

ON GEOCLIMATIC VARIATION IN BASIC DENSITY OF SCOTS PINE WOOD

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SELOSTE:

ILMASTOTEKIJÖIDEN VAIKUTUS MÄNNYN PUUAINEN TIHEYTEEN

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The effect of temperature and water supply on the basic density of Scots pine (*Pinus sylvestris* L.) wood was studied on the basis of material obtained from the literature. On a monthly basis, the basic density increased with increasing mean temperature for June, July and August. The rainfall in these months had no detectable effect on the basic density except through the difference between rainfall and evaporation in July. On a yearly basis, the basic density increased with increasing mean temperature, temperature sum and length of growth period. The effect of water supply on the basic density was evident and a linear relationship between basic density and annual rainfall was detected. The variation in basic density was, however, explained only partially by the chosen factors. Possible reasons for the poor explanatory power have been discussed.

INTRODUCTION

The strength properties of wood products, as indicated by the basic density, are determined by the diameter and wall thickness of the tracheids. Both dimensions change during the growing season since earlywood is composed of wide thin-walled cells and the latewood of narrow thick-walled ones. Van BUIJTENEN (1958) considers the main reason for the variation in tracheid wall thickness and diameter to be variations in air temperature. In particular, low night temperatures accelerate growth of the tracheid wall thus indicating that there is a linear relationship between substrate availability and tracheid growth (cf. also LARSON 1964, RICHARDSON 1964). This correlation is supported by DENNE's and SMITH's (1971) results, which show linear correlation between day length and growth of tracheid wall and tracheid diameter (cf. also GORDON and LARSON 1968). In addition, van BUIJTENEN (1958) has emphasized the role of water supply in tracheid growth, and demonstrated the effect of water deficiency on the formation of thick-walled tracheid cells. The site quality can also be correlated with the basic density of the wood of several tree species (cf. for example HAKKILA 1966, UUSIVAARA 1974).

The aim of the present paper is to try to explain the geographic variation in the basic density of pine (*Pinus sylvestris* L.) wood by means of environmental factors.

The main emphasis is set on the role of temperature, water supply and other climatic factors. The possible effect of nutrient supply or other comparable factors is omitted.

MATERIAL

The results of HAKKILA's (1968) study concerning the geographical variation in the basic density of Scots pine in Finland have been utilized. Each observation represents mean of 150 stems. Hence, between-stem variation in basic density is eliminated from the variation explained in the present analysis.

The role of day length and radiation is of great importance in determining the availability of photosynthates for tracheid growth, and their importance is emphasized in most studies, as discussed above. However, these factors are not likely to have any detectable effect on the basic density owing to the similar pattern of solar radiation in different parts of the country during the growing season. Therefore the variation in basic density, as presented by HAKKILA (1968), should be correlated with temperature and water supply and related factors, as argued above (cf. for example van BUIJTENEN 1958, SAIKKU 1975).

SAIKKU (1975) has emphasized the effect of the mean temperature for June through August on the basic density of Scots pine, and it has hence been included into the analysis. However, the temperature sum (degree days which exceed 5° C) is perhaps preferable for describing the temperature

METHODS AND RESULTS

Effect of temperature

As the first step of the analysis each environmental variable was correlated with basic density. This was first carried out on a monthly basis, *i.e.* basic density was correlated with the climatic characteristics during growing seasons *i.e.* June, July and August. In the second phase, annual regressions were obtained correlating basic

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climate pattern in which trees grow (cf. KOLKKI 1966). In addition, the length of the growing season (number of days which exceed 5° C) were included into the material as assumed on the basis of studies carried out by MIKOLA (1950). All these factors emphasize the length of the season available for tracheid growth (cf. for example RICHARDSON 1964), and introduce the various physiological processes of growth into the analysis.

The water supply has been described by means of annual rainfall and rainfall during June, July and August (cf. HELIMÄKI 1967). In addition, the difference between soil evaporation and precipitation in July as described by SOLANTIE (1976) and accumulation of snow have been used in the analysis (cf. HUOVILA 1970). The latter factor describes the water resources available after snow melt, and may correlate with tracheid growth as demonstrated by LEDIG *et al.* (1975). On the other hand, snow accumulation includes information about the temperature factor. The difference between soil evaporation and precipitation in July indicates the amount of water available for growth during the active growth period. Also annual rainfall indicates the available water resources.

density with climatic characteristics for the whole year. Standard statistical methods were applied in calculating regressions.

There was considerable variation in relationships based on monthly material and in each case the correlation coefficients remained low (cf. Table 1). The correlation with mean temperature in June, July and August was 0.521, 0.598 and 0.550, respectively. All the regressions were statistically signi-

Table 1. Correlations between basic density and environmental factors.

Variable	0	1	2	3	4	5	6	7	8	9	10	11	12
Basic density	1.000												
Log mean temperature in June ..	.521	1.000											
Log mean temperature in July ..	.598	.888	1.000										
Log mean temperature in August ..	.550	.859	.893	1.000									
Rainfall in June185	.147	.079	-.130	1.000								
Rainfall in July253	.239	.152	.111	.394	1.000							
Rainfall in August121	.282	.257	.162	.202	.015	1.000						
Log difference between rainfall404	.812	.825	.859	-.027	.007	.150	1.000					
and evaporation in July								.820	1.000				
Log mean annual temperature603	.848	.893	.930	-.050	.133	.149	.859	.968	1.000			
Log length of growing season520	.882	.893	.942	-.131	.131	.151	.881	.919	1.000			
Log temperature sum495	.898	.889	.923	-.059	.123	.221	.881	.919	1.000			
Depth of snow cover	-.018	-.293	-.336	-.519	.693	.272	-.004	-.438	-.516	-.587	1.000		
Mean annual rainfall533	.751	.748	.666	.346	.257	.477	.629	.676	.648	.423	1.000	
											.343	-.042	1.000

ficant ($p < 0.001$). The values of basic density culminate when the mean temperature in July exceeded 14–15° C. In June the culmination took place at 12–13° C and in August at 13–14° C. The regression between basic density and mean temperature for July is presented in Fig. 1.

Also on a yearly basis the variance in basic density was explained only partly by the chosen factors. The correlations between temperature sum, length of growing season and annual mean temperature were 0.495, 0.520 and 0.603 (cf. Table 1). All the regressions were statistically significant ($p < 0.001$). The values of basic density culminate when the temperature sum exceeds 1 000 dd, *i.e.* between the 62 nd and 64 th latitudes in central Finland, where the length of the growing season exceeds 150 days. In terms of annual mean temperature, culmination takes place when the annual mean temperature exceeds 2–3° C. The

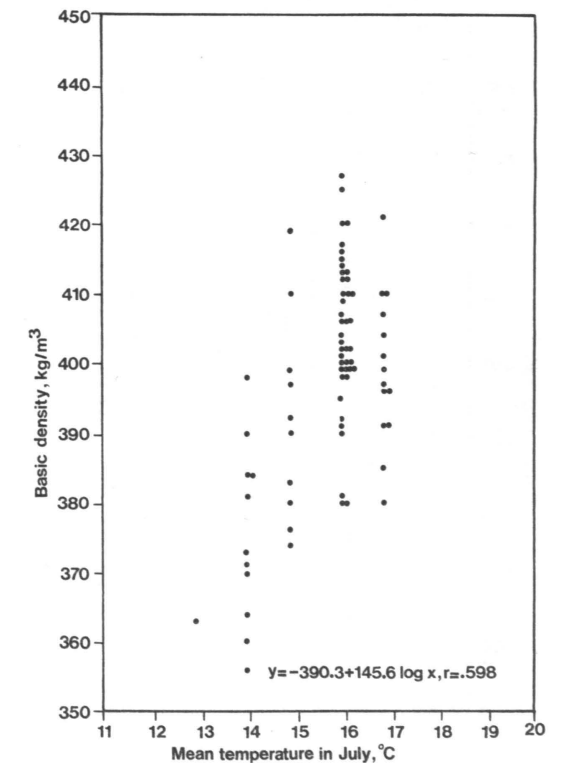


Fig. 1. Dependence of basic density on mean temperature in July.

regression between basic density and the annual mean temperature is presented in Fig. 2.

Effect of water supply

The basic density was first related to monthly characteristic depicting water supply, i.e. rainfall in June, July and August and the difference between rainfall and evaporation in July. The correlations between basic density and rainfall in June, July and August were 0.185, 0.253, 0.127 (cf. Table 1). These regressions were not statistically significant ($p > 0.10$) except for the regression between rainfall in July and basic density. The basic density was also poorly but statistically significantly ($p < 0.05$) correlated with the difference between rainfall and evaporation in July. The correlation coefficient was 0.404. The values of basic density culminated when

rainfall and evaporation were in balance as presented in Fig. 3.

Also on a yearly basis the values of basic density were poorly explained by characteristics describing water supply (cf. Table 1). There was no correlation between basic density and snow accumulation, i.e. correlation between these characteristics was -0.018 ($p > 0.10$). The correlation between basic density and mean annual rainfall was 0.553 and was statistically significant ($p < 0.001$). The regression between these characteristics was linear as can be seen in Fig. 4.

Interaction between temperature and water supply

The significance of various factors was studied with the help of stepwise regression analysis, in which basic density is the

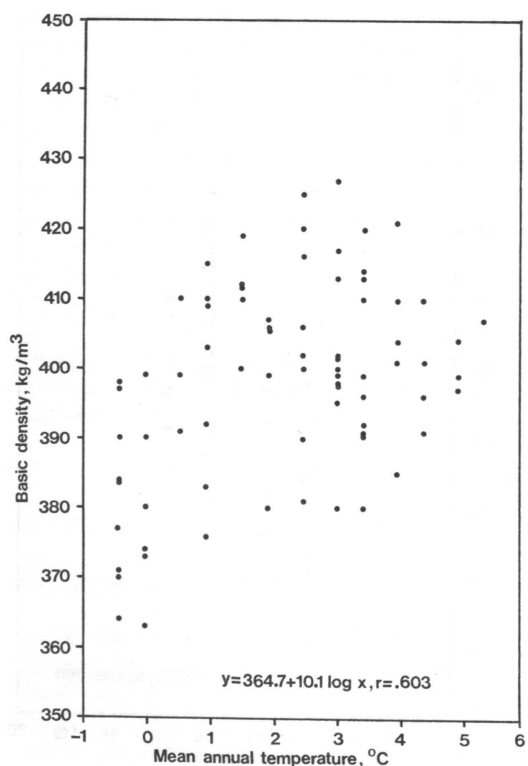


Fig. 2. Dependence of basic density on annual mean temperature.

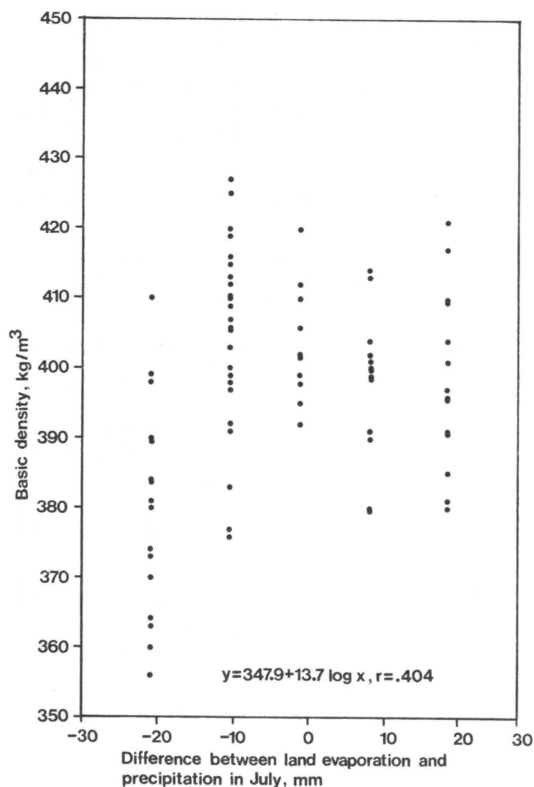


Fig. 3. Dependence of basic density on difference between rainfall and evaporation in July.

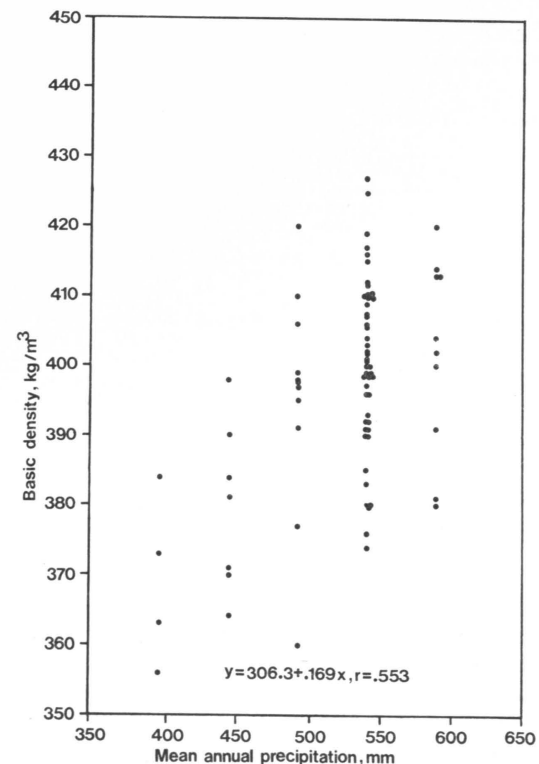


Fig. 4. Dependence of basic density on annual rainfall.

dependent variable and the environmental characteristics the independent variables. This enables evaluation of the sensitivity of basic density to different factors and construction of the model for predictive purposes. Several combinations were produced in which each entering variable was statistically significant as indicated by Student's test ($p < 0.10$). The analysis was carried out separately on a monthly and an annual basis. The highest explanatory power was given by the combinations presented in Table 2.

As expected both mean temperature in July and the difference between rainfall and evaporation in July were included in the monthly model. On an annual basis, the highest explanatory power was given by the mean annual temperature and the annual rainfall both being in logarithmic form. In the former case the percentage of explained variance was 46 and in the latter case 41. When both monthly and annual characteristics were used as independent variables, the best result was given by a model in which mean annual temperature, annual rainfall and the difference between rainfall and evaporation in July were introduced into the model in logarithmic

Table 2. Regression models for interaction between environment and basic density.

Independent variable	Constant for the whole combination	Regression coefficient (and its deviation)	R
Model 1			
Log mean temperature in July	-305.4	254.9(35.1)	.67
Difference between rainfall and evaporation in July		-0.6(0.1)	
Model 2			
Log mean annual temperature	177.4	7.1(1.9)	.64
Log annual rainfall		40.9(18.6)	
Model 3			
Log mean annual temperature	50.1	11.3(2.2)	.70
Log annual rainfall		49.3(17.8)	
Difference between rainfall and evaporation in July		-0.4(0.1)	

form, apart from the difference between rainfall and evaporation. The percentage of explained variance was in this case 49.

Interpretation of the models in Table 2 is obscured by the interactions between the independent factors (cf. Table 1). In particular, the correlation between mean temperature and the difference between evaporation and precipitation in July is high. Thus temperature seems to have a strong effect on the basic density through the latter factor. The correlation between mean annual temperature and annual rainfall is much lower. This fact suggests that both factors may play independent roles in

determining the values of the basic density of Scots pine wood as indicated by partial correlations between basic density and annual mean temperature and annual rainfall. In the former case the correlation was 0.345 when the effect of rainfall on basic density was eliminated. In the latter case the correlation was 0.262 when the effect of temperature on basic density was eliminated. The partial correlation between basic density and mean temperature in July was 0.511, *i.e.* the independent effect of the difference between rainfall and evaporation in July on basic density was negligible.

DISCUSSION

There is considerable variation in the basic density of Scots pine growing within Finland (cf. HAKKILA 1968). The variation may be a result of genetic differentiation or it may merely indicate variability in the physiological response to varying sets of environmental factors. According to ELLIOTT (1970), the basic density is strongly controlled by genetic factors (cf. also PERSSON 1972). For example, van BUIJTENEN (1958) has interpreted the geographical variation in the basic density of pitch pine (*Pinus rigida* Mill.) as deriving partly from genetic differentiation. HAKKILA (1966) suggests that genetic factors are of importance in explaining the variation of the basic density of Scots pine (cf. also SAIKKU 1975).

VELLING (1974) has demonstrated the high heritability of the basic density of Scots pine. Later, however, she has concluded on the basis of provenance trials that the genetic differentiation may play only a minor role in the variation of the basic density of Scots pine growing in Finland, and that there is no clear basic density grouping according to latitude or altitude, even though there are significant differences in basic density between different provenances of Scots pine and Norway spruce (VELLING 1976). VELLING's results suggest that the role of the genotype is of minor importance compared to the effect of environment on the basic density. The results presented by KLEM (1965) and

NYLINDER (1967) suggest that environmental factors may play a dominant role in the variation of the basic density within a limited geographical area. For example, LEDIG *et al.* (1975) attribute the main part of the geographical variation in the wood characteristics of pitch pine to environmental differences. There is, however, a need for additional studies concerning the role of genetic factors in determining the basic density of Scots pine.

The basic density correlated with all variables used to describe the temperature factor. Also LEDIG *et al.* (1975) have emphasized the role of temperature or related factors in determining the basic density of pitch pine (*Pinus rigida* Mill.). According to SAIKKU (1975), a change of one degree in the average temperature for June through August implies a change of 15 kg m^{-3} in the basic density of Scots pine as detected also in the present analysis. The controlling role of temperature factor was evident up to 900–1 000 dd, where the basic density of Scots pine culminates. Especially in northern parts of Finland, *i.e.* at low mean temperature values, the role of temperature is dominating, as indicated by the smaller deviation compared with the deviation at highest temperature values (cf. ZAVITKOVSKI 1976). Also MIKOLA (1950) has demonstrated the role of temperature in wood formation of Scots pine, and especially near the tim-

ber line temperature seems to be limiting factor for growth (cf. also SIRÉN 1961).

According to HAKKILA (1966), the percentage of latewood explains best the variation in basic density of Scots pine. LARSON (1964) found that formation of thick-walled latewood tracheids coincided with the maximum photosynthetic activity of new needles when they start to export photosynthates (cf. also DENNE and SMITH 1971). According to RICHARDSON (1964), tracheid wall thickness can be attributed to the effect of environment on the availability of photosynthates. Van BUIJTENEN (1958) has demonstrated that tracheid wall thickness increases with decreasing temperature in several conifers (cf. also RICHARDSON 1964). This process seems to be attributed to the availability of photosynthates for growth as suggested by the greater effect of night temperature on wall thickness compared with day temperature (RICHARDSON 1964, DENNE 1971). Culmination of the basic density of Scots pine at a specific temperature may be caused by the depletion of photosynthates in respiration at higher night temperatures in southern Finland, thus reducing the availability of substrates for growth (cf. DENNE 1971, DENNE and SMITH 1971).

The amount of late-wood is also related to the length of time during which late-wood is formed and the prevailing temperature, *i.e.* mean temperature in July and August (cf. MIKOLA 1950). According to LEIKOLA (1969), the walls of late-wood cells with small vacuoles may thicken from the end of June through the middle of September. As a matter of fact, early- and late-wood are comparable as regards the tracheid diameter but they differ in cell wall thickness. Therefore the prevailing temperature in late summer seems to be of importance for late-wood formation and high values of basic density as demonstrated also in the present analysis. Also SIRÉN (1961) has emphasized the importance of mean temperature for June through August, especially the mean temperature in July, in the formation of Scots pine wood near the timber line in Scandinavia. According to MIKOLA (1950), the period needed for formation of earlywood is constant, and

the amount of earlywood can not be related to the prevailing temperature.

The basic density of Scots pine also correlated with the variables describing the supply of water, apart from snow accumulation on a rainfall in June and August. According to MIKOLA (1950), the water supply originating from accumulated snow cover is not dependent on the amount of snow but the weather pattern during snow melting and succeeding growth period. Therefore growth is not related to the amount of accumulated snow. MIKOLA (1950) suggests that only the rainfall during active growth period is crucial for growth as indicated by the relationship between basic density and the difference between rainfall and evaporation in July and rainfall in June. There was therefore no detectable correlation between basic density and accumulation of snow cover as supposed on the basis of the results of LEDIG *et al.* (1975).

The relationship between basic density and annual rainfall was linear and it emphasizes the effect of a sufficient water supply on the formation of the substrates needed in tracheid growth (cf. also LEDIG *et al.* 1975). The relationship between density and the difference between rainfall and evaporation in July also supports this assumption. The culmination of basic density when rainfall and evaporation are balanced suggests that an insufficient water supply may reduce the photosynthates available for growth, and may have a considerable effect on the productivity of Scots pine even in Finnish conditions (cf. HALLMAN *et al.* 1978). On sandy soils, in particular, an insufficient water supply is evident. On the other hand, the water supply may directly control the growth rate of conifers as argued by BUECH (1976). SOLANTIE's (1974) calculations suggest that evaporation may frequently exceed rainfall during the formation of late-wood, and drought may thus have an influence on the basic density of Scots pine. According to SIRÉN (1961), the role of rainfall near the timber line is negligible compared with temperature.

Both temperature and water supply appear to exert an independent effect on the values of the basic density of Scots pine.

Combining these factors, however, yielded an explanatory power of only 40–50 per cent of the total variation. This result suggests that there may be other factors, both external and internal, which have a greater effect on basic density than those included in the analysis. For example, the role of the radiation regime was assumed to be of the same magnitude in different parts of Finland during the growing season as suggested by MIKOLA (1950). Carbohydrates stored in photosynthesis are, however, basic for growth, and therefore more detailed studies are needed to verify the present hypothesis. Especially, the annual total photosynthesis seems to determine the growth level of several conifers and thus may also have an effect on the basic density of conifers (cf. LEDIG 1976). For example, MIKOLA (1950) has paid attention to the role of annual photosynthesis in tracheid growth, and he assumes that photosynthesis during winter may be of importance (cf. also EMMINGHAM and WARING 1977). MIKOLA (1950) suggests also that the effect of temperature is partly explained through an increased level of photosynthesis during mild winters. It is noteworthy that basic density in the present analysis was correlated with annual mean temperature, which may support the hypothesis suggested by MIKOLA (1950).

The variation in basic density was only partially explained by temperature and water supply. This fact may indicate the poor explanatory power of pure environmental factors as regards tracheid growth (cf. for example LEDIG *et al.* 1975) or problems concerning the available material and the study approach. The effect of environment on growth and basic density is determined by several physiological processes, and it is evident that there are only a few environmental factors directly effecting tracheid growth and basic density. For example, GORDON and LARSON (1968) have demonstrated that the onset of thick walled late wood production and cessation of leader growth are synchronized. The onset of needle growth at the same time obscures, however, the interpretation of this result, which may be caused either by the improved supply of photosynthates or the hormonal control of leader and needle

growth, as suggested by WAREING *et al.* (1964) (cf. also LARSON 1964). According to ESKOLA's (1976) results, the structure of latewood can be correlated with the concept of maturation suggested by HARI (1972), which refers to the role of hormonal control in tracheid growth.

The results obtained by WAREING *et al.* (1964) suggest that the response of tracheid growth to the environment varies during the period of active growth and therefore the changing physiological status of the lateral meristem should be taken into consideration. In the boreal zone, the annual development cycle of forest trees has been found to be closely correlated with temperature (SARVAS 1972). Thus, temperature may play a dual role in controlling tracheid growth, *i.e.* temperature affects tracheid growth both directly and through physiological processes (cf. HARI *et al.* 1970, HARI 1972, ESKOLA 1976, KANNINEN 1977). It is suggested that the extent of tracheid growth is determined by the mutual independent effects of the environment on growth rate and rate of development (cf. van DOBBEN 1962). Therefore a more dynamic approach is needed for explaining the basic processes of tracheid growth which have an effect on the basic density of Scots pine (cf. KELLOMÄKI 1977).

ZOBEL and McELWEE (1958) have also referred to the role of physiological processes through the effect of age on basic density. In juvenile wood (age 1–10 years) the basic density of Loblolly pine (*Pinus loblolly* Mill) increased parallel with tree age, in mature wood (age 11–) the basic density had stabilized. HAKKILA (1966, 1968) and UUSVAARA (1974) have shown that the basic density of Finnish conifers levels off in mature stands. Basically, this is due to the change in the ratio between early and late-wood and may be derived from the availability of photosynthates for growth.

The material utilized in the present analysis represents pulp wood which must fulfil particular minimum dimensions. Therefore the material from northern Finland represents considerably older trees than the material from southern Finland. Owing to this, the values of basic density representing northern Finland are decreased and

values of basic density representing southern Finland are increased if the basic density values are reduced to the same age level. Therefore, the effect of different environmental factors, especially the effect of temperature, is more pronounced than presented in the analysis. The material from southern Finland also includes more small-dimensioned pulp wood than the material from northern Finland which has the same effect on the real values of basic density as the differences in the age. In addition, there are other sources of error

which remain uncontrolled in the present analysis (cf. HAKKILA 1968). On the other hand, the relating of weather statistics for 1930 through 1961 with values of basic density for a longer period can describe only the basic features of the effect of weather factors on basic density due to the levelling off the annual variation in both factors. Only the analysis carried out on a yearly basis as regards both basic density and weather factors can give a more detailed explanation of the effect of climatic factors on basic density (cf. SAIKKU 1975).

REFERENCES

- BUECH, R. 1976. Tree shoot elongation in northern Wisconsin and relationships with temperature and precipitation. *Can. J. For. Res.* 6: 487–498.
- BUIJTENEN, VAN J. P. 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.
- » — & 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.
- DOBBEN VAN W. H. 1962. Influence of temperature and light conditions on dry matter distribution, development rate and yield in arable crops. *Neth. J. agric. Sci.* 10: 377–389.
- ELLIOTT, G. K. 1970. Wood density in conifers. Commonwealth Agricultural Bureaux. *Tech. Commun.* 18.
- EMMINGHAM, W. & WARING, R. H. 1977. An index of photosynthesis for comparing forest sites in western Oregon. *Can. J. For. Res.* 7: 105–174.
- ESKOLA, T. 1976. Männyn ja koivun päivittäisen paksuuskasvun riippuvuus lämpötilasta ja sisäisestä säätelystä sekä paksuuskasvun vuotuinen kasvurytmi vuosina 1973 ja 1974. Ms. Thesis. University of Helsinki. Department of Silviculture.
- GORDON, J. C. & LARSON, P. R. 1968. Seasonal course of photosynthesis, respiration, and distribution of ¹⁴C 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 of some properties of pine and spruce pulpwood in Finland. *Seloste: Eräiden mänty- ja kuusipaperipuun ominaisuuksien vaihtelu Suomessa.* *Commun. Inst. For. Fenn.* 66.8.
- HALLMAN, E., HARI, P., RÄSÄNEN, P. K. & SMOLANDER, H. 1978. The effect of planting shock on transpiration, photosynthesis, and height increment of Scots pine seedlings. *Seloste: Istitutushokin vaikutus männyn-taimien transpiraatioon, fotosynteesiin ja pituuskasvuun.* *Acta For. Fenn.* 161.
- HARI, P. 1972. Physiological stage of development in biological models of growth and maturation. *Ann. Bot. Fenn.* 9: 107–115.
- » — , LEIKOLA, M. & RÄSÄNEN, P. K. 1970. A dynamic model of the daily height increment of plants. *Ann. Bot. Fenn.* 7: 375–378.
- HELMIMÄKI, V. I. 1967. Taulukoita ja karttoja Suomen sadeoloista kaudelta 1931–1960. Liite Suomen meteorologiseen vuosikirjaan nide 66, osa 2. Tables and maps of precipitation in Finland, 1931–1960. Supplement to the meteorological yearbook of Finland. Vol. 66, part. 2.
- HUOVILA, S. 1970. Tilastoja lumipeitteen syvyydestä Suomessa. Ilmatieteen laitos. Tutkimusseloste 16.
- KANNINEN, M. 1977. Männikön puuston ja varvuston maanpäällisen osan päivittäisen kuiva-ainetuotoksen dynamiikka. Ms. Thesis. University of Helsinki. Department of Silviculture.
- KELLOMÄKI, S. 1977. Dynamics of dry matter production in forest ground cover communities with special reference to their successional development. University of Helsinki. Department of Silviculture. *Research Notes* 16.
- KLEM, G. S. 1965. Variation in the specific gravity of foreign softwood species and Norway spruce from South and West Norway. *Medd. fra Norske Skogforsöksv.* 74.3.
- KOLKKI, O. 1966. Taulukoita ja karttoja Suomen lämpötiloista kaudelta 1931–1960. Liite Suomen meteorologiseen vuosikirjaan nide 65, osa I a. Tables and maps of temper-

- ature in Finland during 1931–1960. Supplement to the meteorological yearbook of Finland. Vol 65, part 1 a.
- LARSON, P. R. 1964. Some indirect effects of environment on wood formation in forest trees. In: The formation of wood in forest trees. (ed. M. H. Zimmermann), pp. 345–365. Academic Press. New York.
- LEDIG, F. T. 1976. Physiological genetics, photosynthesis and growth models. In: Tree physiology and yield improvement (ed. M.G.R. Connel and F. T. Last), pp. 21–54. Academic Press. London. New York. San Francisco.
- » —, ZOBEL, B. J. & MATTHIAS, M. F. 1975. Geoclimatic patterns in specific gravity and tracheid length in wood of Pitch pine. Can. J. For. Res. 5: 318–329.
- 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 kasvatustutkimuksissa. Summary: On variations in tree growth and their significance to growth studies. Commun. Inst. For. Fenn. 38.
- NYLINDER, P. 1967. Non-destructive field sampling systems for determining the wood density of standing timber over large areas, variation within and between species, and the influence of environmental and measurable factors on wood density. Rapp. Uppsats. Instn. Virkeslära Skogshögsk. 56.
- PERSSON, A. 1972. Studies on the basic density in mother trees and progenies of pine. Stud. For Suec. 96.
- 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.
- SAIKKU, O. 1975. The effect of fertilization on the basic density of Scots pine (*Pinus sylvestris* L.). Lyhennelmä: Lannoituksen vaikutus männyn (*Pinus sylvestris* L.) puuaineen tiheyteen. Densitometritutkimus. Commun. Inst. For. Fenn. 85.3.
- SARVAS, R. 1972. Investigations on the annual cycle of development of forest trees. Commun. Inst. For. Fenn. 76.3.
- SIRÉN, G. 1961. Skogsgränstallen som indikator för klimatfluktuationerna i norra Fennoskandien under historisk tid. Commun. Inst. For. Fenn. 54.2.
- SOLANTIE, R. 1974. Kesän vesitaseen vaikutus metsä- ja suokasvillisuuteen ja linnustoon sekä lämpöolojen välityksellä maatalouden toimintaedellytyksiin Suomessa. Summary: The influence of water balance in summer on forest and peatland vegetation and bird fauna and through the temperature on agricultural conditions in Finland. Silva Fenn. 8(3):172–184.
- UUSVAARA, O. 1974. Wood quality in plantation-grown Scots pine. Lyhennelmä: Puun laadusta viljelymännikössä. Commun. Inst. For. Fenn. 80.2.
- VELLING, P. 1974. Männyn (*Pinus sylvestris* L.) puuaineen tiheyden fenotyypisestä ja geneettisestä vaihtelusta. Summary: Phenotypic and genetic variation in the wood basic density of Scots pine (*Pinus sylvestris* L.). Folia For. 188.
- » — 1976. Mänty- ja kuusiprovenienssien puuaineen tiheyden vaihtelusta. Summary: The wood basic density variation of pine and spruce provenances. Folia For. 257.
- WAREING, P. F., HANNEY, C. E. A. & DIGBY, J. 1964. 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.
- ZAVITKOVSKI, J. 1976. Ground vegetation biomass production and efficiency of energy utilization in some northern Wisconsin forest ecosystems. Ecology 57: 694–706.
- ZOBEL, B. J. & McELWEE, R. L. 1958. Natural variation in wood specific gravity of Loblolly pine, and an analysis of contributing factors. Tappi 41: 158–161.

SELOSTE:

ILMASTOTEKIJÖIDEN VAIKUTUS MÄNNYN PUUAINEN TIHEYTEEN

Männyn (*Pinus sylvestris* L.) puuaineen tiheyden riippuvuutta lämpö- ja kosteustekijöistä on tutkittu kirjallisuudesta saadun aineiston perusteella. Havaittiin kesä-, heinä-, ja elokuun keskilämpötilojen korreloituvan tiheyteen, heinäkuun keskilämpötilan kuitenkin kaikkein kiinteimmin. Näiden kuukausien sadannalla ei ollut havaittavaa vaikutusta tiheyteen. Sen sijaan heinäkuun sadannan ja haihdunnan ero korreloitui tiheyden kanssa. Tämä vaikutus osoittautui kuitenkin johtuvan pääasiassa lämpötilasta.

Vuotuisella pohjalla tehty tarkastelu osoitti vuoden keskilämpötilan, lämpösunnan ja kasvukauden pituuden korreloivan männyn puuaineen tiheyden kanssa. Myös vuotuinen sadanta korreloituu tiheyden kanssa. Sekä lämpö- että kosteustekijän vaikutukset osoittautuivat vuotuisella pohjalla tehdyssä analyysissä suhteellisen itsenäisiksi. Yhdessä lämpö- ja kosteustekijät selittivät kuitenkin suhteellisen vähän männyn puuaineen vaihtelusta niin kuukausi- kuin vuotuispohjalta tehdyssä analyysissä.