pine wood (*Pinus sylvestris* L.) was investigated on the basis of material obtained from the literature. Solar radiation seemed to affect basic density during the formation of earlywood. Temperature had the greatest effect on basic density in late summer. The varying effects of solar radiation and air temperature seemed to be associated with the dynamics of the crown system of the trees. Especially the capacity of the crown system to produce photosynthates needed in tracheid growth was assumed to be of importance in controlling the variation in the basic density of Scots pine wood. Growth of tracheids from the point of view of photosynthate supply is dicsussed.

## INTRODUCTION

Basic density is frequently used to indicate the properties of wood. For example, the strength properties of wood and the pulp yield per unit volume of timber are related to this characteristic (cf. for example, Hakkila 1966, Kärkkäinen 1977, pp. 200–203). Hence attainment of a high basic density should be an important aim of management practices in the growing of high-quality timber for industrial purposes.

Basic density is determined by the diameter and wall thickness of the tracheids (cf. Richardson 1964, Denne and Smith 1971). Considerable variation occurs in these characteristics during the growing season since the earlywood is composed of wide, thin- walled, cells and latewood of narrow, thick-walled ones. The change in tracheid dimensions associated with variation in the environment, and especially in temperature, seems to be the main factor determining cell development (cf. van Buijtenen 1958, Richardson 1964, Denne and Smith 1971).

The basic density of conifers seems especially to be related to the proportion of latewood formed as demonstrated, for instance, by Pillow (1955), Hakkila (1966, 1968), Uusvaara (1974) and Saikku (1975). The proportion of latewood explains in the 40 to 70 per cent of the total variation in the basic density of conifers (cf. for example, Larson 1957, Hakkila 1966, 1968, Uusvaara 1974). Through the proportion of latewood the basic density is associated with the temperature of the growing season as shown, for example, by Ledig *et al.* (1975), Saikku (1975) and Kellomäki (1979).

The influence of earlywood on the basic density is clearly evindent, as demonstrated, for example, by Richardson (1964), but its explanatory power is not comparable to that of latewood (cf. for example, Hakkila 1966). Among conifers, especially in Scots pine, the proportion ef earlywood determined on the basis of width measurements seems to be independent of the prevailing air temperature, in contrast to latewood percentage, as shown by Mikola (1950) and Leikola (1969). Furthermore, the time span of earlywood formation seems to be approximately the same from year to year. Hence only negligible year-to-year variation occurs in the earlywood percentage. As a consequence, the low explanatory power of the earlywood percentage is due to its negligible variation, respectively.

The different response of earlywood and latewood formation to temperature also suggests that there are differences in the underlying control mechanisms. Kramer (1964) refers to the role of the supply of photosynthates in tracheid growth, especially in earlywood formation. Also Ford *et al.* (1978) have emphasized the supply of photosynthates in earlywood formation and its dependence on external factors. Hence the influence of earlywood on basic density would be attributable to the interaction between the plant and its environment throught the photosynthetic processes.

The aim of the present paper is to study the effect of environment on the basic density of Scots pine *(Pinus sylvestris* L.) wood. Especially the role of solar radiation is emphasized among controlling factors. The physiological processes affecting earlywood and latewood formation are discussed.

The manuscript has been read by prof. Matti Kärkkäinen and prof. Matti Leikola. Their criticism has been valuable and is acknowledged.

## EFFECT OF ENVIRONMENT ON BASIC DENSITY: A HYPOTHESIS

The effect of environment on basic density is assumed to be different as regards earlywood and latewood formation, as stated above. The contribution of earlywood is further assumed to be associated with the supply of photosynthates as suggested by Ford *et al.* (1978). The following underlying control mechanism is implied as developed by Ford *et al.* (1978).

Ford *et al.* (1978) divide earlywood formation into the following phases: cell production, cell expansion, cell wall thickening and maturation of the cells. Earlywood formation between cell production and final maturation is assumed to be a process in which cell growth proceeds through each phase. Thus, the more rapidly the cells are produced the longer they will take to achieve maturity. An increase in the cell production rate implies larger and thicker-walled cells, if the cell expansion rate and cell wall thickening rate are assumed to be constant. An unchanging rate implies, however, that an increase in cell production is accompanied by an increase in the supply of photosynthates. Hence the size of the supply of photosynthates should have a detectable effect also on the basic density through earlywood formation. Solar radiation is assumed then to be of importance in controlling basic density.

The transition from earlywood to latewood formation has been related to the completion of terminal shoot elongation and is assumed to be associated with a decrease in auxin formation (cf. for example, Larson 1964, Richardson 1964, Leikola 1969). The onset of needle growth also coincides, however, with the onset of latewood formation, which hence may be associated with an increase in the availablity of photosynthates for secondary wall thickening (cf. Larson 1964, Gordon and Larson 1968). The importance of the photosynthate supply in latewood formation is also emphasized by van Buijtenen (1958), Richardson (1964), Denne (1971) and Denne and Smith (1971). The assumption is made, however, that photosynthate supply increased by the formation of new needles is sufficient to meet the requirements of latewood formation. Hence substrate availability is not limiting to latewood formation as is the case with temperature as suggested, for instance, by Mikola (1950) and Leikola (1969).

The effect of the environment on basic density is supposed to be as follows. Earlywood formation is assumed to be controlled mainly by solar radiation and latewood formation by temperature. Both processes are assumed to be separate. Thus emphasis is put on the radiation conditions prevailing during the formation of earlywood and the air temperature prevailing during the formation of latewood. According to Leikola (1969), the transition of earlywood to latewood takes places in late June and early July. Hence, solar radiation in May and June and air temperature in July, August and September are the main factors determining tracheid growth and its subsequent effect on the basic density of wood.

# TESTING THE HYPOTHESIS

## Material

The results of Saikku's (1975) study concerning the effect of fertilization on the basic density of Scots pine *(Pinus sylvestris* L.) were utilized. Only the submaterial used to study the proper sample height in determining of the avarage wood density was included in to this study. It consists of 31 trees, where the wood density was determined at heights 2, 6 and 10 meter above soil level. Values of wood density at these heights were pooled in calculations.

The annual values of basic density for years 1950–1970 were used in explaining by the annual amount of total radiation in June and the mean temperature in July. Radiation and air temperature observations made at the Climatological Station of Jokioinen (60° 49′ N, 23° 30′ E, 103 m.a.s.l.) were utilized (Ilmastohavainnot 1950–1970, Rossi 1976, Säteily- ja auringonpaistehavainnot 1957–1960, 1967–1968, 1969–1970). Temperature observations cover the whole twenty-year period. Radiation measurements made before 1957 were not systematic and were rejected as being uncomparable with those made during 1957–1970. Study of the contribution made by selected factors was thus limited to the period 1957–1970. In addition, information concerning solar radiation, air temperature and rainfall also during other summer months of the current and previous years were included in the analysis carried out for the further study of the selected hypothesis. The material for Saikku's (1975) study was collected near Heinola, (61° 13″ N, 20° 02″ E, 100 m a.s.l.) and hence the weather observations and basic density observations are not exactly comparable.

## Methods and results

As the first step in the analysis the values of the basic density were correlated separately with solar radiation in June and mean air temperature in July (Figs. 1 and 2). For comparison purposes radiation and temperature values of the other months are also shown. The intercorrelations between the independent and dependent variables are also presented in Table 1.

The regression between the amount of solar radiation in June and the basic density was, as expected, statistically significant ($p < 0,05$). This regression was, however, close also in May and July ($p < 0,05$). It appears from Fig. 1 and Table 1 that the values of basic density are also related to the mean air temperature for May, June, and July. Therefore the effect of temperature on the regression between radiation and basic density was eliminated by means

Table 1. Intercorrelation between basic density of Scots pine wood and solar radiation and air temperature in different months.
*Taulukko 1. Männyn puuaineen ja ympäristötekijöiden sekä ympäristötekijöiden keskinäiset korrelaatiot.*

| Variables<br>Muuttajat | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Basic density ..............................<br>*Tiheys* | 1 | 1.000 | | | | | | | | | | |
| Radiation in May ......................<br>*Toukokuun säteily* | 2 | .453 | 1.000 | | | | | | | | | |
| Radiation in June ......................<br>*Kesäkuun säteily* | 3 | .500 | .619 | 1.000 | | | | | | | | |
| Radiation in July .........................<br>*Heinäkuun säteily* | 4 | .643 | .403 | .422 | 1.000 | | | | | | | |
| Radiation in August ...................<br>*Elokuun säteily* | 5 | .282 | .370 | .741 | .526 | 1.000 | | | | | | |
| Radiation in September ..............<br>*Syyskuun säteily* | 6 | .327 | .247 | .406 | .679 | .461 | 1.000 | | | | | |
| Temperature in May ....................<br>*Toukokuun lämpötila* | 7 | .487 | .577 | .471 | .210 | –.090 | .283 | 1.000 | | | | |
| Temperature in June ...................<br>*Kesäkuun lämpötila* | 8 | .030 | .326 | .546 | –.078 | .345 | –.048 | .160 | 1.000 | | | |
| Temperature in July ......................<br>*Heinäkuun lämpötila* | 9 | .814 | .449 | .473 | .633 | .356 | .296 | .536 | .113 | 1.000 | | |
| Temperature in August ................<br>*Elokuun lämpötila* | 10 | .601 | .231 | .499 | .568 | .358 | .335 | .193 | .018 | .422 | 1.000 | |
| Temperature in September ............<br>*Syyskuun lämpötila* | 11 | .094 | .138 | –.064 | .028 | –.376 | .021 | .161 | –.145 | –.384 | .193 | 1.000 |

of analysis of partial correlations. After elimination, the values of the partial correlation between radiation and basic density in May through September were as follows (value of total correlation in brackets): 0,240 (0,453) in May, 0,557 (0,500) in June, 0,283 (0,643) in July, 0,282 (0,099) in August, and 0,323 (0,327) in September. Only the regression between radiation in June and the basic density appeared to be somewhat stable and statistically significant ($p < 0,05$). This can be considered to support the earlier made hypothesis derived from the results presented by Ford *et al.* (1978).

The effect of temperature on basic density was treated in the same way as that for radiation (cf. also Figs. 1 and 2). The regression between mean air temperature in July and the basic density was, as expected, statistically ($p < 0,001$) significant.

This regression was also close in other months ($p < 0,05$), except in June ($p > 0,10$). Elimination of the effect of radiation on regression showed that the regressions for July and August were rather stable. The value of the partial correlation (value of total correlation in brackets) was 0,309 (0,487) in May, −0,335 (0,030) in June, 0,686 (0,814) in July, 0,558 (0,601) in August and 0,092 (0,094) in September. Correlations are statistically significant ($p < 0,01$) only in July and August. The result is in accordance with the earlier made hypothesis and emphasizes the role of temperature during latewood formation (cf. for example, Mikola 1950).

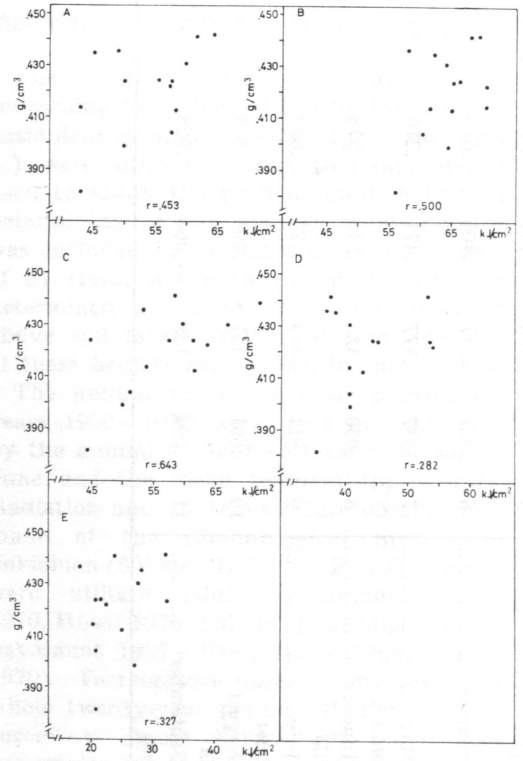

Fig. 1. Basic density of Scots pine wood as a function of total solar radiation in a: May, b: June, c: July, d: August, and c: September.
*Kuva 1. Männyn puuaineen tiheys a: toukokuun, b: kesäkuun, c: heinäkuun, d: elokuun ja e: syyskuun kokonaissäteilyn funktiona.*

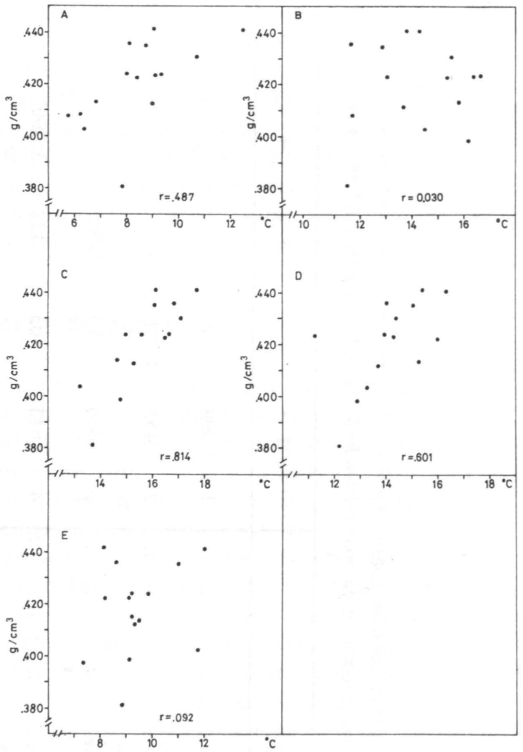

Fig. 2. Basic density of Scots pine wood as a fuction of mean air temperature in a: May, b: June, c: July, d: August and e: September.
*Kuva 2. Männyn puuaineen tiheys a: toukokuun, b: kesäkuun, c: heinäkuun, d: elokuun ja e: syyskuun lämpötilan funktiona.*

As the second step in the analysis the role of current rainfall and solar radiation and air temperature during the previous year was studied. These factors had no detectable effect on the values of the basic density ($p > 0,10$). Hence the solar radiation during earlywood formation and the air temperature during latewood formation seem to be the only factors capable of affecting the basic density of Scots pine wood.

As the third step in the analysis an attempt was made to explain the basic density values by means of the radiation in June and mean temperature in July (Table 2). The percentage of explained variation out of the total variation in basic density was 68. From Table 1 it appears that the inter-correlation between these variables is 0,473, which obscures interpretation of the resulting model. Therefore analysis of the partial correlation was applied in order to determine the relationsip between the independent variables and values of basic density. The partial correlation (the total correlation in brackets) between radiation and basic density was 0,224 (0,500), and 0,756 (0,814) between temperature and basic density, respectively. Only the correlation between temperature and basic density was statistically significant ($p < 0.001$). In other words, the effect of radiation remains small as compared with that of temperature.

As the fourth step in the analysis an attempt was made to include all the information contained in the correlation matrix, shown in Table 1, in the analysis in order to investigate the variation of basic density within the weather pattern prevailing during the whole summer period. To remove the intercorrelations between various weather factors, factorial analysis was used in the analysis of radiation and temperature in May through September (cf. Leikola 1969). Eigen values greater than one yielded a three factor principle component model. Its Varimax solution is given in Table 3.

Solar radiation in July and September and air temperature in July and August had the greatest loadings in the first factor, this being interpretated as »the weather of late summer». Radiation in May and June and air temperature during the same months had the greatest loadings in the second factor, respectively, this being interpretated as »the weather of early summer». It was not possible to give the third factor any meaningful interpretation.

The factor scores of the two factors were employed in explaining the variation in basic density with the help of regression analysis. Several alternative models were tried. The greatest explanatory power was given by a model in which both factors were in a linear form (Table 4). The per-

Table 2. Effect of solar radiation in June and air temperature in July on the basic density.
*Taulukko 2. Kesäkuun säteilyn ja heinäkuun lämpötilan vaikutus tiheyteen.*

| Independent factor<br>*Selittävä muuttuja* | Regression coefficient<br>*Regressio-kerroin* | Value of[1]) Student's test<br>*t-testin arvo* | Constant term for the whole combination<br>*Vakioarvo koko yhdistelmälle* | Total[2]) correlation<br>*Kokonais-korrelaatio* |
|---|---|---|---|---|
| Radiation in June ................<br>*Kesäkuun säteily* | 0,002 | 0,762 | 229,929 | 0,824 |
| Temperature in July ............<br>*Heinäkuun keskilämpötila* | 0,986 | 3,841 | | |

[1]) $p < 0,100$, $t \geqq 1,796$

[2]) F-value for the whole combination 11,661 (2,11), $p < 0,01$.
F-arvo koko yhdistelmälle.

Table 3. Varimax solution of three factors concerning solar radiation and air temperature in May through September.
*Taulukko 3. Kolmen faktorin Varimax-ratkaisu koko kasvukauden säteily- ja lämpösuhteista.*

| Variable<br>*Muuttuja* | Factors<br>*Faktorit*<br>1 | 2 | 3 | Communality estimate<br>*Kommunaliteetin estimaatti* |
|---|---|---|---|---|
| Radiation in May<br>*Toukokuun säteily* | ,313 | ,713 | –,071 | ,612 |
| Radiation in June<br>*Kesäkuun säteily* | ,422 | ,729 | ,325 | ,815 |
| Radiation in July<br>*Heinäkuun säteily* | ,866 | ,112 | ,079 | ,768 |
| Radiation in August<br>*Elokuun säteily* | ,490 | ,273 | ,712 | ,822 |
| Radiation in September<br>*Syyskuun säteily* | ,732 | ,074 | ,046 | ,543 |
| Temperature in May<br>*Toukokuun lämpötila* | ,253 | ,640 | –,391 | ,626 |
| Temperature in June<br>*Kesäkuun lämpötila* | –,186 | ,599 | ,384 | ,541 |
| Temperature in July<br>*Heinäkuun lämpötila* | ,565 | ,410 | ,106 | ,498 |
| Temperature in August<br>*Elokuun lämpötila* | ,621 | ,186 | –,025 | ,420 |
| Temperature in September<br>*Syyskuun lämpötila* | –,002 | ,036 | –,554 | ,308 |
| Cumulative row sums of squared loadings<br>*Latausten neliöiden sarakkeittainen summa* | 2,604 | 2,106 | 1,244 | 5,954 |

Table 4. Effect of prevailing weather conditions in early and late summer on the basic density.
*Taulukko 4. Alkukesän ja loppukesän sääsuhteiden vaikutus puuaineen tiheyteen.*

| Independent factor<br>*Selittävä muuttuja* | Regression coefficient<br>*Regressio-kerroin* | Values of 1) Student's test<br>*t-testin arvo* | Constant term for the whole combination<br>*Vakioarvo koko yhdistelmälle* | Total 2) correlation<br>*Kokonais-korrelaatio* |
|---|---|---|---|---|
| Factor: Weather in early summer<br>*Faktori: Alkukesän sää* | 30.903 | 1.908 | –110.214 | .768 |
| Factor: Weather in late summer<br>*Faktori: Loppukesän sää* | 54.726 | 3.184 | | |

1) $p < 0.100$, $t \geqq 1.796$

2) F-value for the whole combination 7.909 (2,11), $p < 0,01$.
F-arvo koko yhdistelmälle.

centage of explained variation remained, however, lower than that given by solar radiation in June and air temperature in July. The present model puts more emphasis on the weather during early summer than the model based solely on radiation in June and temperature in July. In particular, temperature also seems to have an effect on basic density in early summer.

## DISCUSSION AND FURTHER ELABORATION

The annual variation in the basic density of Scots pine *(Pinus sylvestris* L.) wood was related to the total amount of radiation in June. The detected relationship was interpretated as supporting the hypothesis made by Ford *et al.* (1978) concerning the effect of enviromental factors on cell production and differentation in the earlywood of conifers. According to them, a highly significant correlation exists between short-term variation in tracheid development in earlywood of Sitka spruce *(Picea sitchensis* (Bong) Carr.) and radiation during earlywood formation. The effect of temperature and water supply were also considered in their study but they were found to have a negligible effect on tracheid growth during earlywood development. This conclusion is also supported by the present study.

The effect of temperature in July on the basic density was pronouced, as demonstrated by Saikku (1975), and was in agreement with the findings of, for example, van Buijtenen (1958), Larson (1964), Richardson (1964), Denne and Smith (1971) and Leidig *et al.* (1975). Mikola (1950) has also emphasized the importance of temperature in tracheid growth during latewood formation. Leikola (1969) has demonstrated that the walls of latewood cells thicken from the end of June through the middle of September. Accordingly, the prevailing temperature in late summer seems to be of importance for latewood formation and high basic density values, as indicted also in the present analysis (cf. also Sirén 1961). The effect of solar radiation in June on latewood formation, is, however, possible due to the time required for the translocation of photosynthates from needles to the cambium (cf. Webb 1977). This possibility cannot be excluded with the help of the available material.

The coefficents of partial correlation showed that basic density was not related to solar radiation in months other than June. On the other hand, the role of temperature in months other than July and August was not detectable. It was expected that the weather conditions prevailing the previous year would have had an effect but this was not found in the statistical analysis (cf. Sirén 1961, Larson 1964). The values of partial correlation between basic density and radiation and temperature in each month seem to be inverse ones. The negative correlation between values of partial correlation for the relationship between basic density and radiation and temperature was $-0,844$ ($p < 0,10$), this can be interpretated as indicating that wood formation is relatively sensitive to different factors during various phases of wood formation.

The sensitivity of wood formation is apparently associated with the growth of the stem and crown systems, as presented in Fig. 3. The sensitivity of wood formation to radiation is especially apparent during the phase of maximum leader and radial growth in early June (cf. Kanninen 1977). The competition for the photosynthates needed in growth appears to be associated with this phenomenon. For example, Larson (1964) has demonstrated that earlywood formation coincides with the extension growth of buds or shoots. Rapid growth depletes the supply of photosynthates unless environmental conditions, *e.g.* incoming radiation, are favourable for current photosynthesis (Krames 1964). The present analysis can be interpretated to indicate that there is keen competition between shoot elongation and radial growth for carbohydrates thus producing the detected sensitivity of basic density to radiation as a consequence of exhausted carbohydrate

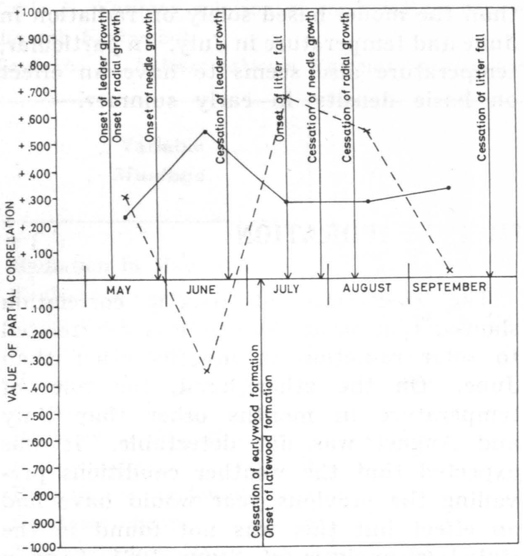

Fig. 3. A schematic presentation of the partial correlations between basic density of Scots pine wood and solar radiation (solid line) and air temperature (dotted line) in different months and some growth characteristics of the crown and stem as adapted from Viro (1955), Leikola (1969) and Kanninen (1977).

*Kuva 3. Kaavamainen esitys männyn puuaineen ja eri kuukausien kokonaissäteilyn (yhtenäinen viiva) ja keskilämpötilan (katkoviiva) välisestä suhteesta sekä latvuksen eräiden kasvutunnusten muutoksista* Viron *(1955),* Leikolan *(1969) ja* Kannisen *(1977) mukaan.*

and nitrogen reserves during the period of most intensive growth. Lehtonen *et al.* (1977) have also demonstrated that there is a considerable decrease in the nitrogen content of needles and shoots of Scots pine as a result of rapid shoot growth.

Wood formation also seems to be sensitive to radiation in late summer and early autumn. This rise apparently coincides with needle fall and may indicate a decline in the supply of photosynthates for tracheid growth in late summer (cf. Leikola 1969). The reduction in the total needle biomass also indicates reduction in the buffer effect of a large needle biomasss. On the other hand, the needle biomass is of the same size in the spring as in the previous autumn; this may also be attributable to the sensitivity of basic density to the amount of radiation in June (cf. Kramer 1964, Ford *et al.* 1978).

Temperature affects the basic density in a different way than radiation, *i.e.* it exerts its greatest effect in July and August and the effect is only negligible in other months. The transition from sensitivity to radiation, to sensitivity to temperature, coincides with the transition from earlywood formation to latewood formation. *i.e.* during early July, as demonstrated, for instance, by Mikola (1950). On the other hand, the current year needles reach maturity at the same time, thus giving rise to a rapid increase in the photosynthetic rate (cf. Freeland 1952, Woodman 1971, Zelawski *et al.* 1973). Hence the contribution made by the new needles in the production of photosynthates for stem growth and wood formation increases.

According to Larson (1964), the effect of needle maturity on the type of latewood wall development is twofold. It decreases photosynthate consumption in needle growth and increases contribution to the growth of other parts of the tree. Once the current year needles have achieved a certain stage of maturation, secondary wall thickening increases rapidly. The sensitivity of basic density to temperature suggests that the supply of photosynthates from the increased needle biomass is probably sufficent to satisfy the needs of tracheid growth even in unfavourable conditions. In other words, the effect of radiation on wood formation is not detectable.

Radiation in June and temperature in July explained 68 per cent of the total variation in the basic density when applied as independent variables in multiple regression analysis. The effect of radiation and temperature during the whole growing season was also included in the analysis by carraying out factorial analysis. The weather conditions prevailing in early summer and late summer represented two separate factors which both had a significant effect on basic density. A degree of determination of 57 per cent was obtained, *i.e.* lower than that obtained when using radiation in June and temperature in July. It seems, however, evident that the mechanism controlling tracheid growth is different in early summer and in late summer weather conditions. Further studies are, however, needed to study the role of translocation processes in wood formation as regards solar radiation and temperature (cf. Webb 1977).

The degree of explained variation in basic density was of the same magnitude as that reported by Saikku (1975). The introduction of radiation in June into the analysis did not essentially increase the explanatory power as compared with the model based only on the temperature factor. The partial correlations showed that the effect of solar radiation remained smaller than expected, as compared with that of air temperature. The application of the weather data recorded in Jokioinen may also result in variance which cannot be controlled in the analysis.

The dominance of temperature originates from several sources. Above all, the density of latewood is approximately three-times higher than that of earlywood. For example, Kollman and Cote (1968, p. 174) give the following density values for pine wood: 300—370 kg/m³ for earlywood and 810—920 kg/m³ for latewood. The effect of temperature is thus greater than would be concluded solely on the basis of the correlation coefficients. The importance of temperature is also emphasized by the length of the period needed for latewood formation (cf. Leikola 1969). There is also more variation in the basic density of latewood than in that of earlywood, as demonstrated by Heger *et al.* (1974). Hence the values of basic density are also more sensitive to temperature than to radiation. The relatively high stability of earlywood as regards its basic density, growth period, tracheid growth etc. generates special problems applying linear models to the analysis (cf. Mikola 1950). Earlywood comprised, however, approximately 70 per cent of the wood volume, and therefore its eco-physiological control system is of importance in the research of wood formation mechanisms.

Acceptance of the hypothesis made on the basis of the present analysis gives rise to the following conclusions. Sunny but cool weather in early summer and a warm late summer yields dense wood. On the other hand, the role of temperature is more pronounced than that of radiation in early summer. Hence, a sunny and cool early summer is not capable of compensating for the loss in basic density dye to a cool late summer. A warm but overcast early summer associated with a cool late summer should yield exceptionally low basic density values.

The importance of the supply of photosynthates for tracheid growth is considered to act through its contribution to tracheid length, tracheid diameter and tracheid wall thickness (cf. also Larson 1964, Richardson 1964, Gordon and Larson 1968, Leikola 1969, Denne 1971). Hence, the effect of environment on tracheid growth is associated with growth of the total growth system and its dynamics, as suggested by the present analysis. Therefore the effect of environment is mainly indirect. For example, Mikola (1950) has suggested that the crown system in the radial growth of Scots pine acts as a source of the photosynthates needed in growth. The crown system acts also as a buffer between the environment and tracheid growth thus obscuring the direct relationship between environment and diameter growth. On the other hand, the apparent relationship between tracheid growth and the dynamics of the crown system introduces the properties of the tracheids within the scope of management.

Only the role of the photosynthate supply in tracheid growth is emphasized. For example, stem girdling of *Picea* and *Pseudotsuga* carried out by Richardson (1966) gave no consistent change in the properties of the tracheid walls even though changes in carbohydrate availability were induced. Wodzicki (1964) was able to relate the formation of thick-walled tracheids in *Larix* to the accumulation of water soluble inhibitors formed during short days. According to Kramer (1964), earlywood formation is associated with an abundant supply of auxins. The transition from earlywood to latewood may primarily be caused by a decreasing supply of auxins. Also Wareing *et al.* (1964) have emphasized the role of leader growth in controlling the growth of the lateral meristem (cf. also Balarinecz and Kennedy 1968, Gordon and Larson 1968, Denne 1971, Denne and Smith 1971). Through the auxin producing organs the tracheid growth is, however, associated with the dynamics of the crown system, too. Hence, the separate roles of photosynthate supply and hormonal control in tracheid growth are hardly distinguishable through linear methods.

## REFERENCES

Balatinecz, J. J., & Kennedy, R. W. 1968. Mechanism of earlywood — latewood differentiation in *Larix decidua*. Tappi 51: 414—422.

Buijtenen, J. P., van. 1958. Experimental control of environmental factors and their effect upon some aspects of wood anatomy in Loblolly pine. Tappi 41: 175—178.

Denne, M. P. 1971. Temperature and tracheid development of *Pinus sylvestris* seedlings. J. Exp. Bot. 22: 362—370.

Denne, M. P. & Smith, C. J. 1971. Daylength effects on growth, tracheid development, and photosynthesis in seedlings of *Picea sitchensis* and *Pinus sylvestris*. J. Exp. Bot. 22: 347—361.

Ford, E. D., Robards, A. W. & Piney, M. D. 1978. Influence of environmental factors on cell production and differentiation in the earlywood of *Picea sitchensis*. Ann. Bot. 42: 683—692.

Freeland, R. O. 1952. Effect of age of leaves upon the rate of photosynthesis in some conifers. Pl. Physiol., Lancaster 27: 685—690.

Gordon, J. C. & Larson, P. R. 1968. Seasonal course of photosynthesis, respiration, and distribution of $^{14}C$ in young *Pinus resinosa* trees as related to wood formation. Pl. Physiol., Lancaster 43: 1617—1624.

Hakkila, P. 1966. Investigations on the basic density of Finnish pine, spruce and birch wood. Seloste: Tutkimuksia männyn, kuusen ja koivun puuaineen tiheydestä. Commun. Inst. For. Fenn. 61.5.

— » — 1968. Geographical variation at some properties of pine and spruce pulpwood in Finland. Seloste: Eräiden mänty- ja kuusipaperipuun ominaisuuksien maantieteellinen vaihtelu Suomessa. Commun. Inst. For. Fenn. 66.8.

Heger, L., Parker, M. L. & Kennedy, R. W. 1974. X-ray densitometry: a technique and example of application. Wood Sci. 7 (2): 140—148.

Ilmastohavainnot 1957—1970. Suomen meteorologinen vuosikirja. Nide 57—70. Osa la-1957-la-1970. Ilmatieteen laitos. Climatological data 1957—1970. Meteorological yearbook of Finland. Volume 57—70. Part la-1957-la-1970. The Finnish Meteorological Institute.

Kanninen, M. 177. Männikön puuston ja varvuston maanpäällisen osan päivittäisen kuiva-ainetuotoksen dynamiikka. Ms. Thesis. University of Helsinki. Department of Silviculture.

Kellomäki, S. 1979. On geoclimatic variation in basic density of Scots pine wood. Seloste: Ilmastotekijöiden vaikutus männyn puuaineen tiheyteen. Silva Fenn. 13(1): 55—64.

Kollmann, F. & Côté, W. A. Jr. 1968. Principles of wood science and technology. I. Solid wood. Berlin.

Kramer, P. J. 1964. The role of water in wood formation. In: The formation of wood in forest trees (ed. M. H. Zimmermann), pp. 519—532. Academic Press. New York.

Kärkkäinen, M. 1977. Puu, sen rakenne ja ominaisuudet. Helsinki. 442 s.

Larson, P. R. 1957. Effect of environment on the percentage of summerwood and specific gravity of Slash pine. Yale School For. Bull. 63.

— » — 1964. Some indirect effect of environment on wood formation. In: The formation of wood in forest trees (ed. M. H. Zimmermann), pp. 345—366. Academic Press. New York.

Ledig, F. T., Zobel, B. J. & Matthias, M. F. 1975. Geoclimatic patterns in specific gravity and trancheid length in wood of Pitch pine. Can. J. For. Res. 5: 318—329.

Lehtonen, I., Westman, L. J. & Kellomäki, S. 1976. Ravinteiden kierto eräässä männikössä: I. Kasvillisuuden ja maaperän ravinnepitoisuuksien vaihtelu kasvukauden aikana. Summary: Nutrient cycle in a pine stand I. Seasonal variation in nutrient content of vegetation and soil. Silva Fenn. 10(3): 182—197.

Leikola, M. 1969. The influence of environmental factors on the diameter growth of forest trees. Auxanometric study. Acta For. Fenn. 92.

Mikola, P. 1950. Puiden kasvun vaihteluista ja niiden merkityksestä kasvututkimuksissa. Summary: On variations in tree growth and their significance to growth studies. Commun. Inst. For. Fenn. 38.5.

Pillow, M. Y. 1955. Specific gravity relative to characteristics of annual rings in Loblolly pine. U.S. For. Prod. Lab., Madison. Rep. 1989.

Richardson, S. D. 1964. The external environment and tracheid size in conifers. In: The formation of wood in forest trees (ed. M. H. Zimmermann), pp. 405—438. Academic Press. New York.

— » — 1966. Studies on the physiology of xylem development. III. Effects of temperature, defoliation and stem girdling on tracheid size in conifer seedlings. J. Inst. Wood Sci. 12: 3—12.

Rossi, V. 1976. Auringon säteilyn mittauksien tuloksia Suomessa 1958—1967. Liite Suomen meteorologiseen vuosikirjaan. Nide 69—70, osa 4, 1969—1970. Ilmatieteen laitos. Results of rediation measurements in Finland during the years 1958—1967. Supplement to the meteorological yearbook of Finland. Volume 69—70, part 4, 1969—1970. The Finnish Meteorological Institute.

Saikku, O. 1975. The effect of fertilization on the basic density at Scots pine *(Pinus silvestris* L.). A densitometric study on the X-ray chart curves of wood. Lyhennelmä: Lannoituksen vaikutuksesta männyn *(Pinus silvestris* L.) puuaineen tiheyteen. Densitometritutkimus puuaineen röntgenkuvista. Commun. Inst. For. Fenn. 85.3.

Sirén, G. 1961. Skogsgränstallen som indikator för klimatfluktuationerna i norra Fennoskandien under historisk tid. Commun. Inst. For. Fenn. 54.2.

Säteily- ja auringonpaistehavainnot 1957—1960, 1967—1968, 1969—1970. Suomen meteorologinen vuosikirja. Nide 57—60, osa 4. Nide 67—68, osa 4. Nide 69—70, osa 4. Ilmatieteen laitos. Measurements of radiation and bright sunshine 1957—1960, 1967—1968, 1969—1970. Meteorological yearbook of Finland. Volume 57—60, part 4. Volume 1967—1968, part 4. Volume 1969—1970, part. 4. The Finnish meteorological institute.

Uusvaara, O. 1974. Wood quality in plantation-grown Scots pine. Lyhennelmä: Puun laadusta viljelymänniközssä. Commun. Inst. For. Fenn. 80.2.

Viro, P. J. 1955. Investigations on fores litter. Commun. Inst. For. Fenn. 45.6.

Wareing, P. F., Hanney, C. E. A. and Digby, J. 1964. The role of endogenous hormones in cambial activity and xylem differentiation. In: The formation of wood in forest trees (ed. M. H. Zimmermann), pp. 323—344. Academic Press. New York.

Webb, W. L. 1977. Seasonal allocation of photo-assimilated carbon in Douglas fir seedling. Plant Physiol. 60: 320—322.

Wodzicki, T. 1964. Photoperiodic control of natural growth substances and wood formation in Larix *(Larix decidua* D. C.). J. Exp. Bot. 15: 584—599.

Woodman, J. N. 1971. Variation of net photosynthesis within the crown of a large forestgrown conifer. Photosynthetica 5(1): 50—54.

Zelawski, W., Szaniawski, R., Dybczybsky, I. & Piechurowxki, A. 1973. Photosynthetic capasity of conifers in diffuse light of high illuminance. Photosynthetica 7(4): 351—357.

## *SELOSTE:*

## *SÄTEILYN JA LÄMPÖTILAN VAIKUTUS MÄNNYN PUUAINEEN TIHEYTEEN*

Auringon säteilyn ja ilman läpötilan vaikutusta männyn *(Pinus sylvestris* L.) puuaineen tiheyteen tutkittiin kirjallisuudesta saadun aineiston perusteella. Säteilyllä havaittiin olevan selvä vaikutus puuaineen tiheyteen alkukesällä, kun kevätpuu muodostui. Ilman lämpötila loppukesällä näytti kuitenkin vaikuttavan puuaineen tiheyteen ratkaisevasti. Säteilyn ja lämpötilan vaikutuksen eriytyminen näyttää liittyvän kiinteästi puiden oksien ja neulasten kasvuun ja sen dynamiikkaan. Erityisesti latvuksen kyky tuottaa trakeidien kasvussa tarvittavia fotosynteesituotteita on kaikesta päättäen keskeisin männyn puuaineen tiheyteen vaikuttava tekijä.