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The Influence of Environmental Factors on the Diameter Growth of Forest Trees. Auxanometric Study

Matti Leikola

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THE INFLUENCE OF ENVIRONMENTAL FACTORS ON THE DIAMETER GROWTH OF FOREST TREES

AUXANOMETRIC STUDY

MATTI LEIKOLA

To be publicly discussed, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, in Auditorium XII on March 8, 1969, at 12 a'clock noon

HELSINKI 1969

Suomalaisen Kirjallisuuden Kirjapaino Oy Helsinki 1969

PREFACE

In the course of the present investigation I have received valuable support and assistance from several persons. The project was made possible through the valuable help of my advisor, Dr. PAAVO YLI-VAKKURI, Professor of Silviculture and Head of the Department of Silviculture, University of Helsinki, and also Dr. GUSTAF SIRÉN, Professor of Silviculture, University of Helsinki, especially in the acquisition of the measuring devices necessary for the field work. Dr. Yli-Vakkuri has shown active interest in the progress of the study; he has also read the manuscript and given valuable advice. In preparation of the study I have also received worthy proposals from Dr. PEITSA MIKOLA, Professor of Forest Biology, University of Helsinki.

During the field work, Mr. AUGUST WÄÄNÄNEN, Field Supervisor of the Forestry Field Station of the University of Helsinki, assisted considerably in establishing the experimental setup, and later, in taking care of it. With commendable care, the field work was carried out in the latter part of summer 1964 by Mr. PENTTI THUNEBERG, B.Sc., and during the 1967 recording period, by Mr. PENTTI PYLKKÖ, B.For.

In the computational part of the study, Dr. PEKKA KILKKI and Mr. JOUKO LAASASENAHO, B.For., have given valuable advice. Mr. Laasasenaho has also carried out the practical aspects of the computation work.

Miss AINO PIISPANEN has prepared the microscopic tissue samples. Numerous persons have assisted me in various phases of preparing the manuscript. I would like to mention especially Mrs. IRJA THUSBERG, Mr. E. MALMIVAARA, and Mr. H. MOISIO.

Mr. KARI MUSTANOJA, M.Sc., is responsible for the language and style of the English version of the original Finnish manuscript. A large part of the translation work has been done by Mrs. ULLA MUSTANOJA. Mr. Mustanoja has also made several valuable comments and suggestions in the manuscript.

The realization of the project was largely carried out while the author was a research assistant of the National Research Council for Agriculture and Forestry. Grants from the Society of Forestry in Finland and the Finnish Cultural

Foundation have aided in financing the study. The Society of Forestry has also kindly accepted the study for publication in Acta Forestalia Fennica.

I wish to express my sincere thanks to the persons and institutions mentioned above.

Helsinki, October 1968

Matti Leikola

CONTENTS

ABBREVIATIONS AND SYMBOLS

Au., aux.	=	Auxanograph, diameter growth recorder
Bi.	=	Birch (*Betula pubescens* Ehrl.)
Day	=	Number of days from the beginning of the growing season
DBH	=	Diameter at breast-height (1.3 m)
D.f.	=	Degrees of freedom
D.h. > ± 0° C	=	Degree-hours with ± 0° C as threshold value
D.h. > + 5° C	=	» » » + 5° C » » »
D.h. > + 10° C	=	» » » + 10° C » » »
Gb.	=	Girth band
Pi.	=	Pine (*Pinus silvestris* L.)
Ppt.	=	Precipitation
r	=	Correlation coefficient
R^2	=	Coefficient of determination
s	=	Standard deviation
S.rad.	=	Solar radiation
Sp.	=	Spruce (*Picea abies* (L.) Karst.)
Tdiff.	=	Difference between the daily maximum and minimum temperatures
Tmin.	=	Minimum temperature
Tmax.	=	Maximum temperature
Tsoil	=	Soil temperature
..	=	No observations
—	=	No results. Hypotheses H_0 approved
*	=	Hypotheses H_0 discarded with a risk level of 5 %
**	=	» » » » » 1 %
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I. INTRODUCTION

Although vague concepts of the true nature of the diameter growth of trees prevailed long, the connection between external environmental factors and the formation of the annual ring was sought as early as in the sixteenth century (reviews of the history in e.g. Erlandson 1936, Glock 1941, 1955, Studhalter 1955). The first efforts to measure the annual diameter growth of trees have been published in the 1750's, and the course of diameter growth during one growing season was already recorded in the 1830's (Studhalter *et al.* 1963). But only after Th. Hartig and his followers, in the latter half of last century, had laid a firm foundation on studies of the physiology of tree growth (e.g. Sanio 1873, R. Hartig 1885, Schwarz 1899), growth studies of various types could be based relatively reliable interpretations.

So long as the researcher had to be satisfied with the weather data from his own general observations and that from weather stations established for other purposes, the efforts to explain the effect of the environmental factors on the diameter growth of trees did not lead to satisfactory results. The first actual forest meteorological stations were established in the 1860's in Saxony and Bavaria (Cajander 1909, p. 18—19); in addition to valuable basic micro-meteorological research, various plant phenological observations were also made at these stations. Tying various phenomena of plant life to the annual ecologic calendar of nature received considerable attention at the end of the nineteenth century. An illustrative example is provided by the ca. 240 forest phenological stations in Germany in the 1890's (Schnelle 1955, p. 15).

Research concerning the effect of climate on tree growth was further developed by the Americans Douglass and Huntington, who started dendrochronological research based on comparing annual ring widths by using so-called cross-dating technique (Laitakari 1920, Boman 1927, Glock 1941, 1955, and others). For analysing the daily diameter growth of trees, several different devices for measurement on top of the bark were developed at the end of the nineteenth and the beginning of the twentieth century (e.g. Friedrich 1897, Mallock 1919, Mac Dougal 1938). The data obtained were used to study the effect of various climatic factors on growth (e.g. Nakashima 1924, Romell 1925). The growth process was also studied from microscope samples taken from the stem at regular intervals (e.g. Wieler 1898, H. Brown 1912, 1915).

The continuous development of micrometeorological theory and techniques of study (reviewed by e.g. GEIGER 1965), applications of statistical computing methods to aid growth studies (e.g. SCHUMACHER and MEYER 1937), proving the growth hormone theory explaining tree growth (e.g. PRIESTLEY 1930, SNOW 1933), and various structural improvements in the devices for measuring growth (REINEKE 1932, and others) further helped to deepen the concepts concerning the diameter growth of trees and the environmental factors affecting it. In general, however, no new, essentially different features were introduced into ecologic growth studies in the years between the two world wars.

Recent advances in growth studies have been considerable. Special attention should be paid to the decisive role of three factors. Growth chambers (»phytotrones») enabling the simultaneous and accurate control of many different growth factors have helped to obtain data e.g. about the regularities in the manner these factors govern the diameter growth of trees (e.g. CROCER 1948, WENT 1957). The general development of meteorological instruments, especially that enabling the use of transistorized ecologic measuring devices (e.g. PLATT and GRIFFITHS 1964, BARNER 1965, HOFMANN 1965, BAUMGARTNER 1967) has enabled researchers to make intensive and accurate measurements, and modern computer technology has facilitated the interpretation of the often large sets of data required for growth studies in the nature. Computers have also been responsible for entirely new mathematical methods previously almost unknown in biological research (see e.g. FREESE 1964, DRAPER and SMITH 1967).

The first modern attempt to explain the effect of several environmental factors on the daily diameter growth of trees in their natural environment was made by FRITTS (1958, 1959, 1960). After these works were published, a large number of research workers have studied these relationships (among the latest publications: WILHELMI 1959, 1962, HARMS 1962, KOZLOWSKI and PETERSON 1962, KOZLOWSKI *et al.* 1962, POPESCU-ZELETIN *et al.* 1962, FRASER 1963, 1966, KERN 1966, MITSCHERLICH *et al.* 1966).

Although research of the relationships between various climatic factors and the diameter growth of trees from annual ring measurements has been carried out in the Nordic countries for a long time and has produced remarkable results (e.g. HESSELMAN 1904, LAITAKARI 1920, BOMAN 1927, ERLANDSON 1936, ORDING 1941, HUSTICH 1948, MIKOLA 1950, EKLUND 1954, 1967, HOLMSGAARD 1955, SIRÉN 1961), very little has been published about the relationships between the daily diameter growth and the environmental factors during the growing season. Among early work, only AMILON (1910), ROMELL (1925), and RONGE (1928) in Sweden have published results of such studies. In Denmark, LADEFOGED (1952) published a growth study based on considerable microscopic data. The study by MORK (1960) in Norway about the formation of the annual ring, and the one by ANDERSSON (1953) in Sweden of the development of late wood in the annual ring, also deserve to be mentioned. — An interesting effort to solve the dependence of tree growth on climatic factors in a somewhat different way is represented by the phyocrologic study by PATERSON (1961) in Sweden.

In addition to the dendrochronological studies mentioned above, only a few Finnish tree-diameter growth studies of this kind have been published. Earlier work is represented by the observations of ILVESSALO (1932) about the time of pine, spruce, and birch diameter growth. In the last years, much interest has been revived in recording the diameter growth of trees, and for instance Huikari has discussed the topic in several publications (HUIKARI 1961, HUIKARI and PAARLAHTI 1967). Among the other studies related to this problem, those of SARVAS (1967) concerning the annual period of development of forest trees and the studies by HEIKURAINEN and SEPPÄLÄ (1965) of the relations between tree growth and the temperature of the growing season on drained peatlands deserve to be mentioned.

— — —

Already the first students of tree growth and its dependence on environmental conditions concluded that contrary to the annual height increment which largely depends on the conditions of the previous growing season, the diameter increment (width of the annual ring) is essentially determined by the conditions of the same growing season (HESSELMAN 1904, CIESLAR 1907, LAITAKARI 1920, HUSTICH 1948, and others). This is the basis for studies concerning the relationships between various environmental factors and the diameter growth of trees, using data collected cursorily through the growing season.

The object of the present study is to throw light on the diameter growht of trees as it is affected by various environmental factors. The data used are composed of daily records, through the growing season, of the diameter growth of trees and various environmental factors; an attempt has been made to interpret the effect of these factors on growth by computational means.

Since the daily recording of the diameter growth of trees is a manyfaceted methodic problem, attention is also paid to various methods of growth measurement and their use in growth studies.

II. MATERIAL AND METHODS

1. SELECTION OF THE METHOD OF STUDY

In studies concerning tree growth, the effect of the environmental factors can be analysed by either of two principal methods: simple or factorial experiments.

In a simple experiment, the effect on growth of the other factors than the one studied has been eliminated as completely as possible either by the experimental design or afterwards in connection with the interpretation of the results. The main advantage of the method is its efficiency: even limited sets of data may provide a realiable basis for the interpretation of the results. This is a primary reason for favoring the simple experiment in all biological research.

However, since all environmental factors act simultaneously in the field — even in simple experiments — methods based on factorial design have been increasingly used in biological growth studies. The greatest advantage mentioned for the factorial experiment is the possibility to consider also the interactions among various factors; the method thus provides more information about the observation than the simple experiment, although the number of observations needed in a factorial experiment may easily run into great numbers (Cox 1958, p. 91—133, Platt and Griffiths 1964, p. 15—55, and others).

The usefulness of data in growth studies based on the simultaneous observation of several growth factors has been greatly increased by the introduction of controlled growth chambers (Crocer 1948, p. 285—342, Went 1957, Lang 1963, Barner 1965, p. 42—45, and others). Research concerning forest trees has, for size limitations, been possible only with small plants in controlled growth experiments; many factors causing uncertainty are present when the results of these young-plant tests are extended to apply also for large trees. Also the inclusion of the time factor and the subsequent continuous variation of the environmental factors in growth studies leads to difficulties. The results may have a considerable theoretic value, but applying them to e.g. practical forestry may meet unexpected difficulties, even surprises (cf. Daubenmire 1962, p. 335—350, L. T. Evans 1963).

The basic method selected for this study was recording the diameter growth of trees and the various environmental factors directly in the field; any analytical

treatment was decided to be carried out by later computations. The following advantages were considered to be gained by this method over the other available ones:

— Full-grown trees in their natural environment could be used in the study.

— The changes in various environmental factors and the entire ecologic environment they form are natural and unsimplified.

— All interactions of the various environmental factors are fully considered.

— The reactions of the sample trees to environmental stimuli are natural.

The following drawbacks of the selected method also deserve, however, to be mentioned:

— The effect of other than the recorded environmental factors on tree growth will not be found.

— Since the environmental effects are actually only those acting in a very narrow zone enveloping the tree, a study of the factors affecting growth has to be limited to the search of the index values of these.

— Tree-to-tree variations can not be adequately described without increasing the volume of data considerably.

2. SELECTION AND GENERAL DESCRIPTION OF THE EXPERIMENTAL STANDS

21. METSÄ-SARAMÄKI

To meet the requirements set by the objectives of the study, special emphasis was placed on the selection of the experimental stands. For instance, it was required of a suitable area that the soil were as homogenous as possible and the stand continued as evenly as possible beyond the main experimental area. It was also required that the stand structure was simple enough to allow maximum generalisation of the results and to provide good criteria for determining their applicability elsewhere.

The first experimental stand selected was a *Vaccinium* -type[1] pine stand on sandy soil in Metsä-Saramäki woodlot owned by the State Board of Forestry, in the commune of Orivesi (61°47′ N, 24°18′ E) (Fig. 1). The stand is 162 m above sea level. The principal stand data are:

Tree species composition: pine (*Pinus sylvestris* L.) 100 %
Stems: 618 per hectare
Basal area: 16.9 sq.m per hectare
Dominant height: 16.0 m
Mean height: 15.3 m
Bottom of canopy (average): 6.5 m

[1] According to Cajander's system of forest (site) types; See e.g. Cajander 1949.

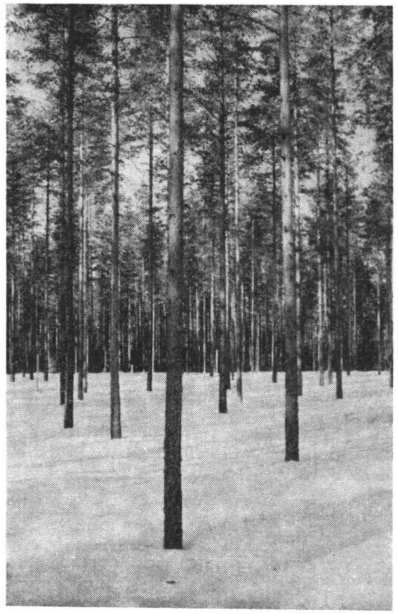

Figure 1. The Metsä-Saramäki experimental stand before the beginning of the field work. Photo March 15, 1964.

Crown closure (Cajanus' cylinder [1]): 43 %
Mean volume: 117 cu.m. per hectare without bark
Age: 60 years

About five years before recording was started, the area had been thinned, and a 1—1.5 m tall spruce understory had been removed. The cutting resulted in slight injury to some trees. Distinguishing these from the uninjured ones was very easy.

The experimental stand was established about two hundred meters from a road; at this distance any disturbance in stand conditions was considered insignificant (cf. Tamm and Troedsson 1955, Nyyssönen and Vuokila 1960).

The stand was marked and a fence was built around it in fall 1963. At the same time, a tower was built in the stand for studying climatic growth factors, and snow-depth rods were installed. Field work started in spring 1964 and was continued to fall 1967 according to the following schedule:

Year	Field work started in the spring	Ended in fall
1964	March 15	September 1
1965	April 27	August 31
1966	April 23	August 31
1967	March 15	September 1

[1] See Sarvas 1953.

Table 1. Placement of environmental recording devices at the Metsä-Saramäki experimental stand. Records have been made through the observation seasons of 1964, 1965, 1966, and 1967 unless other times are specified.

Environmental factor to be measured	Measuring device	Total number	Choice of site in stand: Criterion	Choice of site in stand: Level or depth from soil surf.	Choice of site in stand: Number	Time of records	Remarks (site, year, etc.)
Solar radiation	Solarograph	1	Subject.	1 m high	1	Continuous	In clearing; 1964, 1967
	Sphere pyranometer	1	Subject.	1 m high	1	Continuous	In clearing; 1966, 1967
Air temperature and humidity	Thermohygrograph	3	Subject.	7 m high	1	Continuous	In weather chamber
				2 m high	1	Continuous	In weather chamber
				1.5 m high	1	Continuous	In plastic chamber; 1964
Max. air temperature	Max. thermometer (mercury)	3	Subject.	7 m high	1	Once a day	In weather chamber
				2 m high	1	Once a day	In weather chamber
				1.5 m high	1	Once a day	In plastic chamber; 1964
Min. air temperature	Min. thermometer (alcohol)	3	Subject.	7 m high	1	Once a day	In weather chamber
				2 m high	1	Once a day	In weather chamber
				1.5 m high	1	Once a day	In plastic chamber; 1964
Temperature of tree cambium	Thermometer (mercury)	2	Subject.	1.3 m high	2	3 times a day	Only 1964
Precipitation	Recording rain gauge	1	Subject.	1.5 m high	1	Continuous	In clearing
	Summer rain gauge	24	System.	1 m high	24	After rain	Only 1964
	Stemflow gauge	7	Subject.	1.5 m high	7	After rain	Only 1964
Snow depth	Snow depth rod	24	System.	0—1 m high	24	Every 3. day	
Wind velocity	Cup anemometer	2	Subject.	9 m high	1	Continuous	Only 1964
				2 m high	1	Continuous	Only 1964
Soil temperature	Thermograph	2	Subject.	10 cm deep	1	Continuous	One with two, other with three bulbs
				20 cm deep	1	Continuous	
				50 cm deep	1	Continuous	
Max soil temperature	Max. thermometer (mercury)	2	Subject.	10 cm deep	1	Once a day	
				20 cm deep	1	Once a day	
Min. soil temperature	Min. thermometer (alcohol)	2	Subject.	10 cm deep	1	Once a day	
				20 cm deep	1	Once a day	
Soil moisture	Gypsum resistance meter	1	System.	10 cm deep	10	Every 3. day	Only 1964
				20 cm deep	10	Every 3. day	Only 1964
				30 cm deep	10	Every 3 day	Only 1964
				50 cm deep	10	Every 3 day	Only 1964
Depth of frozen soil	Frozen soil depth rod, direct measurement	1	System/ Subject.	0—30 cm deep	20	Every 3 day	Only 1964, 1965, and 1967

Figure 2. The Metsä-Saramäki experimental stand during the field work. Photo June 8, 1964.

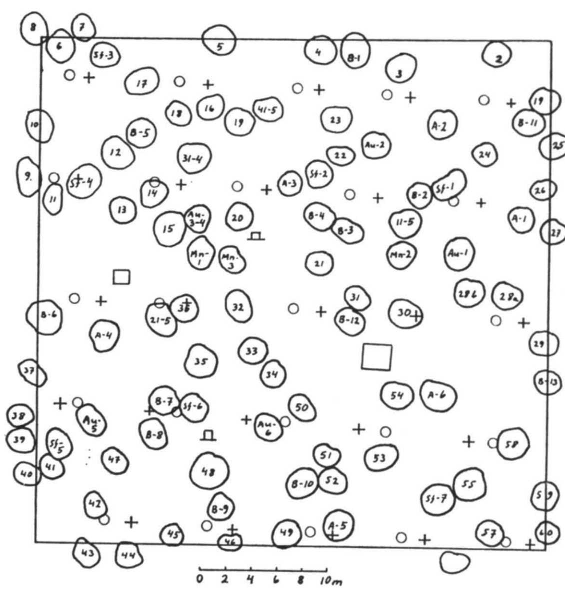

Figure 3. Crown map over the Metsä-Saramäki experimental stand. Legend: ⊙ = tree, □ = thermohygrograph, ☐ = tower for measurements, ⊓ = soil thermograph, + = snow depth rod, ○ = rain gauge.

Table 2. Dimensions of trees studied in the Metsä-Saramäki experimental stand. Breast-height diameters are averages of largest and smallest diameter. Location of trees in stand are shown in figure 3. The other trees in stand are described in appendix 1. All the trees are pines. Measurement in 1964.

Number and symbol of tree	DBH, cm	Height, m	Bottom of canopy, m	Canopy class	Remarks (recording device, year, etc.)
Au — 1	21	17.0	6.0	I	Auxanogr. 1964, 1965, 1966, 1967
Au — 2	21	16.5	6.0	I	Auxanogr. 1964, 1965, 1966, 1967
Au — 3-4	23	17.0	7.0	I	2 auxanogr. 1964, 1 auxanogr. 1965—1967
Au — 5	20	16.0	6.0	I	Auxanogr. 1964, 1965, 1966, 1967
Au — 6	21	16.5	6.5	I	Auxanogr. 1964, 1965
A — 1	21	16.0	7.0	I	Girth band 1964, 1966, 1967
A — 2	24	17.0	7.0	I	» » 1964
A — 3	15	14.0	6.5	I	» » 1964, 1966, 1967
A — 4	19	16.5	6.0	I	» » 1964, 1966, 1967
A — 5	20	17.0	7.0	I	» » 1964, 1966, 1967
A — 6	19	16.0	6.5	I	» » 1964, 1966, 1967
B — 1	21	16.0	7.0	I	» » 1964, 1966, 1967
B — 2	16	14.0	5.5	I	» » 1964, 1966, 1967
B — 3	20	17.5	8.5	I	» » 1964, 1966, 1967
B — 4	16	14.5	6.5	II	» » 1964, 1966, 1967
B — 5	22	17.0	7.5	I	» » 1964, 1966, 1967
B — 6	21	16.0	7.0	I	» » 1964, 1966
B — 7	18	15.0	5.5	II	» » 1964, 1966, 1967
B — 8	20	15.5	6.0	II	» » 1964, 1966, 1967
B — 9	20	16.0	7.0	I	» » 1964, 1966, 1967
B — 10	18	15.5	6.5	I	» » 1964, 1966, 1967
B — 11	23	17.5	8.5	I	» » 1964, 1966, 1967
B — 12	20	16.0	6.0	I	» » 1964, 1966, 1967
B — 13	18	16.0	7.0	I	» » 1964, 1966, 1967
11 — 5	18	17.0	7.0	I	5 girth bands 1964, 1 girth bd. 1966, 1967
21 — 5	22	17.5	6.5	I	5 » » »
31 — 4	20	16.0	7.0	I	4 » » »
41 — 5	18	16.0	6.5	I	5 » » » , 1 girth bd. 1966
Mn — 1	17	15.5	6.5	I	Tissue sampl. 1964
Mn — 2	19	16.5	7.0	I	» » 1964
Mn — 3	21	16.5	6.5	I	» » 1964
Mn — 4	19	16.0	6.5	I	» » 1966
Mn — 5	18	16.0	7.0	I	» » 1966

The experimental setup at Metsä-Saramäki (Fig. 2) was supplemented by a recording site in a 400 × 400 m clearing 450 meters away. Records were started here in May 1964 and continued according to the same schedule as at the main stand.

The crown projections and the sites of the measuring devices in the stand are shown in figure 3. The measurements made in the stand are summarized in table 1. The measurement of the various environmental factors is described in detail in chapter II 3. The sample trees are described in table 2 and the other trees of the stand in appendix 1.

The temperature records of the springs 1965 and 1966 were supplemented with data from Hyytiälä weather station about six kilometers north of the area.

222. HUIKKO

In spring 1966, the study was extended to include another experimental stand (Fig. 4) in the commune of Juupajoki, near Huikko river, about four kilometers north of Metsä-Saramäki. The area is ca. 140 m above sea level. The criteria for selecting the stand included those already described for the Metsä-Saramäki stand plus the tree species composition and soil drainage. The new stand, Huikko, was a young, mixed birch-spruce-pine stand on peatland, ordinary spruce swamp (VK) according to Cajander's forest type classification.[1] The little river maintained approximately even soil moisture conditions throughout the growing season. The principal mensurational data for the stand are:

Tree species composition: birch[2] 50 %, spruce[3] 26 %, pine[4] 24 %
Stems: 537 per hectare
Basal area: 12.9 sq. m per hectare
Dominant height: 15.3 m
Mean height: 14.5 m
Bottom of canopy (average): 6.6 m
Crown closure: 56 %
Mean volume: 100 cu.m per hectare without bark
Age: 45 years

Figure 4. The Huikko Experimental stand during the field work. Photo May 25, 1966.

[1] See footnote 1. on page 14.
[2] (*Betula pubescens* Ehrl.)
[3] (*Picea abies* (L.) Karst.)
[4] (*Pinus sylvestris* L.)

Table 3. Placement of environmental recording devices at the Huikko experimental stand. Records have been made through the observation seasons of 1966 and 1967.

Environmental factor to be measured	Measuring device	Total number	Choice of site in stand: Criterion	Choice of site in stand: Level or depth from soil surf.	Choice of site in stand: Number	Time of records	Remarks (site, etc.)
Air temperature and humidity	Thermohygrograph	1	Subject.	2 m high	1	Continuous	In weather chamber
Max. air temperature	Max. thermometer (mercury)	1	Subject.	2 m high	1	Once a day	In weather chamber
Min. air temperature	Min. thermometer (alcohol)	1	Subject.	2 m high	1	Once a day	In weather chamber
Soil temperature	Thermograph	1	Subject.	10 cm deep	1	Continuous	
Max. soil temperature	Max. thermometer (mercury)	1	Subject.	10 cm deep	1	Once a day	
Min. soil temperature	Min. thermometer (alcohol)	1 1	Subject.	10 cm deep	1	Once a day	

The stand had been thinned about five years before the recording was started. Field work started in spring 1966 and continued to fall 1967 as follows:

Year	Field work started in the spring	Ended in the fall
1966	May 15	August 31
1967	May 12	August 31

The crown projections and the sites of the measuring devices in the stand are shown in figure 5. The measurements made in the stand are summarized in table 3. The measurement of the various environmental factors is described in

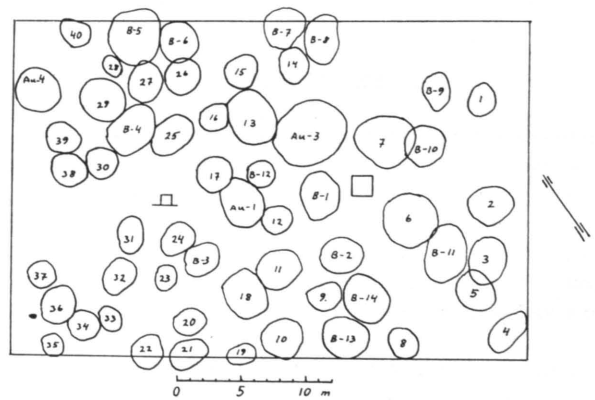

Figure 5. Crown map over the Huikko experimental stand. Legend see fig. 3.

Table 4. Dimensions of trees studied in the Huikko experimental stand. Breast-height diameters are averages of largest and smallest diameter. Location of trees in the stand are shown in figure 5. The other trees in the stand are described in appendix 2. Measurement in 1967.

Number and symbol of tree	Tree species	DBH, m	Height, m	Bottom of crown, m	Canopy class	Explanations (recording device, etc.)
Au — 1	Spruce	25	18	5	I	Auxanogr. 1966, 1967
Au — 2	»	22	17	2	I	Auxanogr. 1966, 1967
Au — 3	Birch	21	17	8	I	Auxanogr. 1966, 1967
Au — 4	»	17	16	7	I	Auxanogr. 1966, 1967
B — 1	Birch	19	18	10	I	Girth band 1966, 1967
B — 2	Pine	21	17	9	I	» » 1966, 1967
B — 3	Spruce	18	16	3	I	» » 1966, 1967
B — 4	Birch	19	16	7	I	» » 1966, 1967
B — 5	»	23	16	8	I	» » 1966, 1967
B — 6	Spruce	21	18	4	I	» » 1966, 1967
B — 7	Birch	15	15	6	I	» » 1966, 1967
B — 8	»	16	15	8	I	» » 1966, 1967
B — 9	Pine	21	17	8	I	» » 1966, 1967
B — 10	»	24	17	9	I	» » 1966
B — 11	Birch	16	15	7	I	» » 1966, 1967
B — 12	Spruce	18	17	4	I	» » 1966, 1967
B — 13	Birch	17	15	6	II	» » 1966, 1967
B — 14	Pine	23	18	10	I	» » 1966, 1967

detail in chapter II 3. The sample trees are described in detail in table 4; the other trees in the stand have been listed in appendix 2.

3. MEASUREMENT OF THE ENVIRONMENTAL FACTORS AFFECTING DIAMETER GROWTH

31. GENERAL

A great number of environmental forces determine the development of forest trees, but it is nevertheless relatively easy to pick out a number of physical and other factors responsible for the major part of the effects on tree growth. In general, the subdivisions of the ecologic environment, proposed by the students of plant growth and of the environmental factors affecting it, have been practically identical (Toumey and Korstian 1947, Billings 1952, Lundegårdh 1954, Kramer and Kozlowski 1960, Walter 1960, Clements 1964, Leopold 1964).

For this study, the following factors were selected for recording in the field. All were presumed to have a direct effect on the growth of forest trees (as judged by available information):

1. Climatic factors
   - solar radiation
   - air temperature
   - precipitation (rain and snow)
   - wind
2. Edaphic factors
   - soil temperature (frost)
   - soil moisture

In addition to the factors listed above, a number of others also affect tree growth, but they were considered to be out of the scope of this study. Factors like changes in soil nutrient levels, the soil CO_2-status, and the soil reaction may sometimes evoke distinctive responses in tree growth (e.g. Voigt 1962, Gaertner 1964), but it was considered impossible to study these, or the biotic influences or those of the gaseous composition of the air, in this connection.

Two methods were available for keeping records at the stands: one or few electronic recording units for several environmental factors (e.g. Ericson 1965, Hofmann 1965, Reifsnyder 1967), or a separate measuring device for the measurement of each factor. The advantages of these two systems will not be discussed. Practical reasons were responsible for choosing the latter alternative. This definitely does not mean that either method would somehow have been unsuited for the purpose of this study.

In the selection of the sites of the measuring devices, no compromises were allowed to subtract from their representativity. It was also required that the devices and the recording work disturbed stand conditions as little as possible.

32. CLIMATIC FACTORS

321. SOLAR RADIATION

Solar radiation consists of a continuous spectrum of rays of different wavelengths. The part of the spectrum between ca. 759 and 400 mμ is called visible light, the longer wavelengths infrared, and the shorter ultraviolet radiation (Franssila 1949 p. 21—26, Mörikofer 1949, Collingbourne 1966, and others). The photosynthetic activity of plants is most directly affected by radiation at 750—350 mμ, or approximately that in the range of visible light, which also transmits a major part of the energy in solar radiation. Thus it seems that a normal light meter (lux-meter) could be used for measuring the radiant energy required for the vital processes of plants (cf. e.g. Walter 1960, p. 351—375). — This is, however, true only with certain reservations. The peak distribution of visible light is at ca. 555 mμ. The photosynthesis of plants is very low at this wavelength; its maxima are at 440 and 650 mμ, and some energy is also received from wavelengths beyond the limits of visible light (Toumey and Korstian 1947, p. 14–29, Curtis and Clark 1950, p. 33–41, Leopold 1964, p. 330, and others).

Therefore, for a device suitable for recording solar radiation, one that measured the total radiation received by the green tree crowns (direct and diffuse solar radiation) was searched for. The device selected for the basic records was Moll-Gorczynski's calorimetric solarigraph with a recorder attachment, manufactured by Kipp & Zonen (no. CM3) in Holland. The sensor consists of fourteen blackened manganese-constantane strips placed under a double glass hood which convert the radiation thermally into electricity registered by a portable automatic recorder. (The principles of use of the device are described by e.g. Platt and Griffiths 1964, p. 72).

The response time of the device is ca. 15 seconds, and it is sensitive to rates of ca. 8 mV/cal/sq.cm/min. The small temperature correction factor of the device is helpful: 0.1–0.2 % per degree (C), as is also the point recording system which facilitates the reading of quickly varying radiation, as compared with a normal recorder (Wilhelmi 1959, Platt and Griffiths 1964, p. 73, Drummond 1965).

Since radiation exhibits a continuous pattern of variation under a forest canopy (e.g. Fairbain 1954, Vézina and Pech 1964, Anderson 1966, G. C. Evans 1966, Reifsnyder 1967), it was considered unwise to install the solarimeter in the stand. Instead, it was set up at the recording site in the nearby clearing. The sensor was installed horizontally at a level of ca. 1 m from the ground on a platform, and it was equipped with a white reflection shield. The meter was calibrated and its glass hood was cleaned fortnightly, on an average. The night period, when no radiation was recorded, was used as control (0-level).

The daily radiation total was measured indoors in the following way: Several regular-shaped pieces of recording paper were cut out, their areas were measured accurately with a planimeter, and they were measured with an accurate balance. The radiation area corresponding to the daily total was cut out of the recording paper and weighed, and the daily radiation totals were calculated with the help of the comparative weights obtained in the experimental weighing described above.

In spring 1966, solar radiation measurements were supplemented with a Gunn-Bellani-sphere pyranometer installed at the experimental site in the clearing at Metsä-Saramäki. The device was made by the Davois observatory. It consists of a metal, silver-colored sphere filled with liquid (ethyl alcohol) and placed into an airtight glass sphere. A hollow metal tube connected to the metal sphere runs through a ca. 50 cm long graduated glass tube. Solar radiation warming the metal sphere causes evaporation of the alcohol through the porous metal into the space between the two spheres, is condensed and flows into the glass tube (the structure and working principle of the device are described by e.g. Rossi 1951, Courvoisier and Wierzejewski 1954, Pereira 1959, Mac Hattie 1961).

Since the amount of liquid evaporated from the metal sphere is proportional to the amount of radiation falling on the sphere, the daily radiation total could be calculated from the amount of liquid in the glass tube, using the transformation coefficients, depending on air temperature, provided by the maker of the device. The coefficients were different for each pyranometer. According to the instructions of use, the device should be zeroed once a day, but it was found that it had to be zeroed twice on a bright day. The accuracy of measurement (mean error ± 3 %) is constant, according to the makers' statement, for several years, and users have also reported that the device is well suited for e.g. stand ecologic measurements of total radiation (e.g. Vézina 1963, Vézina and Pech 1964, Mitscherlich *et al.* 1965 a).

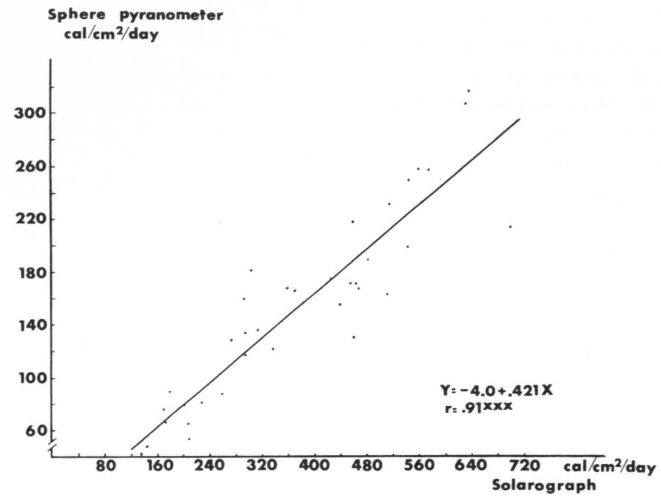

Figure 6. Comparison of solar radiation recorders. Metsä-Saramäki, July 18–August 3, August 7–11, 14–18, 21–25, 28–30 (total 35 days), 1967.

Since the sensor of the solarimeter is a horizontally placed plate, and of the pyranometer an almost perfect sphere, it is natural that the daily radiation values from the two measuring devices (in cal/sq. cm of sensor) are not of the same magnitude. The Bellani pyranometer also measures the reflected terrestrial radiation which is smaller than the total solar radiation (e.g. Berger-Landefelt 1965, Reifsnyder and Lull 1965); the range of the daily readings during the growing season vary from 60 to 280 cal/sq. cm/day, while the solarigraph records showed a range from ca. 120 to 720 cal/sq. cm/day. When the measuring angles of the sensors are transformed so that they register radiation from approximately the same direction (e.g. by covering all but the top of the metal pyranometer sphere), comparisons between these have resulted in well correlated daily radiation sums (r = +.93– +.98 (Pereira 1959, Shaw and Mc Comb 1959)).

The radiation meters used in this study were compared by installing them side by side at a level of ca. 1 meter at the experimental site in the Metsä-Saramäki clearing in late summer 1967. The correlation between the daily radiation values for the 35 days was high (r = +.91***; figure 6). From the results, it was concluded that the meters can replace each other in the present study. It should be remembered that the values of solar radiation, as other environmental factors measured in this study, are primarily used as relative values. In other words, it is concentrated in comparing the obtained daily relative values, and the conclusions are based on these.

Grave doubts can naturally be expressed, despite the discussion above, about the value of the records made by a single radiation meter installed in the open, in obtaining a picture of the total daily amount of radiation received by the trees in the experimental stand. For instance, a part of the needles in the tree crowns is always shaded, and the shaded part continuously shifts around with the relative movements of the sun (ANDERSON 1966, G. C. EVANS 1966). The role of reflected radiation from the sky is much smaller in the stand than in the open (GEIGER 1965, p. 298—309, REIFSNYDER and LULL 1965), and the part of solar radiation falling on the needles, when stomata are closed has a much smaller effect on photosynthesis than the radiation falling on needles with open stomata (POLSTER 1950, KRAMER and KOZLOWSKI 1960, p. 69—71). The spectrum of solar radiation also changes in the stand, depending on the elevation of the sun, in a way not fully computable from calorimetric radiation records; these changes may have an effect on the vital processes of the plant (cf. BERGER-LANDEFELT 1965, COOMBE 1966, HUGHES 1966).

322. AIR TEMPERATURE

Temperature is an expression of kinetic energy, which generally speeds up all biochemical and physiological reactions (e.g. WENT 1953, LEOPOLD 1964, p. 369—392). Although this rule holds true in nature only within relatively narrow temperature limits, and even then with considerable reservations, it nevertheless provides a basis for the relationships between the temperature factor and tree growth.

The rate of the complex series of activities resulting in the diameter growth of the tree stem depends on the temperatures prevailing in different parts of the tree. The temperature of a tissue (in this case the cambium) is always determined in nature by the total effect of two factors, the temperature of the substance surrounding the plant and the heat radiated to and from it. Also the heat conducted from or to the surrounding tissues affects the process (e.g. HUBER 1935, KOLJO 1950, RASCHKE 1960, and others). Therefore air temperature measurements in growth studies are often not directed to obtaining an as realistic picture as possible of the temperature of the plant under study, but rather to finding easily measurable indexes for the relative changes of the temperature of the plant studied (cf. FRITTS 1958, CLEMENTS 1964, MITSCHERLICH *et al.* 1965 b).

In the stand, tree crowns transfer heat during the day to the surrounding air, as they are themselves warmed. Also the soil surface is warmed by the radiation falling on it, and its surface layer conducts heat downwards into the soil and upwards into the air. In the night, the cooling of the soil surface and the cold air flowing from the crowns above, cooled by their own radiation, together cause a declining vertical temperature gradient (e.g. FOWELLS 1948, GÖHRE and LÜTZKE 1956, GEIGER 1965, p. 331—339, MITSCHERLICH *et al.* 1965 b, KERN 1966).

Although wind, especially in daytime, circulates the stand air rather efficiently (e.g. LEIKOLA 1967), the parts of the tree that are mainly responsible for diameter growth through their own processes (root system, stem cambium layer, and green crown) are subject to different temperatures, which causes great difficulties in the measurement.

To get a picture of the temperatures characteristic to the stand canopy, a weather chamber with a thermohygrograph (model Lambrecht no. 252) and a minimum and a maximum thermometer (cf. table 1, figure 3) was set up on top of the tower erected in the Metsä-Saramäki experimental stand. Another thermohygrograph was used in a weather chamber on the two-meter level. The chambers were of the international type used by the Finnish Meteorological Office, and they were erected and the instruments were run according to the general weather observation manual published by the Office (SÄÄHAVAINTO . . . 1951). Both thermohygrographs were calibrated once a day by minimum and maximum thermometers, and fortnightly by an Assman psychrometer (model Lambrecht no. 761). In the Huikko experimental stand, temperature measurement was carried out according to the same principles, but at the level of two meters only (temperature measurements by a thermohygrograph; cf. table 3, figure 5).

The daily minimum and maximum temperatures pertaining to the canopy temperature (at Metsä-Saramäki at seven-meter, at Huikko, at two-meter level) were selected as variables in the growth analysis computations (see chapter III 2). The daily temperature range was also computed for both stands, since some research workers (see e.g. WENT 1953, 1957, LEOPOLD 1964, p. 376—380) have reported its effect on growth, partly through thermoperiodism (WENT 1948, KRAMER 1958, and others), and partly through the effect of the energy it represents on the energy gained in photosynthesis in the daytime and lost in respiration during the 24-hour day (KRAMER 1957, HELLMERS 1962, RICHARDSON 1964).

Since the mentioned temperature values are not adequate to describe the daily temperature conditions, cumulative degree-hours were counted from three alternative threshold temperatures to make up for the deficiency.

From corrected thermograms, the temperature readings for every other (even) hour was read and the daily readings above the threshold temperature were added up; the sum was used in the growth analysis. Since growth was always measured round 8 a.m. (auxanographic tree growth measurements were made from daily maximum to daily maximum, chapter II 42242), this time was used as the limit between two days instead of the normal 12.00 p.m. The highest threshold temperature selected was + 10° C, the intermediate + 5° C which has generally been considered the lower limit of growth (cf. e.g. MAC DOUGAL 1938, HUBER 1950, LADEFOGED 1952), and the lowest ± 0° C. It must be emphasized that the criteria for choosing the temperature thresholds are largely arbitrary. We could just as well have tested e.g. LANGLET's (1936) and VOIGT's (1949)

+ 6° C, or the + 8° C used, for instance, by Mork (1941) in his studies concerning the height growth of spruce.

It is difficult to justify the linear combination of the quantitative level of temperature and its duration, implied by the concept of daily temperature sums, by evidence solely from our knowledge of the effect of temperature on plant reactions (see e.g. Went 1957, Daubenmire 1962, p. 180—187, Hellmers 1962, Leopold 1964, p. 364, 369—383). Still, temperature sums computed according to this very principle have provided a suitable scale especially for plant phenologic studies in the field (Nuttonson 1948, M. Schneider 1952, Schnelle 1955, p. 202—206, Sarvas 1967), and adequate evidence thus seems to be available to warrant the adoption of the described method of computing degree-hours to represent the daily temperature conditions in this study (reservations in the use of temperature sums are also discussed by Wang 1960).

323. TEMPERATURE OF THE CAMBIUM LAYER

In the discussion in the preceding chapter, we were led to assume that the activity of the cambium layer of the tree did not depend exclusively on the

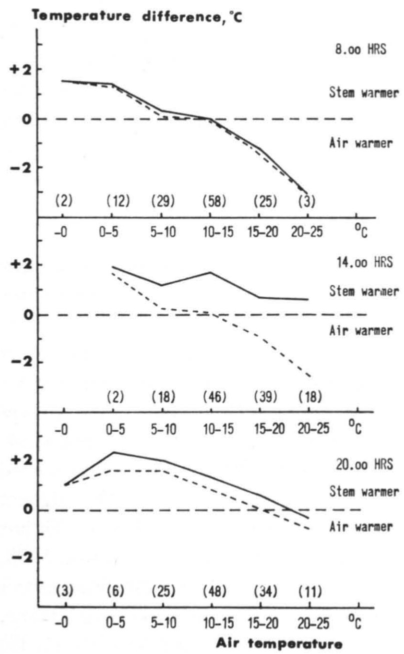

Figure 7. Temperature differences between the open air and the cambium layer of the sample tree 21—5 at various times of the day. The number of observations is given in parentheses. Solid line = south side, dotted line = north side. Records at 2 m. Metsä-Saramäki, April 24 to August 31, 1964.

Figure 8. Plastic chamber in the Metsä-Saramäki experimental stand. The girth bands are above, under, and in the chamber. Photo June 8, 1964.

indirect effects of the crown and root-system temperatures, but that, as has been reported already in early research, also the stem temperature may directly cause local diameter growth variations with fluctuations of temperature within certain limits (e.g. Schwarz 1899). This conforms well with all we know about growth and its dependence on temperature (e.g. Went 1953, 1957, Leopold 1964, p. 369—392).

To get a preliminary picture of the daily changes in the temperature of the stem cambium layer as compared to the air temperature, two mercury thermometers were installed in a tree at 1.3 meters at Metsä-Saramäki in 1964 (figure 3, no. 21-5). Holes were bored to the cambium layer on the north and south side of the stem. The thermometers were installed at a slant, and the holes were tightly sealed by grafting wax. Both thermometers were read regularly three times a day.

Figure 7 shows the differences between the cambium layer temperature and the 2-meter level air temperature. It can be seen that the tree is generally warmer than the cold morning air and cooler than the warm morning air. There is no difference between the temperatures on the opposite sides of the stem. At noon, the south side of the stem is always warmer than the air, and the north side colder, when the air temperature is sufficiently high. In the evening, the clear difference between the two stem temperatures is still found, but the whole

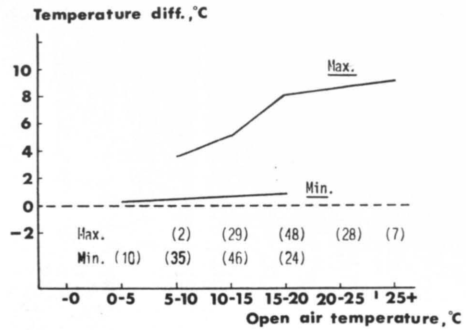

Figure 9. Differences between the open air (2 m) and plastic chamber daily minimum and maximum temperatures. The number of observations is given in parentheses. Records May 9— August 31, 1964.

stem is regularly warmer than the air (cf. e.g. HUBER 1935, p. 99—111, KOLJO 1950, HAARLØV and PETERSEN 1952).

To obtain more information about the effect of stem temperature on diameter growth, a plastic chamber was built around a tree in spring 1964 (figure 8). Two thermometers were installed on the stem, and a thermohygrograph and minimum and maximum thermometers protected from radiation, in the chamber.

Figure 9 shows the differences in the plastic chamber and outside air temperatures (daily minimum and maximum temperatures). In daytime, the chamber temperature has generally been clearly higher than that of the outside air. The higher the outside temperature, the greater the difference. The chamber temperature has probably been about the same as that of the outside air in the night. In daytime, the temperature of the chamber cambial environment has been higher than that of the outside, but in the night the temperatures of the two environments have been of the same magnitude. The effect of the stem temperature on diameter growth is discussed in chapter III 111.

324. PRECIPITATION

The main part of the water trees need for their physiological processes they take from the soil with their roots, and thus the effect of the rain falling on the ground on diameter growth must be considered indirect as compared with the soil water content. Since rain does, however, have a role in maintaining a soil water content favorable for tree growth, and since it also has a significant role in determining the hydrostatic diameter changes of the stem (chapter II 42242), daily precipitation was included in the study as an independent factor.

Precipitation falling above the stand canopy is usually divided into two main portions: that falling on the crowns, and that falling to the ground between crowns (e.g. STÅLFELT 1944, PÄIVÄNEN 1966). Since it is not intended to discuss

the distribution of rainfall in the stand as a separate problem, it has not been considered necessary to give the question more theoretical attention in this connection. Instead of recording the path of rain to the tree rooting layer, only the amount of precipitation falling on the ground layer has been measured (water dropping from the crowns + water falling between the crowns + water flowing down the stems from the crowns).

For measuring precipitation at the Metsä-Saramäki experimental stand, simple cylindrical summer rain gauges with a receiving area of 100 sq.cm were used in 1964 (e.g. SÄÄHAVAINTO . . . 1951). The gauges were emptied regularly after each rain in connection with other measurements, never more often than two times a day. To get a more accurate record of the time of the rain, one recording rain gauge (pluviograph) with a receiving area of 200 sq.cm (Lambrecht no. 1507, model Hellmann) was set up in the clearing. To measure the amount of water running down the tree trunks, rubber water-collection spirals were installed on seven trees in the experimental stand (figure 3, appendix 1). These spirals led all water running down the bark into small-mouthed, large-volume bottles.

The amount of precipitation falling on the soil surface in various types of stands has been extensively studied, also in Finland (LUKKALA 1942, 1946, SIRÉN 1955, SEPPÄNEN 1964, PÄIVÄNEN 1966), but the methodic part of the problem can still be considered partly unsolved (cf. GODSKE and SHIELDRUP-PAULSEN 1949). Also the accuracy of the methods used in this study includes a degree of uncertainty. The main structural sources of error of the summer rain gauges are summarized in the following list:

— The cylindrical gauge creates whirls of wind in the vicinity which direct a part of the rain drops away from the catching area and attract another part into the measuring cylinder. Many kinds of improvements, e.g. various sorts of wind shields and wind muffs have been tried (e.g. PLATT and GRIFFITHS 1964, p. 126—129).

— Some water is evaporated from the rain gauge in dry weather. This did not cause serious errors in this study, since the gauges were emptied quickly after each rain.

— A small amount of water adheres to the gauge at measurement.

— Litter and other particles may block both the recording and manual rain gauges.

The rain gauges were installed in the experimental stand according to the principles of systematic sampling. Twenty-four rain gauges were installed at a level of one meter at regular intervals on five parallel transects. The methods of ascertaining the representativity of the gauge placement will not be discussed in this context, as e.g. GODSKE and SHIELDERUP-PAULSEN (1949) have published a detailed discussion of the subject.

The amount of precipitation falling on the soil surface in the stand was calculated by converting the cubic centimeter quantities measured by the rain gauges into millimeters of precipitation. The stemflow down the trees was calculated by multiplying the average stemflow values for the sample trees by the number of

Table 5. Comparison of precipitation in the open and in the stand. Metsä-Saramäki experimental stand 1964. The method of precipitation measurement is described in the text.

Date, day, month	Ppt. in open, mm	Ppt. on ground surface in the stand, mm	Stemflow, mm	Ppt. on ground + stemflow, mm
1.5	4.8	4.08	0	4.08
3.5	1.3	0.53	0	0.53
4.5	3.9	2.43	0	2.43
7.5 I	6.0	4.77	.0022	4.77
7.5 II	3.5	2.37	.0004	2.37
9.5	12.6	8.19	.0276	8.21
11.5	1.8	1.14	.0013	1.14
12.5	1.0	.72	.0004	.72
14.5	6.0	4.51	.0317	4.54
28.5	2.0	2.34	.0006	2.34
29.5	1.1	1.65	.0018	1.65
1.6	4.2	3.68	.0003	3.68
4.6	3.5	2.68	.0006	2.68
6.6	1.2	.93	.0002	.93
9.6	5.5	4.67	.0296	4.70
11.6	5.4	5.75	.0853	5.83
12.6	5.7	5.43	.0003	5.43
16.6	2.8	2.24	.0005	2.24
18.6	5.9	3.58	.0082	3.59
20.6	1.2	1.03	.0001	1.03
25.6	.7	.61	.0001	.61
30.6	4.1	3.72	.0007	3.72
3.7	7.7	5.38	.0024	5.38
4.7	.4	.48	.0001	.48
9.7	12.8	11.07	.0053	11.07
10.7	1.5	.97	.0002	.97
13.7	.5	.48	.0001	.48
26.7	.8	.35	.0002	.35
28.7	2.5	2.49	.0003	2.49
29.7	.5	.58	.0001	.58
1.8 I	2.2	2.48	.0511	2.53
1.8 II	14.6	12.18	.0204	12.20
4.8	1.9	1.98	.0001	1.98
5.8	8.1	6.98	.0273	7.01
7.8	2.5	1.60	.0002	1.60
16.8	8.4	7.77	.0027	7.80
17.8	3.4	4.15	.0039	4.15
20.8	.8	.67	.0002	.67
21.8	2.7	2.87	.0010	2.87
22.8	2.2	2.71	.0022	2.71
23.8	.7	.59	.0001	.59
25.8	5.5	4.30	.0119	4.31
26.8	2.5	2.53	.0004	2.53
28.8	3.9	3.36	.0002	3.36
30.8	6.3	5.56	.0186	5.58
1.9	2.0	1.69	.0003	1.69

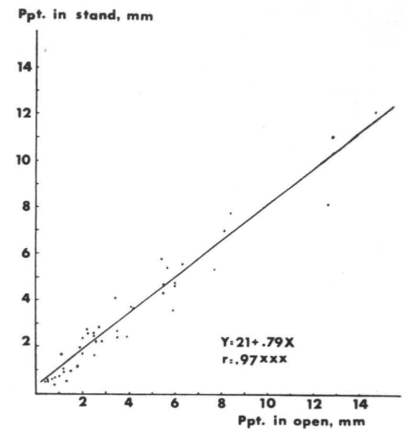

Figure 10. Comparison of precipitation in the stand and in the open. Metsä-Saramäki, 1964.

stems in the stand. The total amount of precipitation was then converted into millimeters of precipitation with the aid of the stand area figures. It was felt that this simplified method was justified by the relative homogenity of the stand, and since stemflow accounted for less than two per cent of the total free precipitation (cf. PÄIVÄNEN, 1966, p. 25—28).

The records derived from the rain gauge measurements at the Metsä-Saramäki experimental stand and the recording rain gauge at the nearby open-area plot in 1964 were examined in detail.

The correlation between the two sets of records is shown in table 5 and figure 10. The degree of correlation is high, and regression is linear. The results were considered an indication that both methods will produce the same relative data. In the following years (1965, 1966, 1967), precipitation measurements in the stand were discontinued, and precipitation was only recorded in the open. Each year's daily precipitation totals were used as such in growth analysis (chapter III 2).

325. THE SNOW COVER AND ITS MELTING

Among the environmental factors determining the beginning of diameter growth, the depth and the melting of the snow cover was recorded at the Metsä-Saramäki experimental stand.

The method of snow depth measurement was the same that e.g. SEPPÄNEN (1961) used in his studies. — In fall 1963, twenty-five 90 cm tall graduated rods were permanently set up in the experimental stand. Snow depth was read, on an average, every third day in March—April. The rods were placed systematically

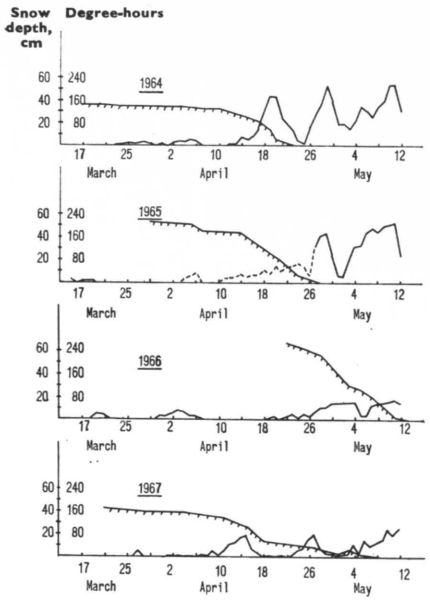

Figure 11. Melting of snow at the Metsä-Saramäki experimental stand during the four springs 1964—1967 (/////////). For comparison, daily degree hours at 2 m are also shown (————).

in the stand, on five transects, at a distance of two meters from the closest summer rain gauge. The mean of the reading was recorded as the mean snow depth of the day of recording.

The average depth of the snow cover in the Metsä-Saramäki stand during the 1964—1967 melting periods is shown in figure 11. The daily degree-hours (threshold $\pm$ 0° C) at the 2 m level are also shown to indicate the role of solar radiation and air temperature in the melting of snow (cf. Sirén 1955, p. 202—204, Seppänen 1961).

It can be clearly seen that at an adequate air temperature, the amount of thermal energy required for snow melt (ca. 80 cal/g, Geiger 1965, p. 219) is reached, and the snow cover disappears more rapidly, the more thermal energy is available for this purpose. — However, the considerable role played by not only solar radiation and air temperature, but also air humidity, in the melting of snow in the stand should be remembered. The rate of melting increases with increasing air humidity (Müller 1953). Also warm rains naturally accelerate this process.

In the spring, the snow cover slows down the thawing of soil both by reflecting a large part of the total radiation otherwise falling on the soil (freshly fallen snow up to 75—95 %, Geiger 1965 p. 15) and by consuming energy for melting. An early snow cover also protects the soil from freezing (e.g. Yli-Vakkuri 1960), and this speeds up the warming of the soil in the spring.

326. WIND

The turbulent flow of air is called wind. Undoubtedly wind can be considered a primary ecologic environmental factor (e.g. Daubenmire 1959, p. 269, Satoo 1962, Geiger 1965, p. 312—315), but its true nature as a factor of tree growth can not be explained simply.

A certain amount of air circulation is necessary for keeping up the gas exchange connected with the assimilation and respiration of a plant (e.g. Deneke 1931, Walter 1960, p. 386—388), but it is uncertain whether we can safely assume rates of circulation in nature below this minimum. The role of wind in determining the form of the tree stem will not be discussed (e.g. Büsgen and Münch 1927, p. 164—177, Jacobs 1939, Ylinen 1952). From the physiological point of view, it is difficult to point out a direct effect of wind on the diameter growth of trees. Wind does, however, have a role, by regulating evapotranspiration and the temperature of various parts of the tree, in the total environment of tree growth (e.g. Sirén 1955, Fritts 1958, 1960, Satoo 1962, Kern 1966).

This study was entirely concerned with measuring wind velocity, for practical reasons. The significance of wind direction was considered secondary, as compared to velocity, from the point of view of the objectives.

Two cup anemometers (model Casella no. 1208) were set up at the Metsä-Saramäki experimental stand in 1964, one on a two-meter pole on top of the tower (nine meters above ground level), the other two meters from the ground. Both meters were read three times a day (8 a.m. 2 and 8 p.m.) in 1964. Only the daily records for the meter on top of the tower were included in the growth analysis (chapter III 2). Recording the wind in the stand and the results obtained are also discussed in an earlier paper (Leikola 1967).

33. EDAPHIC FACTORS

331. SOIL TEMPERATURE

It is commonly held that soil temperature affects the beginning of growth not only of the tree root system, but also its shoots, the length of the growing season, and the rate and total amount of growth (Ronge 1928, Ladefoged 1939, Preston 1942, Sirén 1955, Fraser 1956, Richardson 1958, Yli-Vakkuri 1960, Lyr *et al.* 1967, p. 326—334, and others), although opposing assumptions have also been published (Huikari 1961, Huikari and Paarlahti 1967). For more information about the problem of the effect of soil temperature on the stem diameter growth of trees, this factor was included in the study.

The method of soil temperature measurement (exclusive of the surface soil to 5 cm) is easy as compared to the measurement of the other ecologic environmental factors. Still, several recording sites are necessary for reliable results, since soil temperature varies greatly even within small distances, mainly in relation to the composition of the surface layer of soil and the ground vegetation (e.g. TROEDSSON 1956, FRANSSILA 1960). We know that root temperatures closely follow those in the surrounding layer of soil (e.g. MAC DOUGAL 1938, LADEFOGED 1939), and we can therefore assume that the temperatures of the root tissues of trees are directly known from the changes in the soil temperature.

Soil temperature can be measured with for instance normal glass thermometers (e.g. LADEFOGED 1939, TROEDSSON 1956, FRANSSILA 1960, MITSCHERLICH *et al.* 1965 b), bimetal thermometers or resistance thermistors (SÖDERSTRÖM 1959, WILDE *et al.* 1964, p. 53—54, SIRÉN 1955). The meters can be placed along the sides of a soil pit, but a better and nowadays favored method is to use meters whose sensor can be installed at any desired depth in the soil. No considerable effect of the form or quality of the sensor's surface on the results of measurement have been found in cases where good contact is assured between the soil particles and the sensor's surface (SHANK 1956, PLATT and GRIFFITHS 1964, p. 115—119).

In this study, a thermograph (model Lambrecht no 256) with distant sensors was used in soil temperature measurement in both experimental stands. Two sites per stand were chosen to represent the typical ground vegetation and location in the area. The humus layer was removed in large discs, and on the sides of a soil pit, the lead-covered mercury sensors connected to the recorder by lead cables were installed. Great care was taken to place the sensors in a natural position and into good contact with soil particles, and to tamp the refill soil down well. The humus layer was then replaced, and the site was marked with sticks. Soil temperatures were recorded at depths of 10 and 30 cm from the surface of the mineral soil. The recorder readings were checked once a week in 1964—1966 by matching them to the readings of long mercury glass thermometers designed for soil temperature measurements. In 1967, a thermoelement thermometer (Cu-Ko; model Honeywell no. 2715-S) was used in calibrating the thermographs.

The daily temperature maxima at the depth of 10 cm were used in the growth analysis (chapter III 2). It was assumed that this depth represented the conditions in which the major part of the tree roots are active (e.g. KALELA 1949, p. 27—32).

Such already well-known facts as the daily minimum and maximum temperature time lag from the corresponding air temperatures, and the smoothing down of the temperature fluctuations with increasing depth (e.g. FRANSSILA 1960, GEIGER 1965, p. 142—167), were clearly seen in the results.

322. SOIL WATER CONTENT

To measure the soil water content, soil can be sampled regularly for determinations e.g. in a laboratory, or changes in the water content at various sites can be continuously measured in the field. In this study, the latter method was used, for instance to get rid of any sampling errors. In the Metsä-Saramäki stand, the electric gypsum-resistance-block meter described by BOYOUCOS and MICK (1947) was used in 1964.

The working principles of the meter are: gypsum blocks attached to leads, approximately the size of a match box, are buried in the ground. The block resistance is measured by an accurate Wheatstone bridge. With increasing soil moisture and gypsum block water content, ohmic resistance decreases. With decreasing soil moisture, ohmic resistance increases correspondingly. Calibrated conversion tables are used to compute the water contens.

Gypsum blocks change with time, their resistance and accuracy change also. Therefore only new gypsum blocks were used in the study, and each block was also separately calibrated before beginning field work. The calibration was carried out as follows: in winter 1964, samples were brought from the sites where the blocks would be used. The original metal calibration vessels were found unsatisfactory, and they were replaced by 10 × 10 cm peat pots. One block was placed in the center of each pot, the pots were filled with soil taken from the experimental stand and covered with a plastic cover. The pots were left to stand about half an hour in water, the resistance of the gypsum blocks was measured, and the pots were weighed. The pots were carefully dried at room temperature and weighed three times a day at the same time as the gypsum block resistance was measured. By this method, a calibration curve was drawn for each block. This calibration method was considered superior to those previously used. Water was evaporated from all the walls of the peat pot, and the gypsum block recorded therefore conditions representative of the water content in all the pot soil.

After the pots had dried out until the resistance of the blocks no longer changed, they were carefully dried, and the dry-soil resistance was marked zero. Dividing the difference in weight between the water-saturated and dry pot into hundred equal parts, a direct-reading soil-water-per cent conversion scale was constructed (cf. SIRÉN 1955, p. 244—248).

Water contents were measured in the Metsä-Saramäki stand at ten sites systematically arranged on the previously mentioned five rain and snow measurement transects (figure 3). The gypsum blocks were buried at each site to four depths: 5, 20, 30, and 50 cm from the surface of the mineral soil. The resistance of the gypsum blocks was measured regularly, every third day in 1964, and the mean of the values for the individual sites for a given depth was reported as the soil water content. In the other years, the soil water content was not measured.

The changes in the soil water content at Metsä-Saramäki, during the 1964 period, are shown in figure 12. Even though the soil water content is about the same through the growing season, changes were seen in the order of water contents among the depths of measurement. In early summer, the surface soil was moister than the deeper layers, but in late summer, no clear difference between the various depths was seen. — Although all gypsum blocks were moistened before placing in the soil, it is possible that the low soil water content in the early part of the summer is actually dryness of the gypsum blocks and not the surrounding soil.

The daily precipitation and soil-water content during the 1964 period is shown in figure 12. The heavy rains in the beginning of July have clearly in-

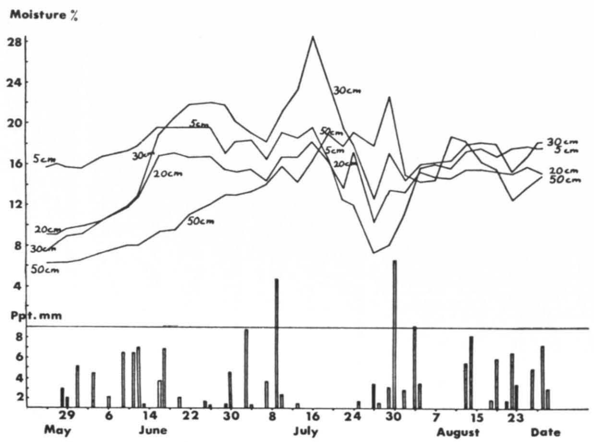

Figure 12. Variation of the average soil moisture content (% dry weight) at various depths at the Metsä-Saramäki experimental stand. For comparison, daily precipitation is also shown. Records April 25—August 31, 1964.

creased the soil water content, and drought two weeks later has decreased it again. The heavy rains in the beginning of August are responsible for the rise of the soil water content to the growing season average.

The accuracy of the gypsum blocks in soil moisture measurements has been criticized in the literature. For instance, it has been emphasized that the resistance values are susceptible to hysteresis (the dependence of the rate of a reversible reaction on the direction of the reaction) when the soil water content changes abruptly, that each block is different and acts differently, and that their ohmic resistance slowly changes in long-time use (e.g. Pereira 1951, Sirén 1955, p. 245, Platt and Griffiths 1964, p. 165). Various technical improvements such as the use of nylon or glass fiber blocks instead of gypsum ones have not been the answer (Colman and Hendrix 1949, Linder and Lötschert 1958, Barner 1965, p. 84—85). — The only good solution offered by modern technology for measuring the water content of mineral soils is the neutron scattering method, but the high price of the equipment has limited its use (Garder and Kirkham 1952, Sartz and Curtis 1961, Wilde *et al.* 1964, p. 44—50, and others).

Since the accuracy of the soil water content measurements was not satisfactory, the effect of this factor on tree growth was not studied. In the selection of the experimental stand at Huikko, most weight was placed on the as small as possible seasonal soil water-content changes. I believe that I succeeded in this attempt.

333. FREEZING AND THAWING OF THE SOIL

The freezing of soil as a growth factor is mainly connected with the warming of soil in the spring. So far as large trees are concerned, the problem has been previously discussed in chapter II 331. Since the methods used in measuring the thawing out of soil differ from those of ordinary temperature measurement, the ones used in this study are discussed here.

Two methods have been used to detect and measure frozen soil: digging soil pits, in which the depth of the frozen layer has been measured with color indicators or by other means (e.g. Ronge 1929, Yli-Vakkuri 1960), or frost rods especially designed for this purpose have been used (Yli-Vakkuri 1960, Mustonen 1965). The first of these two methods is more laborious since it requires digging soil pits into frozen soil. The latter requires an experienced field worker and is less well suited for use on coarse sandy soils (experimental stand) than on e.g. clay soils, for which the frost rod of Wäre, commonly used in Finland, has originally been designed (Wäre 1947).

The frost measurements in this study were made in 1964 and 1965 by the method described first. An area was chosen next to the Metsä-Saramäki stand resembling the tree stand and the soil of the experimental stand as closely as possible. Each frost measurement was made in four subjectively chosen sites. The 1964 results are given here:

Day	Depth of frost, cm from surface of mineral soil
April 4	1—9, none, 7—16, none
May 7	4—12, none, 9—15, 3—8
May 10	4—8, none, none, none
May 13	none, none, none, none

The 1965 means of four observations in the same area:

Day	Depth of frost, cm from surface of mineral soil
April 27	2—7
April 30	1—5
May 3	3—8
May 6	1—5
May 10	none
May 14	none

In 1967, frost measurements were made at Metsä-Saramäki by a different method. Since thawing exhibited great local variations, I considered increasing the number of observation sites necessary. 24 random tests were made with a stone rod (Viro 1947) in the area on each sampling day. The records are summarized in the following:

Day	Frozen soil in number of sites out of 24	% sites frozen
May 4	16	66
May 6	17	71
May 8	16	66
May 10	16	66
May 12	12	50
May 14	6	25
May 16	2	8
May 18	1	4

In the Metsä-Saramäki experimental stand, the soil thawed out about 2—3 weeks after the snow cover had disappeared (figure 11). This agrees with the results of other studies. E.g. Yli-Vakkuri (1960) reports that the soil had thawed out in pine stands in central Finland about two weeks after the melting of snow.

The soil frost observations also agree well with the soil temperature measurements. In 1964, the soil thawed out simultaneously as the daily 10 cm maximum soil temperature rose permanently above the freezing point (ca. May 10—13). In 1965, frozen soil was found five days after passing this temperature limit. In 1967, the soil thawed out at the temperature limit but five days later than in 1964.

4. MEASUREMENT OF DIAMETER GROWTH

41. DEFINITION OF THE CONCEPT

It is very difficult to give a universal definition of tree growth. Two principles are usually considered:

1. If the growing unit is the three-dimensional tree, growth is defined as a **change in tree dimensions** (Ilvessalo 1965, p. 106, and others). This is the usual mensurational definition, according to which tree growth may be positive or negative, permanent or temporary, without conflicting with the definition.

2. When growth is considered in the pure biologic sense, the basic concept is the ability of the living organism to transform the energy and matter it receives into new matter. An **increase of the amount of organic matter,** resulting from the activity of the living cells in the meristematic cells and tissues of trees, thus leads to the biologic growth of trees. This often results in permanent changes in the outward appearance of the tree and the organization of cells within it, even though this can not be considered a regular phenomenon (Whaley 1961,

and others). Biologic growth is basically cumulative and should therefore, considering the implicit meaning of the term, be applied only to the increase of organic matter described above. Any biologic reduction of organic matter should therefore be referred to by other terms.

In addition to biologic growth, changes in tree volume and form due to other reasons also occur. These differ from growth in that they are reversible, and their effect usually vanishes as soon as the factor causing them is no longer present. As a typical example, changes in water balance causes temporary fluctuations in turgor pressure and changes in the volume of various portions of the tree stem (Mac Dougal 1938, p. 21—30, Kozlowski 1964, p. 206—213, and others).

In this study, the biologic definition of growth will be used. When it is not clear that the increase of the organic mass of tree cells is the sole cause of an increase in stem volume, growth and diameter changes will always be discussed separately. Thus the stem may, for instance, grow even when its dimensions decrease.

The growth of the stem is traditionally divided into height, diameter, and form growth (e.g. Ilvessalo 1965, p. 106—107). The term **diameter growth** will be used to refer to the growth resulting from the activity of the secondary lateral growth tissue, the cambium, in the stem of a growing tree. **Height growth,** respectively, is caused by the apical meristematic tissue. When diameter growth has been measured only at one side of the stem in a radial direction, it is referred to as **radial growth.** When diameter growth has been measured as changes in stem girth, the term **girth growth** will be used.

42. DIAMETER GROWTH RECORDS

421. GENERAL

The simplest method to determine the diameter growth of trees is by using a common measuring tape (rod) or a caliper. The diameter (girth) of the bole is determined at intervals, and the differences are assumed to be growth. This method is relatively inaccurate, and it is best suited for the determination of increment during longer periods (5 + years). However, e.g. Ilvessalo's (1932) measurements of the annual duration of diameter growth indicate that satisfactory results are possible by this method. Specially made, accurate calipers have also been successfully used in studies of e.g. the hydrostatic changes of the tree diameter (Mac Dougal *et al.* 1929, p. 7—8).

Determining diameter growth from on the cores of increment borers, or disks or sectors sawed from the bole, is a popular method. Especially when primary emphasis is placed on growth during periods longer than one growing season, the method based on measuring the width of the annual rings is suitable. Textbooks of forest mensuration and detailed literature reviews by e.g. GLOCK (1941, 1955) and STUDHALTER *et al.* (1963) deal with the method.

When diameter growth is measured during basic periods shorter than one growing season, two methods are available: recording diameter growth by devices fastened on the tree bark, or measuring the new cell layers formed in the tree in regularly extracted microscopic samples. Both methods have been used concurrently in this study (chapters II 422 and II 423).

422. RECORDING DIAMETER GROWTH BY DEVICES FASTENED ON THE BARK

4221. Development of the recording devices

The first device suited for measuring diameter growth was a measuring tape. It was used by Marsham already in the 1740's (STUDHALTER *et al.* 1963). It was, however, soon surpassed by waxpaper and metal bands, especially designed for the purpose, which were tightened around the tree trunk by a spring or a rubber strip. Growth during the desired period was read directly from the difference in the distance between the ends of the band. Although excellent results were obtained by these devices — especially the measurements of tree diameter changes during the growing season by v. Mohl and Christison (WIELER 1898) deserve to be mentioned — Pfister is credited for the first device suited for the accurate measurement of diameter growth. The device was presented to the public in 1883 (BÖHMERLE 1883). The device consisted of two decimal levers connected to a steel band tightened around the tree stem. The levers permitted reading the changes in the tree diameter on a scale to the nearest 0.01 mm.

Ten years later REUSS (1893) described a diameter growth meter constructed on a basis totally different. This instrument was screwed on the tree stem; it had a single feeler resting perpendicularly against the bark, and showing the local changes in the tree radius on a micrometer scale.

A model of the first recording diameter-growth meter was already described in 1890 (FRIEDRICH), and a few years later the instrument was complete and ready for use (FRIEDRICH 1897). A nickeled steel band tightened by a weight rested on small rollers attached to the tree. Band movements were vertically transmitted to a stylus, which recorded growth on a revolving drum on fifteen times the actual scale. Later, the inventor developed the device toward increasing accuracy (FRIEDRICH 1905, also KORSTIAN 1921, MITSCHERLICH *et al.* 1966).

In 1919, MALLOCK, in England, described an interesting diameter growth meter: an optical device. An invar band was tightened around the tree stem, and a prism, wich could move in its frame and could be adjusted with micrometer screws, was attached to the band. A small leveling instrument some meters from

the stem caught the ray of light reflected by the prism, and the changes in tree girth could be read with great accuracy, as the prism turned.

Two years later (1921), one of the most notable scholars in the field of tree diameter growth, MAC DOUGAL, published a report about a recording diameter gage constructed in 1912. The device rested on a belt made of invar metal plates; the sensor rested on the two opposite sides of the tree stem. The movement of the sensor could be read on a drum to an accuracy of 0.01 mm.

Thus the basic models of diameter growth recorders, the girth band, the sensor meter measuring radial diameter growth, and the optical meter, were distinctly different types of devices in the beginning of the 1920's, and later developments have been merely technical. Recording devices working on the girth band and sensor principles had also been successfully used.

The Reuss sensor meter was considerably improved by REINEKE in 1932, when he replaced the growth detector by an indicator device commonly used in mechanical engineering. Accuracies of ca. 0.01 mm were attained, and since the only part fastened on the tree was a small perpendicularly bent hook, it was possible to measure a great number of trees with one indicator, cheaply and in a short period of time. This was a considerable advantage, since it was now possible to measure large numbers of trees simultaneously instead of a few only. The device has been further improved and modified by e.g. DAUBENMIRE (1945), TRYON and FINN (1949), WARRACK and JÖRGENSEN (1950), BELYEA *et al.* (1952), Arnberg and Karlberg (KARLBERG 1954), ALVIM (1964), BLUM (1966), HENGST (1966), and SCHELEV (1966). These include a resting plate and a handle for the indicator, replacing one hook by two or three screws far from the point of measurement, and a metal or other plate for resting the sensor on the tree. The popularity of the indicator-meter is indicated by the large number of its users; in addition to those already mentioned, they include DILS and DAY (1952), JACKSON (1952), CANTLON (1953), EGGLER (1955), BOGGESS (1956), TURNER (1956), WILHELMI (1956), AHLGREN (1957), MC CLURKIN (1958), SMALL and MONK (1959), KERN and MOLL (1960), BUELL *et al.* (1961), KERN (1961, 1965), KRAUS and SPURR (1961), POPESCU-ZELETIN (1961), HARKIN (1962), KÜBLER and TRABER (1964), ABETZ (1966), DELLA-BIANCA and DILS (1966), FRASER (1966), and MITSCHERLICH *et al.* (1966).

A device modified after Friedrich of a very accurate girth growth meter was described by ROMELL (1925); after the second World War, growth bands have become popular in various silvicultural studies. A simple girth band has been constructed from aluminium by HALL (1944), LIMING (1957), and MESAVAGE and SMITH (1960). Brass and steel bands have been used in Finland by e.g. HUIKARI (1961) and HUIKARI and PAARLAHTI (1967). Among the recent users of the girth band method, HARMS (1962), BASSETT (1966), and HOYLE (1966) deserve to be mentioned.

Wide-scale use of various growth recording devices has been prevented by the high price of the instruments. Among the other studies than his own, where Friedrich's devices have been used, the through work of NAKASHIMA (1924) should be mentioned. A useful and accurate device working on the same principle has been developed by Mitscherlich (MITSCHERLICH *et al.* 1966). The device designed by Mac Dougal has been used by e.g. KORSTIAN (1921), PEARSON (1924), LODEWICK (1925), HAASIS (1932, 1933, 1934), KIENHOLZ (1934), BEILMAN (1943), FRIESNER and WALDEN (1946), and REIMER (1949). Popescu-Zeletin has also described a modification of the growth recorder (e.g. POPESCU-ZELETIN 1964) used by himself and his coworkers to record the growth of forest trees (POPESCU-ZELETIN and MOCANU 1962, POPESCU-ZELETIN *et al.* 1962).

Fritts introduces a new model of the growth recorder based on the old Reuss' principle (FRITTS and FRITTS 1955). The sensor of the device transmitted the changes in the stem radius from one point on the bark only. This device has also been used elsewhere (KOZLOWSKI *et al.* 1962, KOZLOWSKI and WINGET 1964). The device used in this study is constructed according to the same principle (chapter II 42231).

The optical growth meter has had little use. I need to mention only the studies of KUROIWA with a device of his own construction (KUROIWA 1957, 1958, 1959, KUROIWA *et al.* 1958).

Other growth meters than the ones discussed have received less attention (e.g. NAJERA 1926, PYKE 1941). A new line of development does, however, deserve to be mentioned: the electric growth meter described by PHIPPS and GILBERT in 1960 and later developed by e.g. IMPENS and SCHALK (1965).[1] The indicator of the device is a sensitive potentiometer coil screwed on the tree on a support. The movements of the sensor cause changes in the induction field of the surrounding coil, measurable with a sensitive voltmeter far from the sensing site. Several sensors can be simultaneously connected to a central recorder.

4222. Recording device terminology

The terminology of the devices used in measuring tree diameter growth is rather heterogenous. The inventors of the first devices had their own names for their devices, such as »Zuwachsuhr» (BÖHMERLE 1883), »Zuwachsmesser» (FRIEDRICH 1890), and »Zuwachsautograph» (FRIEDRICH 1897, 1905). In the beginning of this century, all these devices were called »auxanometers» or »auxanographs» according to the Greek word for growth. This term followed the growth measurement terminology of general botany (cf. e.g. RUGE 1961). MAC DOUGAL (1921) called his own device a dendrograph (dendron = tree), and REINEKE (1932) further developed terminology along this line and called his indicator meter a »dendrometer».

[1] The first to report on an electric growth meter usable in the field are probably NINOKATA and MIYAZATO (1959).

Traditionally, forest mensurationists have called a device for measuring from the ground the tree diameter at an arbitrary level, a dendrometer. The device works according to the principle of sighted parallel stem tangents (definitions in e.g. LÖNNROTH 1930, GROSENBAUGH 1963). Nevertheless, the terms »dendrometer» and »dendrograph» were quickly adopted in English-language publications (the scholars using the indicator growth meter and e.g. KRAMER and KOZLOWSKI 1960, p. 36—38). These terms were adopted by German scholars in the 1950's (e.g. WILHELMI 1956, 1959, KERN and MOLL 1959, KERN 1965, MITSCHERLICH *et al.* 1966) and thus refer to two devices constructed for different purposes and on different principles.

For consistency, general growth measurement terminology will be used in this study. The indicator growth meter will be called auxanometer and the recording growth meter auxanograph by their original names.[1] We will thus also avoid any confusion with the »dendrometer» term used in its original context to mean a »distance caliper» (cf. ILVESSALO 1965, p. 60—63).

The simple device for measuring girth increment will be called a »girth band».

4223. The growth-measurement devices used in this study

42231. Auxanograph, or growth recorder

The growth recorder used in this study has been developed from the device described by FRITTS and FRITTS (1955) which they call a dendrograph. A considerable role in the technical designing of the instrument was played by Mr. A. Silvonen who directed the construction of the recorders at the precision-mechanical workshop of Oy Physica Ab. Figure 13 shows the growth recorder installed on a tree stem.

The principal differences from the Fritts' device are:

— The height of the revolving drum has been decreased from 20 cm to 10 cm. The recording marker is thus practically on a level surface, and the marker resistance is always the same. If the angle of the recorder is too great as compared to the diameter, the marker must rise against considerable resistance from the lower part of the paper to the center and go down against much smaller than normal resistance. In the top part of the paper, the phenomena are reversed.

— The sensor has been made of two parts to allow the adjustment of its length while mounted and also the return of the recording marker from the top to the bottom position with ease.

— The sensor ends in a steel ball, on which the steel end of the lever rests. The friction at the

[1] The term »dendroauxograph» introduced by POPESCU-ZELETIN in 1964 is a possible alternative. The term has not been used in this study because of its length.

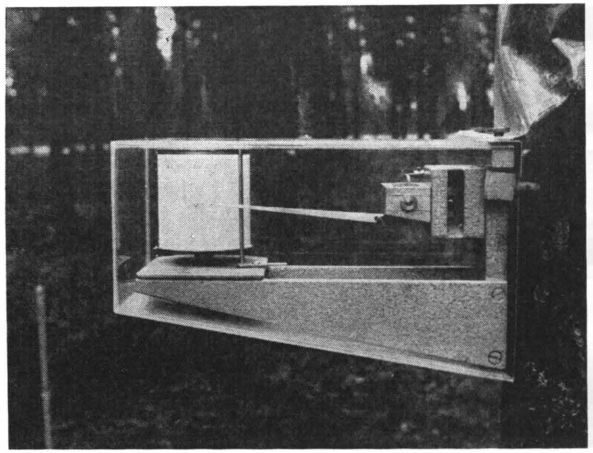

Figure 13. Mounted auxanograph. Photo June 8, 1964.

lever-sensor junction is thus small, and the change of the degree of magnification due to wear is avoided.

– The lever shaft is attached with adjustable screws to allow changes in the degree of magnification.

The device is attached to the tree by first boring the holes for the attaching screws with the help of a model plate. The sensor resting point is carefully evened off, avoiding excessive bark damage. The springs are tightened, and the length of the sensor is adjusted. The growth recorder is protected from weather by a simple plexyglass cover.

The device is lubricated once in about two months with tower clock oil which does not harden in the cold. A few drops are put into the ends of the shafts. Otherwise the device is cared for according to usual maintenance directions for meteorological instruments (Säähavainto . . . 1951).

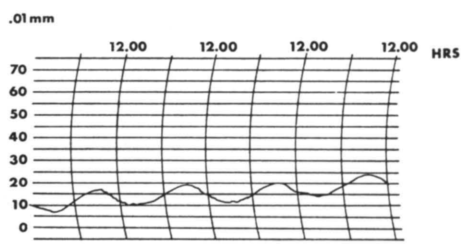

Figure 14. An example of the auxanograph record (auxanogramme): diameter changes of the sample tree Au-1 at the Metsä-Saramäki experimental stand during May 24–27, 1964.

Figure 15. Mounted girth band. Photo June 8, 1964.

The recorder paper was manufactured by Euran Paperi Oy. A sample record (figure 14) is shown for tree no. Ag-1 for the diameter growth from May 24 to 27, 1964.

42232. Girth band

The girth band used in this study differs somewhat from the models described elsewhere in that a separate device is used for the actual measurement (cf. Huikari and Paarlahti 1967). The band itself is not removed for measurement.

A 60 to 80 cm long flexible band made of steel used for measuring tapes or clock springs is fastened on an iron clasp. The band has been punctured at intervals of 2.5 cm, and it is attached to a steel spring used for tightening the device.

When the band is installed on a tree, the bark is first smoothened at the area of measurement. The end of the band is drawn through the clasp and the hook at the free end of the spring is fastened to the holes in the band. The changes in tree diameter are measured with a sliding caliper as the distance between a notch in the clasp and one of the holes. As the tree diameter increases, the measurements are made to the closest hole from the clasp.

When the band is well lubricated, it will not be damaged by weather conditions, and it shows the girth dimension changes accurately so that the accuracy of measurement is that of the sliding caliper: 0.1 to 0.05 mm.

Figure 15 shows a girth band installed on a tree. Plastic or other substances were not used under the band to facilitate the band movements (cf. Huikari and Paarlahti 1967, p. 32—33).

4224. Errors in recording growth

42241. Errors due to growth-recording devices

Several types of sources of error are inevitable in tree diameter growth measurements. A number of these result from the irritation caused by the measuring device in the living tissue. This may lead to abnormal growth, and generalizations of the growth measurements may become questionable.

The most serious disturbances will occur in normal tree diameter growth, when the growth-measurement device is fastened on the stem so that the cambium layer is damaged. The effects of the devices installed entirely on top of the bark are obviously much smaller.

The problem of abnormal growth caused by the fastening screws of the growth meters, and how this is accounted for, is touched in almost every publication in this field (e.g. Reineke 1932, Young 1952, Abetz 1966, Kern 1966), but no universal answers have been obtained. As examples of the discussion, Reineke (1932) concludes on the basis of data from 120 Douglas-firs (*Pseudotsuga Douglasii* Carr.) that the effect of a strange body (in this case, the auxiliary hook of the sensor of an indicator) on the cambium is relatively local in trees of this species. He considers a distance of .65" (ca. 1.65 cm) a sufficiently safe distance between the fastening screw of the growth meter and the site of measurement. Kern (1966 p. 156), on the contrary, reports, on the basis of his measurements concerning nine spruces (*Picea abies* (L.) Karst.) and eight firs (*Abies alba* Mill.), that even the distance between the fastening screws and the site of measurement in an auxanometer model Arnberg (ca. 5 cm) is too small to prevent disturbances. Abetz (1966) arrives at the same conclusion. Blum (1966) found that in the 236 yellow birches (*Betula alleghaniensis* Britt.) he measured, abnormal diameter growth was found no farther than at the vertical distance of ca. 1.25" (ca. 3.17 cm) from the fastening screws.

In connection with this study, auxanograph screws were attached on four pines growing near the Metsä-Saramäki experimental stand in late winter 1965 in a similar pattern as those actually on an auxanograph. Two trees were felled after one growing season and the other two after two, in November. The screw attachment sites were cut out, and the last annual rings were measured and photographed in the laboratory. The effect of the screw could be seen in the immediate vicinity of the damage (figures 16 and 17), but at a horizontal distance of ca. 1.5 cm and a vertical distance of ca. 2 cm, the last annual ring

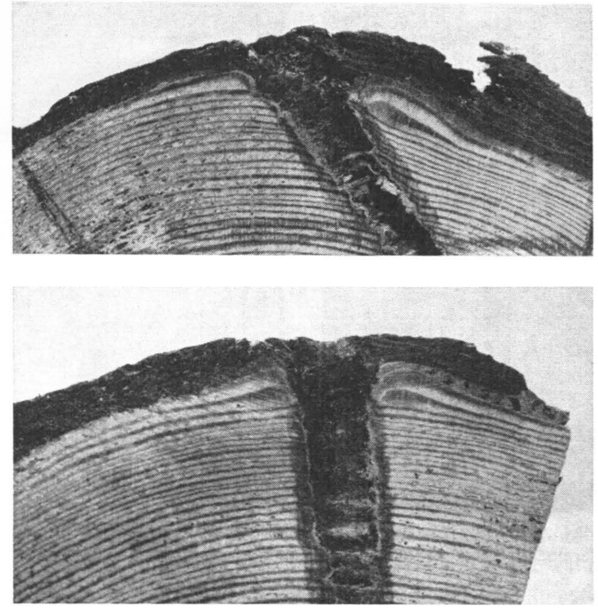

Figure 16. Radial increment due to disturbance by auxanograph screw, after two growing seasons. Pine, Metsä-Saramäki. Cross cut. Photo: Institute of Photography, University of Helsinki.

was quite normal. These observations indicate that the difference between the fastening screws and the sensor in the auxanograph used in the study (6 cm horizontally and 12.5 cm vertically) is sufficient to totally eliminate any errors in the measurement of pine diameter growth caused by the irritation by the screws.

The mechanical decreasing effect of the slight pressure of the girth band or the sensor on cambial growth also remains unknown. Even the pressure exerted by the band is rather small, since the spring tension is under one kilopond.The pressure exerted by the bark on the growing tree is, as we know, considerable (Schwarz 1899, Büsgen and Münch 1927, p. 179, and others). E.g. the experiments of Brown and Sax (C. Brown 1964), using detached cambium cell and undetached cambium tissue cultures, placed under various pressures against the tree, indicate that considerable external pressures are a normal environment for the cambium layer and that their absence leads to abnormal growth.

Since the growth-measurement device is left in the field for long periods of time, it is exposed to great changes in temperature. Attempts have been made to avoid systematic errors due to heat expansion by following two principles:

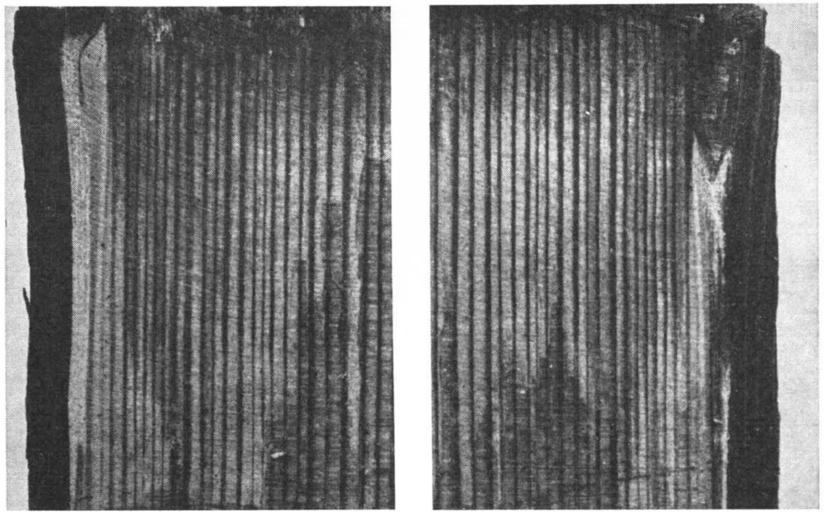

Figure 17. Radial increment due to disturbance by auxanograph screw, after two growing seasons. Pine, Metsä-Saramäki. Radial cut. Photo: Institute of Photography, University of Helsinki.

a suitable material has been selected for the device, or known temperature errors have been eliminated in the computing work later on.

The simplest method is to use materials in the auxanometer that exhibit small volume changes with changes in temperature. The materials mainly used in girth growth measurement devices are aluminum, steel, tungsten, and invar metal (Böhmerle 1883, Mallock 1919, Romell 1925, Mac Dougal 1938, Fielding and Millet 1941, Mitscherlich *et al.* 1966, and others).

The raw material used for the girth bands in this study was high quality measuring tape steel and clock spring steel with a heat expansion coefficient per degree C of 0.0000123 (Insinöörin . . . 1953). An 80 cm long band thus expands ca. 0,39 mm, as the temperature rises 40° C. Since the accuracy of band measurement is 0.1 mm, this error is at the most three units. No temperature corrections have, however, been made in this study, and the heat expansion factor must therefore be kept in mind, when the realibility of the results is considered.

In auxanometers with a single sensor, the best results are secured by constructing the stationary body and the mobile sensor in such proportions and out of such materials that any heat expansion disturbances will be eliminated. Thus an approximately correct reading will be obtained in any temperature conditions.

The temperature correction problem in the auxanograph work in this study

has been carried out in the following way. Since the body part of the device and the marker and its lever are both made of aluminum, no heat expansion differences will occur in the device from the body surface towards the tree stem to the marking point. The length of the aluminum sensor between this surface and the tree is ca. 23 mm, and of the iron fastening screws ca. 45 mm (mean) when they are attached to the tree. The heat expansion differences are thus almost canceled (the example at 40° C difference):

Sensor:

0.0000238 (alum.) × 40° C × 23 mm = 0.0219 mm

Fastening screw:

0.0000123 (iron) × 40° C × 45 mm = 0.0222 mm

Heat expansion — 0.0003 mm

Computational heat expansion correction is another theoretically correct method in eliminating the error. Determining the correct temperature correction factor for each growth measurement requires, however, both additional computing and the data about the band temperature at the time of measurement. This is seldom easily obtainable, since e.g. applying the values from the protected thermometers to the metal bands in sunshine leads to errors in sunny weather. The subjective use of the extreme temperatures may also lead to greater errors than the use of uncorrected band readings. One should also keep in mind the great possible temperature differences among various parts of an individual band.

The other structural problems connected with auxanometers, the deadening of the springs, the expansion of the recording paper in humid conditions, the sinking of the marker due to a weight increase following the absorption of water from the air in rainy weather, etc. are difficulties common with all meteorologic field instruments. It has usually been possible to take precautions to avoid these e.g. by a suitable selection of the quality of materials (Säähavainto . . . 1951, Platt and Griffiths 1964).

42242. *Errors due to hydrostatic tree diameter changes*

The water-conducting tissue of plants is a continuous hydrostatic system, in which water molecules, connected to each other by cohesion, move upwards from the roots in a transpiration suction stream (Kramer and Kozlowski 1960, p. 329—341, Kozlowski 1964). When the amount of water lost in transpiration equals the water taken up by the root system, the conducting tissues are normally tensed by turgor pressure. When transpiration from the leaves increases or water uptake by the roots decreases, water deficiency (dehydration) in the stem follows almost immediately, causing a decrease in the cellular turgor pressure. The decrease of cell volume due to this phenomenon is seen as shrinkage of the tree stem (HAASIS 1934, MAC DOUGAL 1938, KOZLOWSKI 1964, p. 170—219, and others).

The basic daily pattern of expansion and shrinkage is fairly similar in most trees. The largest stem diameter is recorded in the late part of the night, and a decrease will be seen immediately after sunrise. The decrease continues until transpiration has decreased after the stomata are closed or until the water-conducting cells of the tree stem have attained their minimum volume, and their cell walls mechanically prevent shrinkage. After sunset and the cooling of air in the evening, transpiration will generally decrease and the stem diameter will again increase with the increase in the turgor of the water conducting cells.

The daily pattern described above was first reported by Kraus in 1879 (e.g. FRIEDRICH 1897, MAC DOUGAL *et al.* 1929, KERN 1965). Since then, practically every scholar using auxanographs to study growth has found the same phenomenon. The matter has been thoroughly discussed by e.g. HAASIS (1932, 1933, 1934), Popescu-Zeletin (POPESCU-ZELETIN *et al.* 1962), KOZLOWSKI and WINGET (1964), and KERN (1965). The degree of daily shrinkage has been found to depend quite clearly on the weather conditions (in sunny and dry weather, shrinkage is considerable, in rainy and cloudy weather, slight). But also soil moisture, the position of the tree in the stand, the tree species, and the rate of tree growth have an effect on the shrinkage. — It can be said that studies concerning the hydrostatic diameter changes of trees are carried out in the field of water metabolism problems and are connected to growth studies only in their methodic aspects (e.g. MAC DOUGAL *et al.* 1929, KRAMER and KOZLOWSKI 1960, p. 342—367).

Since auxanometers fitted on the tree bark measure all diameter changes, including those due to growth and those due to hydrostatic changes, a major difficulty encountered by scholars has been the elimination of the water-regime effects in the growth records.

A convenient method is offered by the possibility to register growth at standard hydrostatic conditions (e.g. FRASER 1952, KERN 1961, 1966). Reading the bands and auxanometers is recommended in the morning at the time of maximum stem diameter, before the rising sun has started to cause shrinkage. This solution is quite practicable. However, the time of reading would have to be changed, as the time of sunrise changes during the growing season. So far as is known, this method has never been tried. Instead, the readings have been made at a standard time; the resulting error will be small.

Another solution is the use of various comparative data, consisting of diameter changes due to growth plus hydrostatic changes and those due to hydrostatic changes only. HAASIS (1934) and MAC DOUGAL (1936, 1938) have experimented with several comparative methods using variously treated trees. Pruning the lower part of the tree, cropping the crown, and removing the needles decreased the hydrostatic changes, but probably also decreased the rate of tree growth. Using telegraph poles as comparative material was also tried, but the results were not encouraging.

MITSCHERLICH and his coworkers (1966) have tried out a method in which the experimental tree was girdled, and the diameter changes were measured with an auxanometer model Arnberg above and below the girdling site. No diameter growth would occur below the girdle, but the water movement would continue to the crown. The first year of study provided excellent comparative data, but in the next, extremely dry year (1964) the part of the stem below the girdling site shrank permanently in late summer and did not attain its spring diameter before the end of September. The authors conclude that the method will not lead to reliable results in extraordinarily dry years.

The best method to obtain comparative data is probably offered by the method first proposed by HAASIS (1933). He installed three auxanographs above each other on a single tree, one of which measured tree diameter changes normally on top of the bark, another from the surface of the wood, and the third at a depth of ca. 5 cm, at the boundary of sapwood and heartwood. This enabled sufficiently reliable records of the center cylinder of the stem as separated from the actual growth.

Computational corrections have sometimes been recommended for the daily shrinkage (e.g. KERN 1961). This is a fairly simple process when we wish to compare growth recorded in the morning to that recorded in the evening, but comparisons between days may prove difficult because of differences in the hydrostatic conditions; except for a small number of obvious cases, daily hydrostatic changes have contributed to all changes in diameter.

Comparisons based on microscopic samples taken at regular intervals have also been recommended as supplementary data in growth studies. It is possible to distinguish in these samples the cell layers formed before sampling, measure their total dimensions and thus obtain a picture of the true diameter growth of the tree. Growth measurements based on taking microscopic samples is discussed in detail in chapter II 423.

The basis of the growth records used in this study was the maximum diameter in the auxanograph records, occurring at 7-8 a.m. and the tree diameter measured with the girth bands at the same period. Computational corrections were not made, in fear that in converting the basic growth curves without adequate basic data, relevant information (growth resulting from cambial activity) could be unintentionally lost. This introduces a degree of risk in discussions of the results of the study. — The question of hydrostatic tree diameter changes will be dealt with again in chapter III 221.

42243. Errors due to diameter shrinkage at freezing

Sudden decreases of tree volume at sufficiently low air temperatures are mentioned in several growth studies (Friedrich 1897, Romell 1925, Beilmann 1943, Friesner and Walden 1946, Daubenmire and Deters 1947, Byram and Doolittle 1950, Fritts and Fritts 1955, Kuroiwa 1958). The first specific study of this problem was published by Friedrich in 1907. Later, the problem has been discussed by e.g. Small and Monk (1959), Kübler and Traber (1964), and Winget and Kozlowski (1964).

With no doubt the phenomenon is connected with the freezing of the stem cells. This is indicated by the results pointing out the trigger temperatures of freezing shrinkage, from -7° C (Beilmann 1943) to -4.4° C (Small and Monk 1959). Tree shrinkage has been found directly related to decreases in temperature and somewhat different in different tree species (Winget and Kozlowski 1964). The phenomenon is most reliably explained by the formation of ice with a lower osmotic value than in the vacuole, in the intercellular spaces as the stem freezes. Due to the decreasing vapor gradient from the vacuoles to the intercellular spaces, water gradually starts to flow out of the cell, and the volume of the whole tissue decreases (e.g. Levitt 1956, Kübler and Traber 1964). This phenomenon which is common in all plants, is, in trees, mainly found in the phloem portion (Marvin 1958, and others).

In the course of this study, sample trees were found to shrink in the late

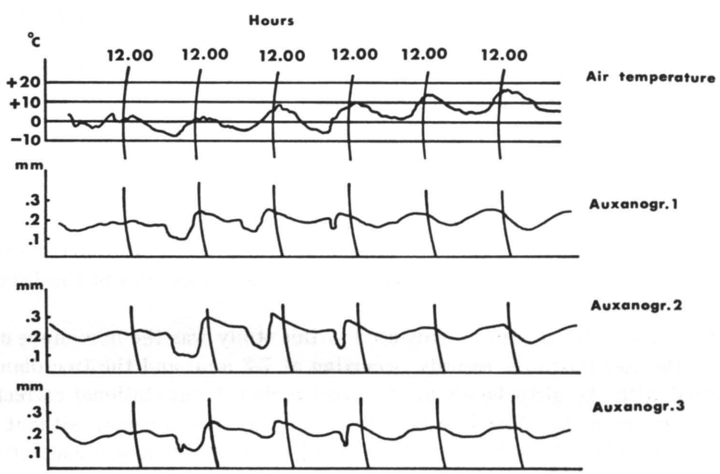

Figure 18. An example of stemwood shrinkage at freezing of sample trees Au-1, Au-2, and Au-3 at the Metsä-Saramäki experimental stand. For comparison, air temperature at 2 m is also shown. Records April 23—29, 1964.

night at sufficiently low temperatures. An example of the nature of the phenomenon is provided by the stem diameter changes registered by three auxanographs during the last week of April in 1964 at Metsä-Saramäki, shown in figure 18. It can be clearly seen that stem shrinkage has lasted only through the period of air temperature below the freezing of water, and the stem has quickly attained its earlier dimensions after this period.

Freezing shrinkage is rather easily eliminated in growth records as a source of error. During the growing season, stem freezing is, of course, exceptional, and at periods of stem freezing we can be sure that no diameter growth will occur. Even in these cases, distinguishing freezing shrinkage from other diameter changes is easy and certain to the naked eye. It is sure that of the factors causing stem diameter changes, the shrinking of the stem at freezing has had no effect on the measurement of growth and the conclusions drawn from the results.

42244. Errors due to the growth of the phloem and the cork layer

The cambium layer of trees produces xylem on the side of the wood and phloem towards the tree bark. According to the majority of published observations, phloem growth starts in the spring slightly later than that of the xylem (Esau 1939, Bannan 1955, 1962, Srivastava 1964). The seasonal rhythm of phloem growth is distinctly different from the pattern common to xylem growth. The formation of cells starts very slowly in the spring and continues without interruptions through the summer to the end of the growing season. E.g. Bannan (1955) reports that the cambium layer of Eastern white cedar (*Thuja occidentalis* L.), growing near Toronto, formed 30—60 xylem cell layers before the end of June, but only two cell layers of phloem, on an average. The cessation of phloem growth occurs at the same time as that of xylem or later (Lodewick 1927, Bannan 1955, 1962, Trendelenburg and Mayer-Wegelin 1955 p. 379).

Since auxanometers installed on top of the bark register all diameter growth of the tree stem, phloem growth is also included in the records. Many scholars have pointed to this error, but a useful method of correction has not been developed (Mac Dougal 1938, Kern 1965, 1966). Therefore this factor must also be kept in mind as a source of error in discussing the results (e.g. Abetz 1966).

Fortunately, phloem growth is small as compared to xylem growth (Lodewick 1928, Esau 1939, H. Schneider 1952, Bannan 1962, Srivastava 1964). We know that phloem growth varies annually much less than xylem growth (Holdheide and Huber 1952, Bannan 1962). It does, however, seem obvious that the basic ecologic requirements for phloem growth are similar to those of the xylem. In other words, good tree growth conditions are also favorable for phloem growth. The danger of erroneous conclusions seems smaller on the basis of this line of thought than would be expected on the basis of the total increment of the phloem.

The surest way to distinguish xylem growth from phloem growth is to measure the increment in tissue samples extracted from the stem. This method is discussed in detail in chapter II 423.

Bark growth resulting from the activity of the cork cambium is a source of error comparable to phloem growth. However, it amounts to so little during the year, as compared to the increment of the xylem, that it will not be discussed in any detail (cf. Srivastava 1964).

42245. Errors due to local variations in cambial activity

It is commonly known that the thickness of the annual ring varies locally in both the horizontal and the vertical direction. A part of the variation is irregular, and a part systematic, depending on tree age, stage of development, prevailing wind direction etc. (e.g. Mikola 1950, Holmsgaard 1955, Trendelenburg and Mayer-Wegelin 1955, p. 380—391). In the following discussion, the danger caused by the phenomenon to the generalization of conclusions in growth studies will be carefully considered.

Comparative records have been made by various scholars in different conditions from cores of increment borers taken next to each other and from the sensing points of auxanometers. These agree fairly well with each other. E.g. Lodewick (1925) reports that the cambium layer and the annual ring formed during measurement below a Mac Dougal's auxanograph exhibited no differences from the tissue next to the point of measurement. Fowells (1941), in a study comparing six tree species, found that the correlation between an increment core and the auxanometer reading at the same site on the stem was high ($r = +.936$, $n = 31$). Similar experiments carried out with spruce and Douglas-fir have given similar results (Warrack and Joergensen 1950, Kern and Moll 1960). If the distance between the compared points is increased to a few centimeters, the correlation seems to be poorer. This was already noted by Wieler (1898); it will be discussed in chapter II 423 in connection with growth measurements from microscopic samples.

A great number of examples are available about growth differences on different sides of the stem. In comparative work on various methods of growth measurement, Bormann and Kozlowski (1962) noticed that the weekly growth measurements from opposite sides of the stem of *Pinus strobus* showed a highly significant statistical difference in four, a significant difference in one, and no significant difference in three pairs of measurements. In his thorough methodic study, Abetz (1966) noticed that four weeks from the beginning of growth, auxanometers installed on the east and west sides of the stems of fifteen spruces recorded growth differences of 35 %, and after ten weeks, up to 45 % in extreme cases. Young (1952) has also found differences in comparative work with *Pinus taeda.*

In the Metsä-Saramäki experimental stand, auxanographs were installed on the north and south sides of the stem of one tree (figure 3; tree Au 3-4). The growth records for 1964 and 1965 are shown graphically for these in figures 24 and 27, together with the records from the other auxanographs. The growth curves confirm the fact that the amount of radial growth in a tree may be different on different sides of the stem, and that the measurable points of the beginning and end of growth may be slightly different (cf. Chalk 1930, Wilhelmi 1956).

When we study the suitability of records for growth analysis from one point of measurement only, it is useful to pay special attention to the relative magnitude and general trend of the growth variations. The difference seems to be relatively small, allowing the use of a single growth-measuring site in studies concerning primarily the variations rather than the absolute amount of growth. E.g. Abetz (1966), who concludes that a radial growth meter (indicator-type) is of no real value, when e.g. the effects of thinnings on diameter growth are studied, reports that the daily relative variation was very consistent in his data (cf. Bormann and Kozlowski 1962, Kozlowski and Winget 1964, Kern 1965, 1966).

The distribution of diameter growth among various levels on the tree stem will be shortly discussed. Several studies (e.g. Kozlowski and Winget 1964, Kern 1965) have indicated great differences in the quantity, but small differences in the pattern of growth. E.g. Huikari and Paarlahti (1967) found differences in the readings of four girth bands at different levels quite close to each other in four pines, spruces, and birches. For all species, however, the relative growth differences were practically the same.

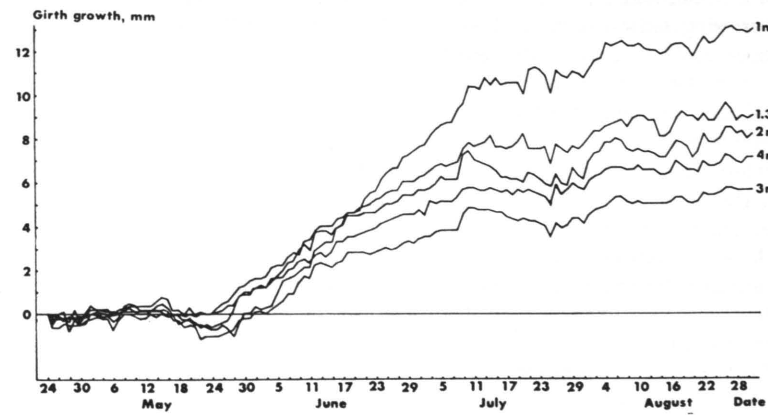

Figure 19. An example of the daily diameter growth of pine at five different levels. Metsä-Saramäki, sample tree 21—5, 1964.

To get a picture of these differences in the Metsä-Saramäki experimental stand, girth bands were installed on three trees, at five levels, in spring 1964. The annual growth curve of sample tree 21-5 (cf. figure 3) is shown in figure 19 as an example. It can be seen that the pattern of growth is not quite the same at the different levels. However, the daily changes are almost similar. In some individual cases, a clear difference can be seen.

The similar growth pattern on the different sides of the tree stem can be explained simply in two ways: either diameter growth depends only little on the unevenly distributed day temperature of the stem (cf. Huber 1935, Koljo 1950), or diameter growth takes place primarily in the night, when the temperature of all sides of the tree is about the same. Also the observations reported on page 66 that diameter growth was the same in the part of the stem in a plastic chamber and that outside during the entire growing season, speak for these conclusions.

423. RECORDING DIAMETER GROWTH BY SAMPLES TAKEN FROM THE TREE STEM

Theodor Hartig was probably the first scholar who (in the 1850's) tried to record the diameter growth of trees from microscopic samples taken from the stem at regular intervals (Ladefoged 1952). The method has gained increasing popularity among students of growth. The literature will not be thoroughly reviewed, since good general reviews have been published by e.g. Ladefoged (1952), Bannan (1962), and Wilcox (1962).

In the first studies, a great number of apparently similar trees were selected from a stand, and these were then felled for sampling one after another during the growing season (e.g. R. Hartig 1885, Amilon 1910, Wight 1933). The samples could be taken with ease from disks sawed from various parts of the tree, and the tissues were always taken from an unharmed tree. However, the sampling error due to tree-to-tree growth variations proved to be overwhelming. Attempts to decrease the inaccuracies by e.g. presenting the ring formed before a certain date relative to the previous observation met with no success. Therefore, the diameter growth of trees is commonly studied from series of samples taken from an individual tree. The sampling error is thus mainly restricted to the local differences of cambial activity in a single tree, and the resulting observations have proved to be more easily handled (Wieler 1898, Chalk 1927, 1930, Rees 1929, Topcuoglu 1940, Ladefoged 1952, von Pechmann 1953, Mork 1960).

Local differences between the samples taken from different parts of the stem are real. One also has to consider the irritating effect of sampling, which may cause traumatic wound reactions in the cambium tissue surrounding the wound.

Samples were taken from the tree, especially in the early period, by an increment borer (Mischke 1890, Wieler 1898, Romell 1925). However, since an ordinary increment borer works on the screw principle, it easily breaks the soft cambium cells separating two hard layers (the bark and the wood). Therefore, Brown (1912) recommended sampling by a specially constructed chisel. Most scholars have followed his example and taken the samples with a knife or a chisel (Lodewick 1928, Rees 1929, Chalk 1930, Hummel 1946, Ladefoged 1952, Mork 1960). Sample extraction has been developed later on by e.g. Fraser (1952; a chisel-cutting tube combination) and Schober (1951; a modified dowel borer). Priestley (1930) developed a totally different method: he carefully removed the bark and scraped the exposed soft cambium and xylem layer in large sheets.

After sampling, the wound is covered by a suitable wax, and the samples are immersed in storing liquid, fixed, cut, and dyed (microtechnique in e.g. Johansen 1940). An efficient dyeing method is described by e.g. H. Schneider (1952).

The microscope samples used in this study were prepared as follows:

The tree bark was ground off into a thin layer. A sample consisting of the rest of the bark and ca. 3 – 4 latest year-rings, was taken by a sharp gouge 6 mm in diameter. The wound was immediately covered by grafting wax. The extracted sample was immediately immersed in a 90:3:7 (volume) solution of 50 % alcohol, strong acetic acid, and formaline (cf. Johansen 1940, p. 41). Three replicate samples were always taken. In the laboratory, the samples were cut down with a razor to 0.3 × 0.3 cm; the best of these blocks were dehydrated, embedded in paraffin, dissected and made into slides according to the method described by Mikola and Persidsky (1951). The dyes used were safranine and »fast green» (Johansen 1940, p. 59, 62, 119). The slides were examined and photographed with a C. Reichert's »Zetopan» research microscope.

The samples were taken as follows: In 1964, samples were taken in the Metsä-Saramäki experimental stand, from three pines (figure 3, nos. Mn 1, 2, 3; table 2) at two levels (1.3 and 4 m) every fourth day. Sampling was started on April 24; the last samples were taken on July 29.

In 1966, two pines were selected from the immediate vicinity of the Metsä-Saramäki experimental stand. The first microscope samples were taken on July 15, and sampling was continued at five-day intervals to September 1. The samples were taken at one level (1.3 m).

424. DISCUSSION OF THE METHODS OF RECORDING TREE DIAMETER GROWTH

Both described methods of recording tree diameter growth have their limitations and drawbacks, but to an extent they supplement each other. The auxanometric readings are tree diameters resulting from the sum effect of several processes. Distinguishing xylem growth from phloem and cork growth is practically impossible, even when temporary short-period diameter changes can be accounted for (e.g. KERN 1965, 1966). In microscope slides, the number and diameter of the tissues produced by cambial activity is easily recorded, and a picture of the real quantity and quality of xylem growth is obtained. In practice, sampling intervals easily exceed a day, and level comparisons must be included, while the continuous auxanometric redings refer to the same site of measurement. Data from several scores of trees, exceeding the practical capacity of the microscopic work or the use of auxanographs, are easily obtained by girth bands or auxanometers. Auxanometers do no damage to the organic tissue of the site of measurement, but microscopic sampling may crush or distort the tender cambium.

III. RESULTS

1. SEASONAL COURSE OF DIAMETER GROWTH

11. BEGINNING OF GROWTH

In the climatic conditions of Finland, tree growth totally ceases for the winter. The cambium, two to three cell layers surrounding the woody part of the stem, has contracted, and the radial walls of individual cambium cells appear equally thick as the tangential ones in a microscopic slide. In the spring before growth actually has started, the cambium cells swell after water starts flowing in the stem (figure 20). The radial walls of the cells become thinner, as the cytoplasm swells from a gel into a solum (figure 21). The cambium layer may thus become twice the original thickness (e.g. LADEFOGED 1952, BANNAN 1955, 1962).

The first cell division takes place in the stem several weeks later (BROWN 1915, LADEFOGED 1952, WILCOX 1962, and others). The development of new cell layers as a result of the periclinal division of the cambium varies greatly, depending on the tree species, the climate etc. In general, however, the vascular cambium produces cells at a considerably slower rate than the smaller cells of the apical meristem. As an example of observed rates, BANNAN (1955) found that in a *Thuja* growing near Toronto, Canada, the cambium produced the second cell layer two weeks after the first, the third ten days after the second, the fourth a week after the third, and the consecutive layers at four- to six-day intervals (cf. figure 21).

It is generally recommended that microscopic samples be used for determining the exact beginning of diameter growth (e.g. ROMELL 1925, LODEWICK 1928, CHALK 1930, TRENDELENBURG and MAYER-WEGELIN 1955). Despite the drawbacks of the method, it is held that growth samples give a better picture of the series of events otherwise revealed only by gradual and extremely small stem diameter changes. Especially the hydrostatic volume changes of the stem, due to changes in the weather conditions, will cause difficulties in interpretation.

During this study, an attempt was made to watch for the formation of the first cell layers in spring 1964 in the Metsä-Saramäki experimental stand (figure 3, trees Mn-1, Mn-2, Mn-3), but a partial failure of the samples of the

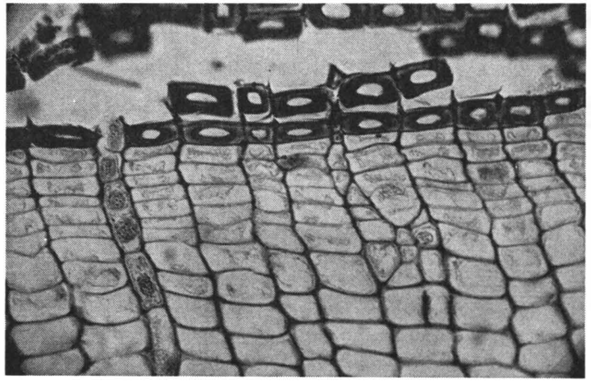

Figure 20. Pine cambium tissue before the initiation of cell division. Previous-year latewood shown at the top of the picture. Cell division has already started in medullary ray on the left. Metsä-Saramäki, sample tree Mn-3. Sampling date May 9, 1964. Magnification 400 x.

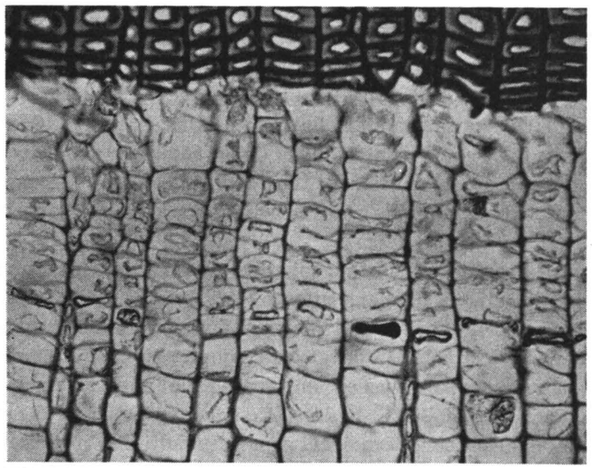

Figure 21. Pine cambium tissue after three periclinal divisions. Previous-year latewood shown at the top of the picture. Metsä-Saramäki, sample tree Mn-3. Sampling date May 29, 1964. Magnification 400 x.

Table 6. Beginning and ending dates of pine diameter growth, and the length of growing season. Metsä-Saramäki experimental stand, 1964—1967.

Measuring device and tree no.	Period of diameter growth, day, month				Duration of diameter growth, days			
	1964	1965	1966	1967	1964	1965	1966	1967
Auxanograph								
Au — 1	20. 5. — 6. 8.	26. 5. — 5. 8.	18. 5. — 11. 8.	25. 5. — 9. 8.	78	71	85	76
Au — 2	20. 5. — 26. 8.	24. 5. — 4. 8.	18. 5. — 11. 8.	25. 5. — 9. 8.	98	72	85	76
Au — 3	20. 5. — 26. 8.	25. 5. — 4. 8.	14. 5. — 11. 8.	25. 5. — 25. 8.	98	71	89	92
Au — 5	20. 5. — 22. 8.	27. 5. — 2. 8.	14. 5. — 11. 8.	21. 5. — 9. 8.	94	67	89	80
Aver.	20. 5. — 20. 8.	25. 5. — 4. 8.	16. 5. — 11. 8.	24. 5. — 13. 8.	92	70	87	81
Girth band								
A — 1	25. 5. — 22. 8.	..	28. 5. — 11. 8.	30. 5. — 9. 8.	89	..	75	71
A — 2	25. 5. — 22. 8.	..	..	..	89	..	..	..
A — 3	25. 5. — 23. 8.	..	28. 5. — 9. 8.	4. 6. — 9. 8.	90	..	73	66
A — 4	24. 5. — 22. 8.	..	28. 5. — 11. 8.	30. 5. — 9. 8.	90	..	75	71
A — 5	24. 5. — 17. 8.	..	28. 5. — 9. 8.	30. 5. — 9. 8.	85	..	73	71
A — 6	25. 5. — 22. 8.	..	28. 5. — 9. 8.	30. 5. — 9. 8.	89	..	73	71
B — 1	26. 5. — 26. 8.	..	..	..	92	..	..	..
B — 2	28. 5. — 28. 8.	..	..	30. 5. — 8. 8.	92	..	..	70
B — 3	28. 5. — 27. 8	..	27. 5. — 9. 8.	30. 5. — 9. 8.	91	..	74	71
B — 4	26. 5. — 22. 8.	..	27. 5. — 11. 8.	4. 6. — 9. 8.	88	..	76	66
B — 5	27. 5. — 28. 8.	..	27. 5. — 9. 8.	4. 6. — 10. 8.	93	..	74	67
B — 6	23. 5. — 28. 8.	..	24. 5. — 11. 8.	..	97	..	79	..
B — 7	26. 5. — 28. 8.	..	29. 5. — 16. 8.	30. 5. — 9. 8.	94	..	79	71
B — 8	26. 5. — 28. 8.	..	2. 6. — 11. 8.	30. 5. — 9. 8.	94	..	70	71
B — 9	26. 5. — 28. 8.	..	27. 5. — 11. 8.	30. 5. — 8. 8.	94	..	76	70
B — 10	26. 5. — 28. 8.	..	27. 5. — 11. 8.	30. 5. — 9. 8.	94	..	76	71
B — 11	26. 5. — 27. 8.	..	25. 5. — 11. 8.	31. 5. — 9. 8.	93	..	78	70
B — 12	28. 5. — 26. 8.	..	29. 5. — 12. 8.	4. 6. — 9. 8.	90	..	75	66
B — 13	24. 5. — 27. 8.	..	28. 5. — 11. 8.	31. 5. — 9. 8.	95	..	75	70
11 — 5 / 12	1. 6. — 23. 8.	..	29. 5. — 7. 8.	1. 6. — 9. 8.	84	..	70	69
21 — 5 / 22	24. 5. — 18. 8.	..	..	..	86	..	..	..
41/— 5 / 42	..	..	28. 5. — 11. 8.	1. 6. — 9. 8.	..	..	75	69
Aver.	26. 5. — 25. 8.	..	27. 5. — 11. 8.	31. 5. — 9. 8.	91	..	75	69

early part of the season resulted in dropping the method. Reattempts in spring 1966 also failed, and it was decided that the beginning of growth would be determined in both experimental stands purely from diameter-change measurements. The day, when stem diameter exhibited a distinct permanent increase, was considered the beginning day of growth. The stem volume could thus have been smaller or greater at the beginning of growth than the volume at the beginning of measurement (0-level) (figures 24—38). The beginning of growth determined in this way is shown in table 6 for the Metsä-Saramäki trees and in table 7 for the Huikko trees.

Table 7. Beginning and ending dates of spruce, pine, and birch diameter growth, and the length of growing season. Huikko experimental stand, 1966—1967.

Tree species	Measuring device and tree no.	Period of diameter growth, day, month		Duration of diameter growth, days	
		1966	1967	1966	1967
Spruce	Auxanogr.				
	Au — 1	17. 5. — 9. 8.	. .	84	. .
	Au — 2	17. 5. — 11. 8.	. .	85	. .
	Aver.	17. 5. — 10. 8.	. .	85	. .
	Girth band				
	B — 3	20. 5. — 7. 8.	30. 5. — 9. 8.	79	71
	B — 6	21. 5. — 17. 7.	30. 5. — 9. 8.	57	71
	B — 12	28. 5. — 17. 7.	29. 5. — 9. 8.	51	72
	Aver.	23. 5. — 24. 7.	30. 5. — 9. 8.	62	71
Pine	Girth band				
	B — 2	23. 5. — 7. 8.	29. 5. — 8. 8.	76	71
	B — 9	20. 5. — 11. 8.	3. 6. — 9. 8.	83	67
	B — 10	29. 5. — 11. 8.	. .	74	. .
	B — 14	28. 5. — 11. 8.	31. 5. — 8. 8.	75	69
	Aver.	24. 5. — 10. 8.	31. 5. — 8. 8.	77	69
Birch	Auxanogr.				
	Au — 3	2. 6. — 9. 8.	. .	68	. .
	Au — 4	11. 6. — 29. 7.	. .	48	. .
	Aver.	7. 6. — 3. 8.	. .	58	. .
	Girth band				
	B — 1	10. 6. — 28. 7.	3. 6. — 8. 8.	48	66
	B — 4	10. 6. — 28. 7.	30. 5. — 24. 7.	48	56
	B — 5	3. 6. — 28. 7.	5. 6. — 10. 8.	55	66
	B — 7	5. 6. — 30. 7.	8. 6. — 1. 8.	55	54
	B — 8	10. 6. — 18. 7.	14. 6. — 4. 8.	38	51
	B — 11	8. 6. — 28. 7.	4. 6. — 8. 8.	50	65
	B — 13	8. 6. — 8. 8.	25. 5. — 14. 8.	61	78
	Aver.	8. 6. — 28. 7.	10. 6. — 5. 8.	51	62

In both sample plots, the tree-to-tree differences within a tree species seem to be relatively small, only a few days, except in a few cases. However, in auxanographic determinations, the beginning date has regularly been a couple of days earlier than in girth-band determinations. This is probably mainly due to the greater sensitivity of the auxanographs and the greater absolute accuracy of these devices (cf. e.g. Bormann and Kozlowski 1962).

Tree species appear to start their annual diameter growth at a distinctly different time. Data from the cool and temperate climatic zones are to be found

in e.g. the following publications: Büsgen and Münch 1927, p. 98—103, Lodewick 1928, Ladefoged 1952, Trendelenburg and Mayer-Wegelin 1955, p. 364—369, Schober 1961, Gaertner 1964, Kern 1966, p. 166—167. It is generally held that ring-porous hardwoods begin diameter growth relatively early, while diffuse-porous hardwoods require a preparative period. Conifers (except larch) begin diameter growth at approximately the same time as ring-porous hardwoods. Of the species studied, pine and spruce diameter growth starts at about the same time and birch diameter growth about two weeks later (Ronge 1928, Ilvessalo 1932, Ladefoged 1952, Huikari and Paarlahti 1967). This agrees well with the results from the Huikko experimental stand: conifer diameter growth starts within one day in 1966 and 1967, birch diameter growth 14—15 days later in 1966 and 10—11 days later in 1967.

A short comparison with results from the other Nordic countries clearly shows that the beginning of growth depends on the geographic location of the area. Huikari and Paarlahti (1967, p. 56—57) found that the diameter growth of pine started about a week earlier in Kivalo (66°27′ N) in 1961—1964 than in Vilppula (62°3′ N). Romell (1925) found that the diameter growth of pine started in Hoting, North-Central Sweden (64°6′ N) on June 6 in 1922; this he considers an average date for the area. According to Ronge's (1928) observations, the diameter growth of pine and spruce started in Norrland, North Sweden, on June 2 in 1922, and Mork (1960) found that the diameter growth of spruce started in Kise (140 m OD), southern Norway before April 29 in 1959, but in Hirkjolen (860 m OD) in the fjelds at the end of May in the same year.

The mechanism of the beginning of tree diameter growth has been much discussed. The subject and the development of the different views are reviewed by e.g. Ladefoged (1952), Trendelenburg and Mayer-Wegelin (1955, p. 367—371), Fraser (1959), Wareing (1956), Bannan (1962), Larson (1962, 1964,) Wilcox (1962), and Romberger (1963). According to the view unanimously accepted today, tree buds and their development have a key role in the beginning of stem diameter growth. The growth hormone that develops in awakening buds causes cell division in the cambium layer immediately below the branch tips, and the stimulus spreads towards the base of the tree. The spreading rate of the growth hormone seems to be closely connected with the general characteristics of the tree species, especially the anatomic structure of the woody stem.

Since tree buds actually transfer the external stimulant of the beginning of tree growth, determinations of the beginning of growth on the basis of diameter change measurements at breast height must be treated with reservation. However, it is considered useful to briefly discuss the environmental factors affecting the beginning of diameter growth, since the conclusions will be based primarily on relative comparisons between the various years.

111. ENVIRONMENTAL FACTORS AFFECTING THE BEGINNING OF DIAMETER GROWTH

It is obvious that, especially in Finnish climatic conditions, temperature has a highly dominant effect in the beginning of diameter growth in the spring (e.g. ROMELL 1925, MIKOLA 1950, MITSCHERLICH *et al.* 1966), and especially the use of various kinds of cumulative temperature sums to explain the awakening in the spring has been promising (NUTTONSON 1948, VOIGTS 1949, SCHNELLE 1955, p. 206—218, SARVAS 1967). Table 8 shows the degree-hours accumulated in four recording years before the day on which growth started, using three different threshold temperatures (about degree-hour computations see p. 25). When the values for the different years are compared, they seem to agree fairly well, except spring 1966 with much fewer than average cumulative degree-hours. It seems natural that in spring 1966, the sudden warm period following a long cold period started the diameter growth of trees earlier than could be judged merely on the basis of the average degree-hour level. It should be mentioned in this connection that e.g. MITSCHERLICH *et al.* (1966) have emphasized the role of minimum temperatures in slowing down the beginning of growth (cf. also HUIKARI and PAARLAHTI 1967). Although supplementary evidence would be necessary before concluding that the temperature-time combinations used provide a complete framework of conditions required for the beginning of diameter growth, the result nevertheless clearly implies that indexes like the temperature sum are useful in explaining the beginning of the diameter growth of trees in the spring. When different threshold temperatures are compared, the smallest amount of variation results from using the lowest one, ± 0° C, which can therefore be considered the best of those used. The coefficient of variation[1] for + 5° C differs only slightly from the one for ± 0° C, but the one for + 10° C is much

Table 8. Cumulate degree-hours at beginning of pine diameter growth. Metsä-Saramäki, 1964—1967.

Year	Starting date of growth, auxanogr. measurement.	Temperature limit ± 0° C	+ 5° C	+ 10° C
		Cumulate degree-hours		
1964	May 20	2 307	745	145
1965	» 25	2 505	901	233
1966	» 16	1 775	591	95
1967	» 24	2 570	901	211
Mean		2 289	784	171
Standard deviation		361	148	63
Coefficient of variation		15.8	18.8	36.8

[1] Coefficient of variation (C) = $s/\bar{x}$ (e.g. SNEDECOR 1956, p. 44, 62—64).

bigger. In the literature, the most commonly used threshold temperature is + 5° C, considered the lowest average temperature of tree growth (e.g. POLSTER 1950, LADEFOGED 1952, SIRÉN 1961), but the results of this study indicate that when thermometers are used in weather chambers protected from solar radiation, the threshold temperature could be some degrees lower.

The problem 'to what extent do the beginning dates of growth shown in tables 6 and 7 represent average dates in normal conditions' can be elucidated further by a summary of the monthly average temperatures of the area (Juupajoki and Orivesi), in which the study was carried out, relative to the normal (1931—1960 averages) values:

Year → / Month	1964	1965	1966	1967
	Deviation of mean monthly temperature from normal, °C[1]			
March	− 1.5	± 0.0	± 0.0	+ 4.5
April	+ 0.5	+ 1.0	− 2.5	+ 0.5
May	+ 0.5	− 2.0	± 0.0	± 0.0
June	− 0.5	+ 0.5	+ 3.0	− 0.5

It seems that the spring 1964 has been slightly warmer than normal, spring 1965, especially May, cold, April 1966, cold, but the following June very warm, and the spring 1967, about normal except for the very warm March. It seems that in a normal year, the diameter growth of pine starts approximately on May 22—24, and that a half-degree deviation in the April-May temperature means causes a corresponding 1—2 day shift.

Especially in older forestry literature, it is mentioned that local cambium-layer temperatures affect the beginning of diameter growth (e.g. SCHWARZ 1899, AMILON 1910, also CHALK 1930, p. 12). Although this theory is no longer valid in its original form, we must remember that however strong the hormonal stimulus, the rate of growth and cell division always depends also on local temperatures (e.g. WENT 1953, 1957, LUNDEGÅRD 1954, p. 134—142, LEOPOLD 1964, p. 369—392). Mostly, in the field, the rhythm of temperature rise in the buds and in the stem is the same, and both temperatures are important for diameter growth. A solution to the problem is offered by the experimental procedure used by e.g. MAC DOUGAL (1936 and 1938) and RICHARDSON (1964). The stems or parts of the stems of the trees under study are subjected to temperatures

[1] The data are derived from the monthly reports of the Finnish Meteorological Office on weather conditions in Finland.

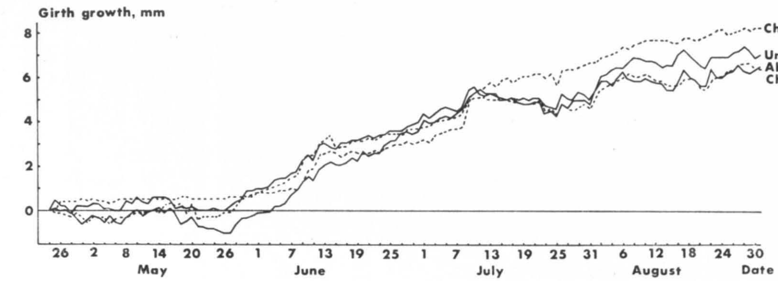

Figure 22. Daily diameter growth of sample tree 31—4 in the part of the stem in plastic chamber, and above and under it. Ch = girth band in plastic chamber, Un = under the plastic chamber, Ab = above the plastic chamber. Metsä-Saramäki, 1964.

distinctly higher than the temperature of the outside air, and growth is measured by instruments or microscopic samples.

In the Metsä-Saramäki experimental stand, a two-meter portion of a pine stem was isolated in a plastic chamber built around the tree (chapter II 323). Figure 22 shows the girth growth of this tree as measured by girth bands above the chamber, below it, and at two sites within it. No sign of earlier growth in the chamber than outside can be detected. Later on, no distinct differences are seen in the course of growth during the summer. The measured girth growth appears to vary irregularly at the different levels. The negative results agree with the results obtained by MAC DOUGAL (1938) and also HUIKARI and PAARLAHTI (1967).

Figure 23 summarizes the changes in some environmental factors in the springs of the four years of measurement in the Metsä-Saramäki experimental stand. The poor agreement of the dates of snow melting and soil thawing with the beginning of diameter growth are especially conspicuous. Although the date of soil thawing was different in different parts of the stand (cf. p. 37), the great time differences observed in growth are not explained by e.g. measurement errors. It must be assumed that soil temperature variations, especially soil thawing in the spring, have a less decisive role in determining the beginning of tree growth in the spring than was expected. The same conclusion is reached by e.g. HUIKARI and PAARLAHTI (1967) in studies of the beginning of pine diameter growth in sites kept cold by straw covers.

Solving the true effect of the rise of the soil temperature in the spring would require larger and multifactorial series of experimental data. However, the following summary lists the soil temperatures at the beginning date of pine diameter growth in the different years in the experimental stand at Metsä-Saramäki:

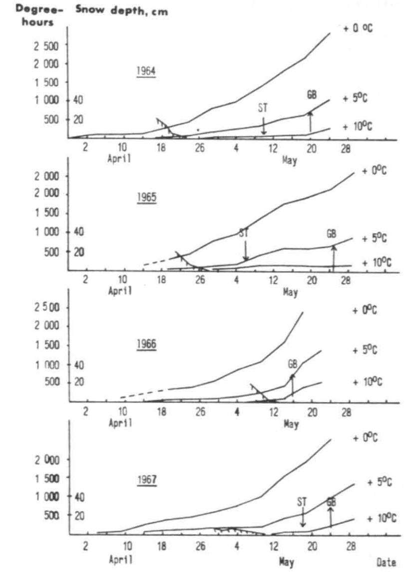

Figure 23. Changes in various ecological factors at the Metsä-Saramäki experimental stand during the four springs 1964—1967. For comparison, the first day of pine diameter growth as indicated by auxanograph records is shown. ST = soil thawed out, GB = first day of diameter growth, ////// = melting of snow, ———— = degree-hours, cumulative.

Year	Beginning date of diameter growth, auxanogr.	Soil temperature at 10 cm depth, daily max., °C
1964	May 20	5.5
1965	May 25	7.5
1966	May 16	5.0
1967	May 24	4.0

For better comparison, the soil temperature at the beginning of pine diameter growth in the two experimental stands is also given:

Year	Beginning date of pine diameter growth, girth bands		Soil temperature at 10 cm depth, daily max., °C	
	Metsä-Saramäki	Huikko	Metsä-Saramäki	Huikko
1966	May 27	May 23	6.5	4.5
1967	May 31	May 30	12.0	6.0

A definite solution to the problem of the effect of the soil temperature on the beginning of diameter growth can not be given. However, soil temperature was distinctly lower in the experimental stand at Huikko (peaty soil) than in the

Metsä-Saramäki stand (mineral soil) on the beginning date of pine diameter growth, probably indicating that the significance of soil temperature is secondary to that of air temperature, a fact which is not always distinct in the ecologic calender of nature.

12. GROWTH CURVE

The basic pattern of growth is same everywhere in the living nature. The initially slow rate of organic matter increase gradually increases, reaching a peak, then gradually decreases, and finally growth stops. The growth curve has been extensively analysed in highly variable conditions and using different types of series of data (e.g. Smith 1939, Lyr *et al.* 1967, p. 379—396). The growth curve found has basically been a sinus curve, the upward and downward gradients of which are not symmetrical (e.g. Curtis and Clark 1950, p. 651—688, Went 1957, p. 200—210, Whaley 1961, and others).

This model seems to hold also for the seasonal cumulative diameter growth curve measured by auxanographs and girth bands from the sample trees (figures 24—38). Accidental environmental phenomena cause irregularities, but the general growth curve pattern is easily distinguishable.

Additional information about the seasonal course of diameter growth was obtained from microscopic samples (chapter II 423). The course of diameter growth on two levels in three sample trees is shown in table 9 and also in figures 39 and 40. It is seen that new cell layers are formed in the pine xylem every second or third day during the period of most rapid growth, but the rhythm of periclinal cell division that can be considered normal is usually one in four days. This

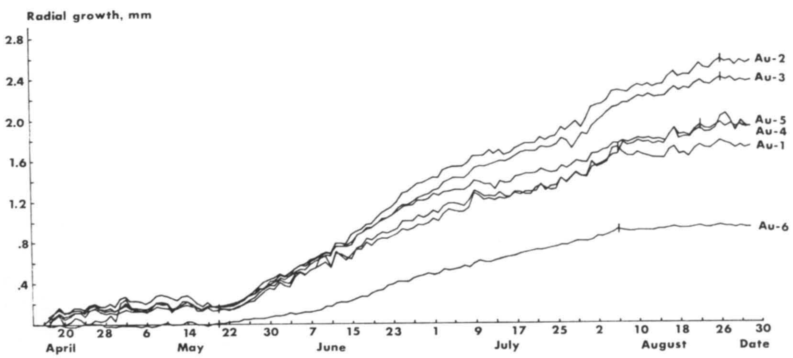

Figure 24. Diameter growth of pine according to auxanograph measurements during the 1964 growing season. Beginning and end of growth are indicated by small vertical lines. Au-3 and Au-4 are the north and south sides of the same tree; Au-6 discarded from final analysis. Metsä-Saramäki.

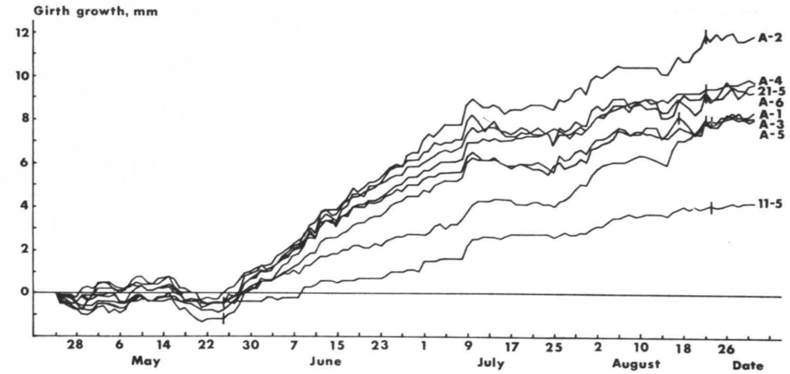

Figure 25. Diameter growth of pine according to girth band measurements during the 1964 growing season. Beginning and end of growth are indicated by small vertical lines. Metsä-Saramäki, girth bands, series A and the sample trees 11—5 and 21—5.

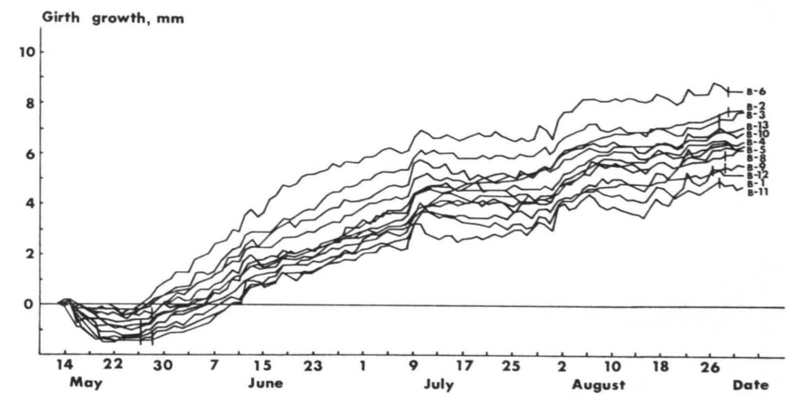

Figure 26. Diameter growth of pine according to girth band measurements during the 1964 growing season. Beginning and end of growth are indicated by small vertical lines. Metsä-Saramäki, girth bands, series B.

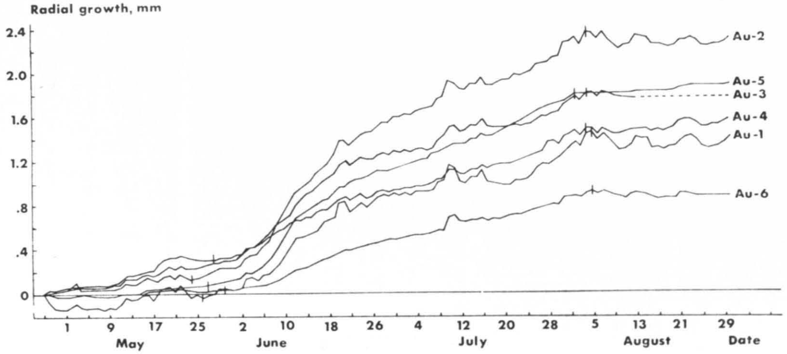

Figure 27. Diameter growth of pine according to auxanograph measurements during the 1965 growing season. Beginning and end of growth are indicated by small vertical lines. Au-3 and Au-4 are the north and south sides of the same tree; Au-6 discarded from final analysis. Metsä-Saramäki.

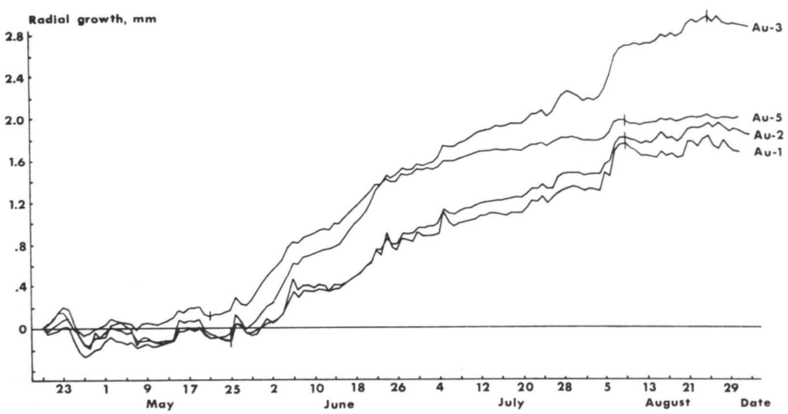

Figure 28. Diameter growth of pine according to auxanograph measurements during the 1966 growing season. Beginning and end of growth are indicated by small vertical lines. Metsä-Saramäki.

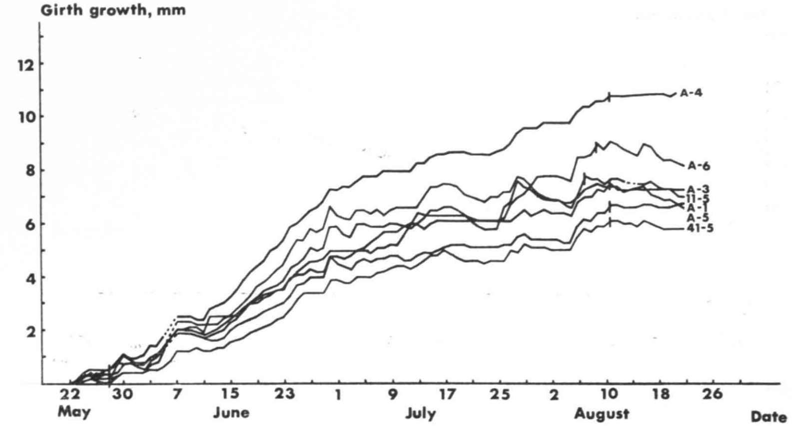

Figure 29. Diameter growth of pine according to girth band measurements during the 1966 growing season. Beginning and end of growth are indicated by small vertical lines. Metsä-Saramäki, girth bands, series A and the sample trees 11—5 and 41—5.

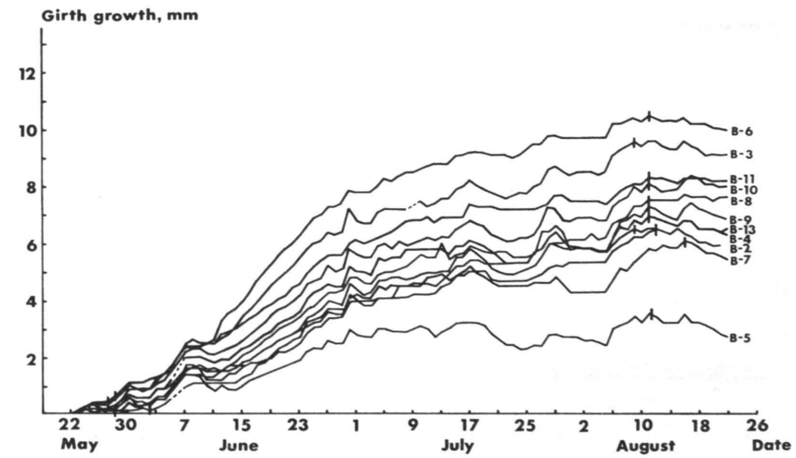

Figure 30. Diameter growth of pine according to girth band measurements during the 1966 growing season. Beginning and end of growth are indicated by small vertical lines. Metsä-Saramäki, girth bands, series B.

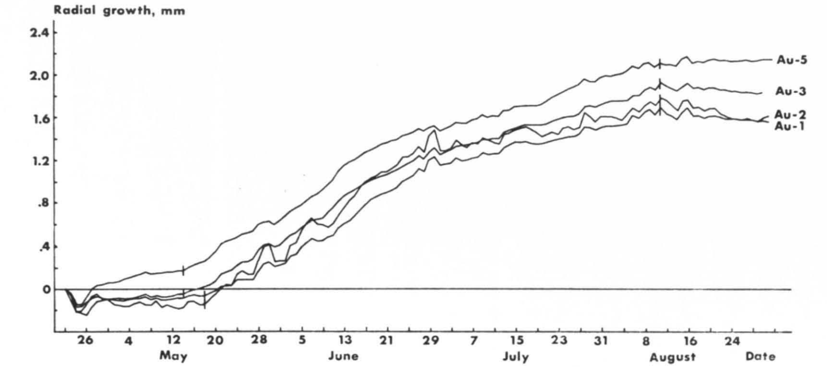

Figure 31. Diameter growth of pine according to auxanograph measurements during the 1967 growing season. Beginning and end of growth are indicated by small vertical lines. Metsä-Saramäki.

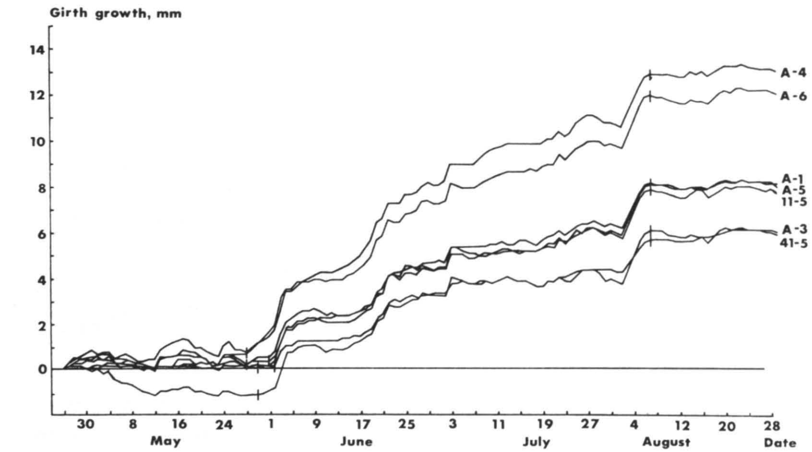

Figure 32. Diameter growth of pine according to girth band measurements during the 1967 growing season. Beginning and end of growth are indicated by small vertical lines. Metsä-Saramäki, girth bands, series A and the sample trees 11—5 and 41—5.

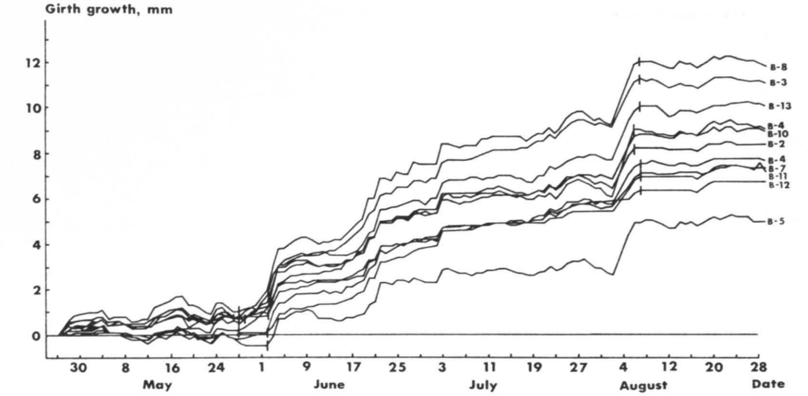

Figure 33. Diameter growth of pine according to girth band measurements during the 1967 growing season. Beginning and end of growth are indicated by small vertical lines. Metsä-Saramäki, girth bands, series B.

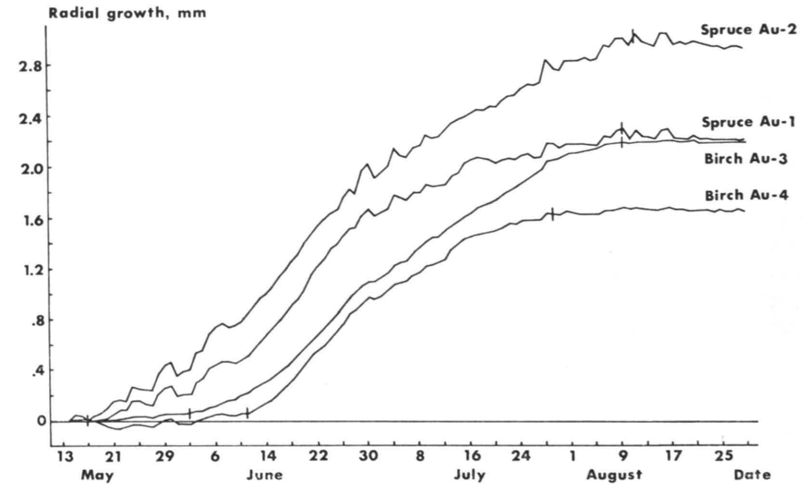

Figure 34. Diameter growth of spruce and birch according to auxanograph measurements during the 1966 growing season. Beginning and end of growth are indicated by small vertical lines. Huikko.

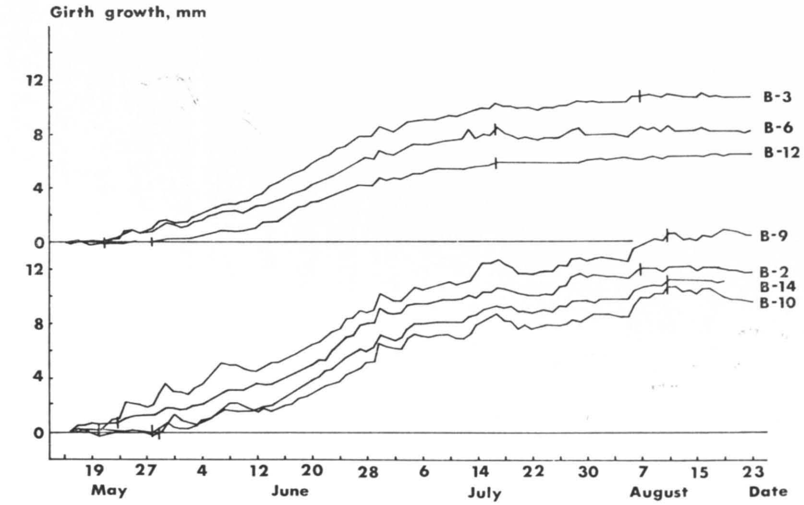

Figure 35. Diameter growth of spruce (above) and pine (below) according to girth band measurements during the 1966 growing season. Beginning and end of growth are indicated by small vertical lines. Huikko.

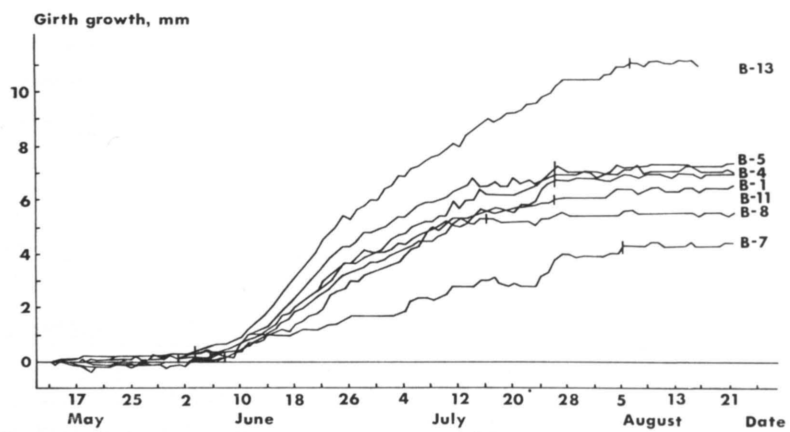

Figure 36. Diameter growth of birch according to girth band measurements during the 1966 growing season. Beginning and end of growth are indicated by small vertical lines. Huikko.

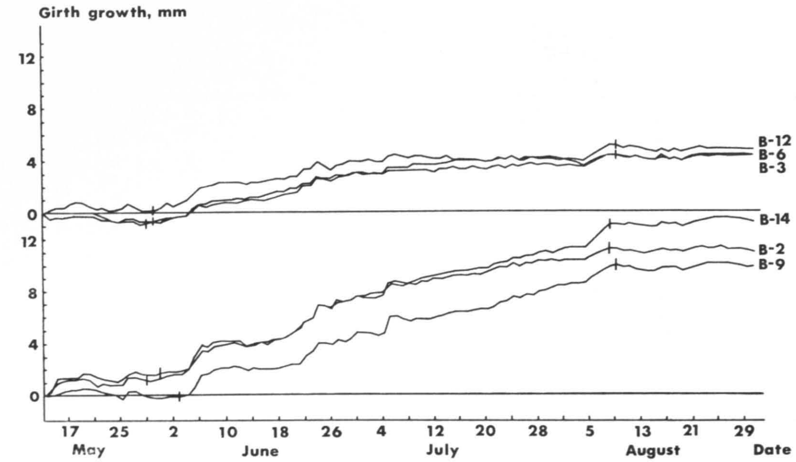

Figure 37. Diameter growth of spruce (above) and pine (below) according to girth band measurements during the 1967 growing season. Beginning and end of growing season are indicated by small vertical lines. Huikko.

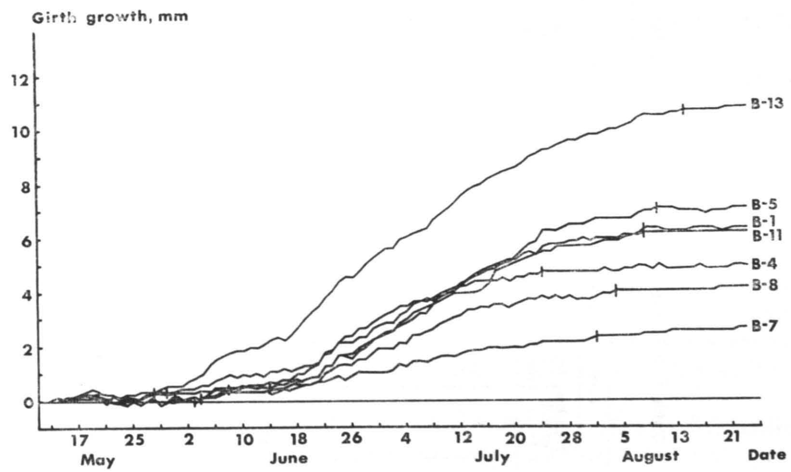

Figure 38. Diameter growth of birch according to girth band measurements during the 1967 growing season. Beginning and end of growth are indicated by small vertical lines. Huikko.

Table 9. The course of diameter growth in 1964 in sample trees M-1, M-2, and M-3 according to the tissue samples. Each value is an average of several samples.

Sampling date	Tree M-1/1.3 m			Tree M-1/4 m			Tree M-2/4 m			Tree M-3/1.3 m			Tree M-3/4 m		
	Number of cell layers	Difference, no./days	Ring width, mm	Number of cell layers	Difference, no./days	Ring width, mm	Number of cell layers	Difference, no./days	Ring width, mm	Number of cell layers	Difference, no./days	Ring width, mm	Number of cell layers	Difference, no./days	Ring width, mm
May 29	—		—	—		—	3		.07	—		—	2		.05
June 6	4		.087	—		—	—	1/3	—	3		.06	—		—
June 10	—		—	4		.08—.1	6—8		.25—.26	—		—	7—8		.17—.20
June 15	—		—	5	1/5	.14—.15	—	5/9	—	—		—	—	2/9	..
June 19	—		—	6—7	1/2	.22—.25	12		.47	7—8		.27—.30	10—11	..	.32—.35
June 23	—		—	10—11	3/4	.38—.40	13—15	2/4	.52—.56	9—11	3/4	.35—.37	9—11	1/4	.40—.42
June 27	8		.38	9—10	1/4	.27—.31	16—17	3/4	.61—.64	10—12	1/4	..	10—11	1/4	.29—.30
July 1	9	1/4	.36—.38	12—13	1/2	.38—.41	17—18	1/4	.64—.68	14—15	1/1	.52—.55	14—15	1/1	.42—.43
July 5	13—14	5/4	.47—.48	12—14	1/4	.42—.45	16—18	..	.56—.60	18—19	3/4	.64—.67	10—12	..	.24—.26
July 9	14—15	1/4	.53—.56	16—17	3/4	.46—.50	18—20	1/2	.66—.69	16—18	..	.51—.52	15—17	1/1	.51—.53
July 13	..	1/8	..	15—16	..	.47—.48	23—24	3/4	.93—.94	22—24	3/2	.77—.81	18—19	1/2	.52—.56
July 17	15—18	..	.53—.57	16—17	1/4	.55—.60	..	..	..	19—21	..	..	15—16	..	.38—.40
July 21	18—20	3/4	.57—.58	14—16	..	.38—.41	..	..	..	22—23	1/2	.60—64.	..	5/7	..
July 24	16—17	..	.51	15—17	1/3	.48—.53	22—23	..	.74—.77	..	..	..	20—21	..	69—.72.
July 29	..	..	..	21—23	6/5	.78—.80	26—28	4/5	.81—.84	..	..	..	..	..	..

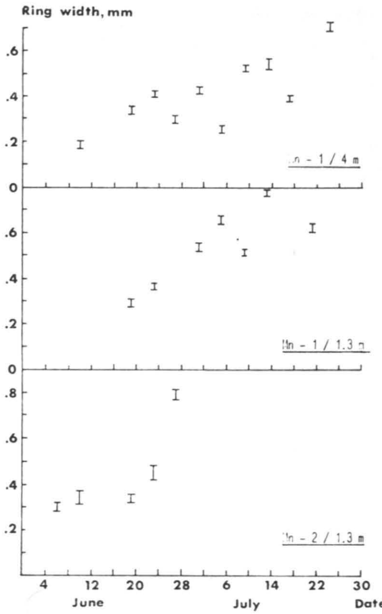

Figure 39. Diameter growth in two pines at two levels, according to microscopic samples, Metsä-Saramäki, sample trees Mn-1 and Mn-2, 1964.

agrees well with the picture given by e.g. Romell (1925), Ladefoged (1952), Bannan (1955) and Mork (1960) about the rhythm of cell division in fairly similar climatic zones.

The period of summer growth inhibition (sommerliche Ruhepause), which several workers have found elsewhere in the middle of the growing season in conifers (e.g. Friedrich 1897, Brown 1915, Chalk 1930, p. 15, Topcuoglu 1940, Trendelenburg and Mayer-Wegelin 1955, p. 375—377, Romberger 1963, p. 80, Valenziano and Scaramuzzi 1967), was not found in the growth records (figures 24—38). It seems that the short and relatively uniform summer conditions in the north allow continuous diameter growth. Reasons for this phenomenon are difficult to say, but many of the scholars listed have connected it with environmental factors, especially drought, and the end of weight growth and the beginning of late wood formation. The growth cessation period has not been always found (Chalk 1930), or it has only been distinct in a certain part of the stem (Lodewick 1928, Fraser 1966).

Figure 41 shows the comparative courses of diameter growth as determined by the auxanographic records and the tissue samples. The last day of the 1964 observation series (July 29) has been denoted 100 for both methods, and all records are shown as relative values. The figure provides weighty evidence to

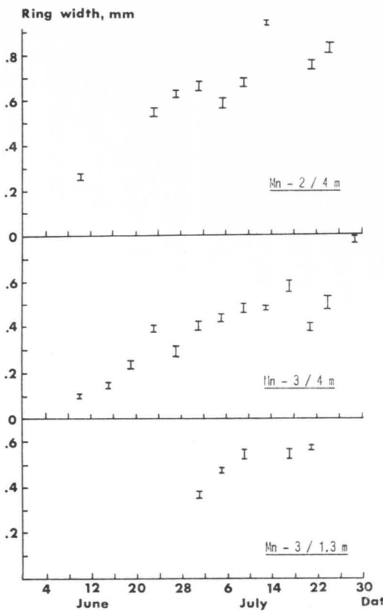

Figure 40. Diameter growth of two pines at two levels, according to microscopic samples. Metsä-Saramäki, sample trees Mn-2 and Mn-3, 1964.

the view that the sampling error connected with the use of microscopic samples is so large that determinations of the amount of diameter growth entirely by this method is extremely hazardous. This result partly led to the decision to include only the auxanographic and girth band data in the growth analytical computations (chapter III 2).

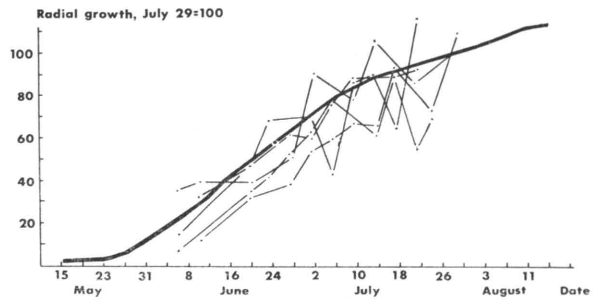

Figure 41. Diameter growth of pine according to two different methods of measurement. Thick line = radial growth as measured by auxanographs, 4-day moving average. Thin lines = radial growth as measured from microscopic samples, trees Mn-1 — Mn-3, at breast height. Diameter on July 29 = 100. Metsä-Saramäki, 1964.

Some research workers, including Romell (1925) and Kern and Moll (1960), have found a better agreement between tissue sample and auxanometric determinations, but the limitations listed earlier in chapter II 323 appear to be generally valid.

13. END OF GROWTH

According to early views, the diameter growth of trees in the temperate and cool climatic zones continued in the fall to the first frosts, until the freezing of the stem stopped cambial activity, but later studies have shown that diameter growth ends long before this, in environmental conditions appearing to provide the possibility for the formation of new cell layers in the annual ring (e.g. Lodewick 1928, Chalk 1930, Mac Dougal 1938, Trendelenburg and Mayer-Wegelin 1955, p. 370—371, Wareing 1956, Wilcox 1962, Romberger 1963, Mitscherlich *et al.* 1966).

Even though the exact determination of the beginning of diameter growth may be difficult, determining accurately the date, when diameter growth ends, is impossible (e.g. Chalk 1930, Schober 1951, Andersson 1953, Wilhelmi 1956, Kern 1966). In this study, the end date of diameter growth was that on which regular diameter increase ended and subsequent diameter changes were temporary and static in relation to diameter growth.

When the ending dates of diameter growth shown in table 8 and figures 34—38 for the tree species studied in the experimental stand at Huikko are compared, it is seen that the difference between pine and spruce is not great, but that the diameter growth of birch ended much earlier (cf. e.g. Ilvessalo 1932). The differences in the years are best shown by the results for the Metsä-Saramäki pines in table 6. In 1964, diameter growth continued rather late — it ended around August 25 — but in the other years, growth ended on August 5—10. It can be seen that tree-to-tree differences are greater than at the beginning of growth.

A fact that e.g. in figures 24 and 31 draws attention, in addition to the annual differences in the ending of growth, is the clear positive correlation of the time of the ending of growth of the Metsä-Saramäki pines in 1964 and 1967 with the total amount of growth. In other words, the later the date growth ended, the wider the annual ring. The same phenomenon is clearly seen in the birches (figures 34 and 36) and spruces (figures 34 and 35) in the Huikko experimental stand in 1966, but hardly at all in the Metsä-Saramäki pines in 1965 and 1966 (figures 27—30).

This dependence relationship has been described by e.g. Ladefoged (1952) who reports that the trees with the narrowest year-rings in his material stopped diameter growth already at the end of July or the beginning of August, but the trees producing most wood continued to grow to the end of August and even the beginning of September. He judges that this general characteristic, seemingly quite independent of tree species, tree age etc. is mainly due to the nutritional differences of trees at the end of the growing season. He considers the nutritional status of low-production trees unfavorable for the continuation of annual ring development, as compared to the high-production trees, and causes the earlier cessation of diameter growth. Also KOZLOWSKI and PETERSON (1962), KERN (1965), BASSETT (1966), and MITSCHERLICH *et al.* (1966) report that the growth of stand dominants is greater and continues longer than that of the suppressed, physiologically weaker trees (e.g. HENGST 1966 and HOYLE 1966, however, support a contrary view).

The question of the relationship between the amount of diameter growth and the ending time of the growing season is further discussed in chapter III 14 in the discussion concerning the length of the growing season.

The observations of the times of the ending of tree growth are generally in good agreement with the data published in the other Nordic countries. According to ILVESSALO (1932), pine and spruce diameter growth ends in southern Finland between August 6 and 18, and birch, between July 29 and August 24. In Sweden, ANDERSSON (1953) has reported that pine diameter growth usually ends, depending on the year, between August 12 and 24, and spruce growth a few days earlier. ROMELL (1925) reports that pine diameter growth ends in Hotingen, North-Central Sweden, usually around August 25 (in 1921—1923), and according to Ronge's (1928) observations, pine and spruce diameter growth ended in Norrland, North Sweden, around August 10 and 12, respectively. According to MORK (1960), spruce diameter growth ended in South Norway already on August 4 in 1959. Toward Central Europe, the growing season generally extends further in the fall, as expected (SIEGMOND 1936, TOPCUOGLU 1940, SCHOBER 1951, KERN and MOLL 1960, and others).

The views on the reasons of the ending of diameter growth have not been compounded into a consistent theory. The first factor concerned is the hereditary annual growth rhythm of the tree, the relationships of which to the environment are unexplained. Another concept relates to the activity of the tree itself in transforming the conditions so that cell growth stops after a certain period of time. This is so far the only explanation for e.g. the periodicity of the trees growing in regions with no clear seasonal climatic changes.

It has been stated in several studies that the ending of growth is primarily a series of activities regulated by the growth hormones, but this is no explanation to the variation of hormonal quantities or the development of inhibitory substances during the growing season. Several climatic factors have been suggested. One can in this connection give only passing attention to e.g. the theories constructed on the basis of experiments in the warm climatic zone concerning the anaerobic respiration of young buds due to warm nights, and the resulting inhibitory products harmful to trees (e.g. KRAMER 1957) and the conclusions

from many regions that regular summer drought has a dominant effect in stopping growth (BYRAM and DOOLITTLE 1950, DILS and DAY 1952, BOGGESS 1956, MC CLURKIN 1958, KRAUSS and SPURR 1961, HARKIN 1962, BASSETT 1964). In many years with warm late periods, it is also futile to present the cooling of air as a factor.

Forest tree seedlings have been induced dormant in laboratory conditions prematurely by changing the environmental photoperiod (WAREING 1950, DOWNS 1958, FRASER 1959). It is fairly common in the literature to state shorter days as the reason for the cessation of growth, and several experiments with e.g. induced growth hormones support the theory (WAREING 1956, KRAMER and KOZLOWSKI 1960, p. 477—485, LARSON 1962, 1964, ROMBERGER 1963). It may, however, prove difficult to apply the theory directly in Finnish conditions. Usually the critical photoperiod has been about 14 to 15 hours (e.g. FRASER 1959), but even in South Finland (ca. 60° N) the time between sunrise and sunset is over 18 hours at the end of diameter growth, and in North Finland (ca. 66° N), the days are 20 to 21 hours long at the end of diameter growth.

It may be concluded that none of the many theories so far presented has been unanimously accepted (cf. PAULEY 1958) or explains well the ending of growth in Finnish climatic conditions. The true factor may be an indigenous mechanism connected with e.g. the growth and activity of the leaves and needles and modified by the environmental conditions. Several of the hypotheses listed above seem promising, but this is all that can be said so far about the basic effect of the environmental factors on the ending of diameter growth.

14. DURATION OF GROWTH

The duration of diameter growth is defined in this study as the time from the beginning of annual diameter growth to its ending. Some research workers have adapted a definition according to which diameter growth is considered to start, when a certain part of the annual ring (mostly 5—10 % of the final width) has been formed, and the growing season ends when a similar part of the annual ring is still to be formed (e.g. JACKSON 1952, HUIKARI and PAARLAHTI 1967). This method is said to provide a more reliable basis for various comparisons especially when the exact beginning and ending dates of diameter growth are uncertain.

The duration of diameter growth is given for the Metsä-Saramäki trees in table 6 and the Huikko stand trees in table 7. The shortness of the birch growing season as compared to that of the conifers is clearly shown by table 7; table 6 illustrates the considerable annual variation of the duration of growth.

It is known that the duration of diameter growth is generally shorter in mountains than on plains and in the north than in the south (e.g. BÜSGEN and MÜNCH 1927, p. 98—103, SCHOBER 1951, KRAMER and KOZLOWSKI 1960, p. 35), and many scientists have stated that the dominant trees of the stand grow in more favorable conditions than the suppressed and that their growing season is longer (e.g. Kozlowski and Peterson 1962, Kern 1966, Mitscherlich *et al.* 1966). It is therefore reasonable to assume that the duration of diameter growth is determined not only by the tree species, the physiological condition of the tree etc. but also by general environmental factors. In Finnish conditions, a possible factor is the the accumulation of temperatures exceeding a threshold in relation to time.

Cumulative degree-hours were computed from temperature observations made at canopy level in Metsä-Saramäki during the four years of observation, using three alternative temperature thresholds (cf. p. 25), for the average period of diameter growth as determined on the basis of auxanographic measurements. The results are shown here:

Year	Average growing season		Cumulative degree-hours using different threshold temperatures		
	Dates	Duration, days	± 0° C	+ 5° C	+ 10° C
1964	May 20 – August 20	92	152 025	96 675	46 920
1965	May 25 – August 4	70	108 585	64 075	27 482
1966	May 16 – August 11	87	158 920	106 506	58 180
1967	May 24 – August 13	81	145 830	97 485	52 055

The temperature sums for the different years are so different that the results of this study can not be considered evidence for the assumption that these dominate in determining the duration of diameter growth.

The relationship between the amount of diameter growth and the length of the whole growing season was also studied. The total radial increment of the trees of the experimental stands at Metsä-Saramäki and Huikko is shown in tables 10 and 11. It has been computed by subtracting the auxanometer reading of the day growth started from the corresponding reading on the day growth ended. The auxanograph readings of pine growth at Metsä-Saramäki during four field years were used to compute the radial increment growing season length relationships (figure 42). Since overall correlation was studied, it was considered possible to combine the data from all four years into the same analysis. A significant positive correlation was found, indicating a close connection between the length of the growing season and the total radial increment. The same process was repeated, for the birch data from Huikko (figure 43), and the same results obtained. No significant correlation was, however, found for the Metsä-Saramäki girth band records for pine, which was probably primarily due to the similarity of the growing season lengths of the trees (cf. table 6).

The great effect of the temperature conditions during the growing season on

Table 10. Total diameter growth of pine in the Metsä-Saramäki experimental stand 1964–1967.

Measuring device and no of tree	1964		1965		1966		1967	
	Girth increm., 0.1 mm	Radial increm., 0.01 mm	Girth increm., 0.1 mm	Radial increm., 0.01 mm	Girth increm., 0.1 mm	Radial increm., 0.01 mm	Girth increm., 0.1 mm	Radial increm., 0.01 mm
Auxanograph								
Au – 1	..	157	..	143	..	177	..	189
Au – 2	..	238	..	213	..	168	..	200
Au – 3	..	225	..	150	..	181	..	296
Au – 5	..	179	..	178	..	198	..	189
Aver.	..	199.7	..	171.0	..	181.0	..	218.5
Girth band								
A – 1	87	138	..	..	63	100	79	126
A – 2	130	207	..	..	..	..	..	..
A – 3	86	137	..	..	69	110	59	94
A – 4	105	167	..	..	104	165	124	197
A – 5	85	135	..	..	69	110	78	124
A – 6	99	158	..	..	82	130	114	181
B – 1	68	108	..	..	..	..	..	..
B – 2	82	130	..	..	..	..	81	129
B – 3	76	121	..	..	87	138	106	169
B – 4	81	129	..	..	63	100	69	110
B – 5	72	115	..	..	31	49	53	84
B – 6	91	145	..	..	99	158	..	..
B – 7	73	116	..	..	54	86	65	103
B – 8	77	122	..	..	75	119	112	178
B – 9	71	113	..	..	69	110	81	129
B – 10	71	113	..	..	77	122	83	132
B – 11	59	94	..	..	79	126	75	119
B – 12	70	111	..	..	59	94	66	105
B – 13	72	115	..	..	61	97	94	149
11 – 5/12	46	73	..	..	68	108	79	126
21 – 5/22	98	156	..	..	..	..	..	..
41 – 5/42	..	..	..	..	56	89	72	115
Aver.	80.9	128.7	..	..	70.3	111.7	82.8	131.7

the total diameter increment has been much emphasized in the Nordic countries (e.g. Laitakari 1920, Romell 1925, Hustich 1948, Mikola 1950, Holmsgaard 1955). Langlet (1936) has also given attention to the role of the length of the growing season in regulating growth. After studying experimental pine plantings of different provenances in various parts of Sweden, he also tested the significance of growing season lengths computed by using different temperature thresholds in determining total tree dry matter production. He found that the number of days with an average air temperature over + 6° C was best, reducing the total dry-matter production variance from 1.435 to 0.889 (*op. cit.*, p. 352).

Table 11. Total diameter growth of spruce, pine, and birch in the Huikko experimental stand, 1966—1967.

Tree species	Measuring device and no. of tree	1966 Girth incr., 0.1 mm	1966 Radial incr., 0.01 mm	1967 Girth incr., 0.1 mm	1967 Radial incr., 0.01 mm
Spruce	Auxanogr.				
	Au — 1	. .	220	. .	. .
	Au — 2	. .	295	. .	. .
	Aver.	. .	257.5	. .	. .
	Girth band				
	B — 3	105	167	52	83
	B — 6	79	126	42	67
	B — 12	77	123	58	92
	Aver.	87.0	138.7	51.0	80.7
Pine	Girth band				
	B — 2	116	185	101	161
	B — 9	144	229	99	158
	B — 10	94	150	. .	. .
	B — 14	110	175	114	181
	Aver.	116.0	196.3	104.6	166.6
Birch	Auxanogr.				
	Au — 3	. .	218	. .	. .
	Au — 4	. .	164	. .	. .
	Aver.	. .	191.0	. .	. .
	Girth band				
	B — 1	69	110	63	100
	B — 4	70	111	49	78
	B — 5	73	116	70	111
	B — 7	44	70	26	41
	B — 8	55	87	41	65
	B — 11	65	103	62	99
	B — 13	109	174	107	170
	Aver.	69.3	110.1	59.7	94.8

A similar study was carried out for the auxanographically obtained mean pine growth at Metsä-Saramäki. The daily mean temperatures from the Hyytiälä weather station about 6 km north of the experimental stand (mean of 8 a.m., 2 p.m., 8 p.m., and computed 2 a.m. temperatures) were summed for the years 1964—1967 for five alternative threshold temperatures (table 12). The threshold recommended by Langlet, + 6° C, proved best in correlation analysis (figure 44). The result is a further indication of the great significance of sufficiently warm weather during the growing season for the total diameter growth of trees.

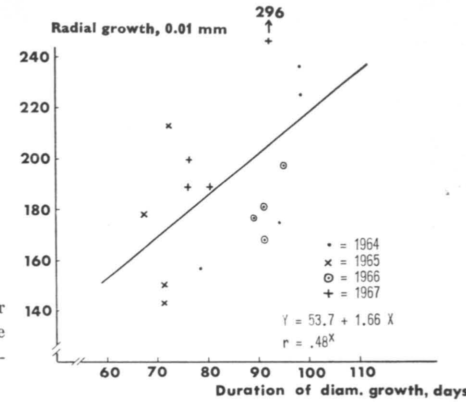

Figure 42. The dependence of diameter growth of pine on the length of the growing season. Metsä-Saramäki, auxanographs, 1964—1967.

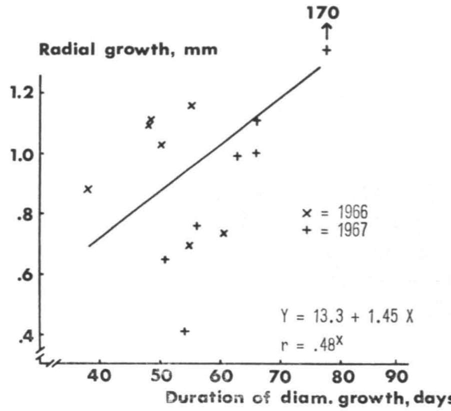

Figure 43. The dependence of diameter growth of birch on the length of the growing season. Huikko, girth bands, 1966—1967.

Table 12. Number of days with the average temperature exceeding various limits, Metsä-Saramäki, 1964—1967.

Year	Radial increment, .01 mm	Average-temperature limit, °C + 2	+ 4	+ 6	+ 8	+ 10
		Number of days				
1964	200	195	181	156	124	101
1965	171	195	172	149	130	103
1966	181	180	166	140	126	102
1967	218	189	174	162	134	120
Correlation between growth and no. of days. D. f. = 3		Correlation coefficient (r)				
		+.04	+.49	+.83*	+.37	+.76

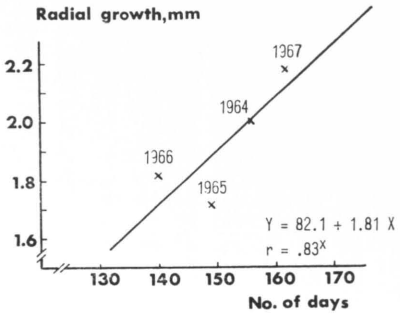

Figure 44. The dependence of diameter growth of pine on the number of days withan average temperature over + 6° C. Metsä-Saramäki, auxanographs, 1964—1967.

15. FORMATION OF LATE WOOD

The annual ring of conifers is traditionally divided into two parts by the anatomic properties of its cells: early wood and late wood. Earlywood cells have large vacuoles and thin walls, latewood cells small vacuoles and thick walls. Mork's method is commonly used in classification: earlywood consists of the cells with a vacuole larger than twice the double cell wall. All the cells with a vacuole smaller than or equal to this are latewood (Wiksten 1945, Andersson 1953, Trendelenburg and Mayer-Wegelin 1955, p. 441—412).

Annual ring formation in the pines of the Metsä-Saramäki experimental stand was studied from microscopic samples in the summers 1964 and 1966 (chapter II 423). The formation of latewood and the time of formation were also studied. In the cells formed before the end of July 1964, the cell wall did not thicken enough to enable distinguishing earlywood and latewood. A distinct trend toward smaller vacuoles was, however, seen (figures 45 and 46). In 1966, smaller vacuoles were produced from the end of June, and the walls of the latewood cells with small vacuoles thickened approximately between the beginning of August and the middle of September (figures 47 and 48).

These observations support the assumption that the cell characteristics distinguishing earlywood and latewood, cell wall thickness and vacuole diameter, are partly independent of each other physiologically. Latewood formation has been explained on highly different grounds, by the increasing mechanical pressure exerted by the bark on the cambium in late summer, by nutritional difficulties, and by pure teological theories (reviews in e.g. Schwarz 1899, Büsgen and Münch 1927, p. 177—183, Ladefoged 1952, Studhalter *et al.* 1963). The most realiable today appears to be the growth hormone theory, supported strongly by e.g. Larson (1962, 1964) by various experiments, stating that the change from early- to latewood is due to the amount of growth hormone produced in the

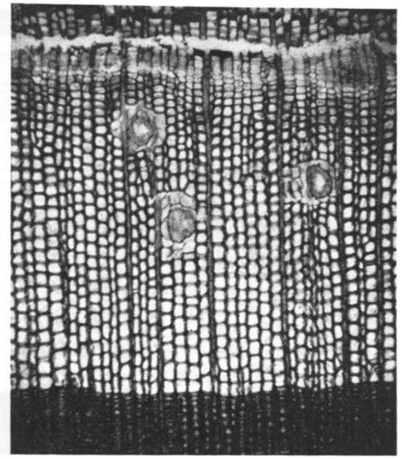

Figure 45. An example of the formation of late wood in pine. Cambium layer shown at the top of the picture. Metsä-Saramäki, sample tree Mn-2. Sampling date July 24, 1964. Magnification 60 x.

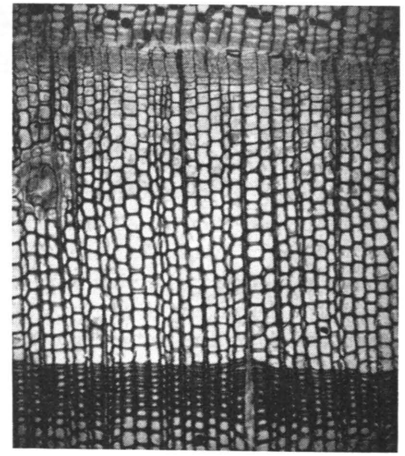

Figure 46. An example of the formation of late wood in pine. Cambium layer shown at the top of the picture. Metsä-Saramäki, sample tree Mn-3. Sampling date July 24, 1964. Magnification 60 x.

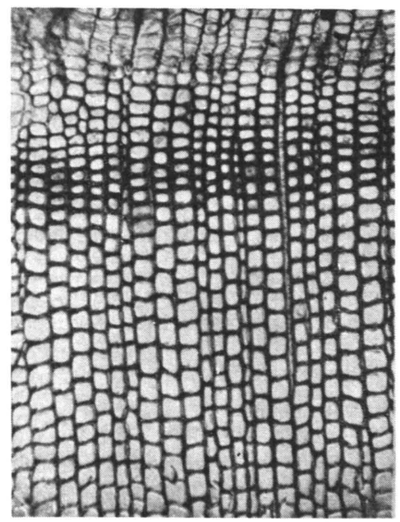

Figure 47. An example of the formation of late wood in pine. Cambium layer shown at the top of the picture. Metsä-Saramäki, sample tree Mn-4. Sampling date August 5, 1966. Magnification 80 x.

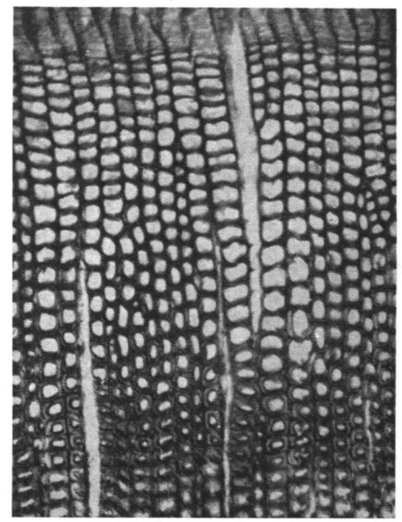

Figure 48. An example of the formation of late wood in pine. Cambium layer shown at the top of the picture. Metsä-Saramäki, sample tree Mn-5. Sampling date August 15, 1966. Magnification 80 x.

green crown in connection with the ending of height growth and the development of the needles. According to this theory, the size of the vacuole in conifers depends primarily on the ending of height growth and the development of buds in the new shoots, while the thickening of cell walls is connected with needle growth. The actual situation is, however, more complex, and the continuing photosynthetic production has been shown to play a considerable role in the thickening of cell walls (e.g. RICHARDSON 1964).

In this connection the physiological mechanism of early- and latewood formation will not be discussed further. However, it ought to be mentioned that e.g. MIKOLA (1950) reaches similar conclusions in his year-ring analytical study. He found that the amount of earlywood formed by pine in Finland is relatively independent of the temperature prevailing during this period, but that the amount of latewood depends on the earliness of the beginning of growth and the temperature of the late part of the summer.

2. DEPENDENCE OF THE DAILY DIAMETER GROWTH ON ENVIRONMENTAL FACTORS

21. COMPUTING THE FIELD DATA

211. REGESSION ANALYSIS IN GROWTH STUDIES

The most common objectives of regression analysis in scientific work are the following (FREESE 1964, p. 9):

— To find a mathematical function that can be used to describe the relationship between a dependent variable and one or more independent variables.

— To test a hypothesis about relationships between a dependent and one or more independent variables.

This study has been carried out with mainly the latter objective in mind.

The simplest multiple regression model is linear (e.g. EZEKIEL 1941, SNEDECOR 1956, DRAPER and SMITH 1967):

$$y = b_0 + b_1x_1 + b_2x_2 + b_3x_3 \ldots b_nx_n,$$

and the individual variables are pretransformed to fit this equation, if their relationships otherwise are non-linear (e.g. DRAPER and SMITH 1967, p. 128—134). This method has been used by e.g. FRITTS (1958, 1959, 1960) in analytical studies of the growth of American beech (*Fagus grandifolia* Ehrl.) in Ohio, USA, and HARMS (1962) in analytical studies of yellow poplar (*Liriodendron tulipifera* L.) growth in West Virginia, USA. In Finland, multiple regression analysis has been used by HUSTICH and ELFVING (1944) in dendrochronologic studies concerning the effect of various climatic factors on the annual diameter growth of pine at northern timber line. Regression analysis has been much used in forest mensurational growth studies (e.g. KUUSELA and KILKKI 1963).

When regression analysis is used, the data must meet certain requirements, and certain restrictions must be kept in mind in the interpretation of the results (cf. FREESE 1964, MÄKELÄ 1968). Some of the basic concepts relevant to this study are listed below:

The methods of collecting data by field measurements and their reliability must be known. No careful and complete computational procedure can be interpreted at a greater accuracy than the representativeness and accuracy of the data. The problem has been thoroughly discussed in chapters II 3 and II 4, separately for measuring the environmental factors and the diameter growth.

When several presumably independent variables are studied simultaneously, sufficient amounts of data must be available for a desired level of probability (cf. e.g. MÄKELÄ 1968, p. 38). In this study, one day (24 hours) was chosen as the basic unit for each variable. The number of replications per variable is thus the same as the number of days in the growing season (tables 6 and 7). In this respect, high requirements are met by the data.

All sets of data analysed by methods based on the assumption that the values are normally distributed, must also meet the following requirements:

— The standard deviation of each value of the dependent variable must be independent of the other values of this variable. However, the weight of this requirement depends considerably on the structure of the set of data studied (cf. e.g. EZEKIEL 1941, p. 349—358). It is clear that the growth observations made on consecutive days may exhibit mutual correlations. E.g. the general pattern of growth described on page 68 may have a role in determining the amount of diameter growth possible at a given position on the curve.

If any considerable autoregression occurs between consecutive increment measurements, it will be included in the residual variance. Thus the ratio of this variance to the variance explained by the independent variables, measured by various tests of reliability, ultimately determines the significance of autoregression to the realiability of the results. — This aspect will be further discussed on page 105.

— The variance of the set of data must be homogeneous. In this study, the daily variation of diameter growth must be independent of the absolute amount of diameter growth, whatever the effect of the environmental factors acting as independent variables in the analysis. — This question will also be discussed later, in connection with the construction of the basic growth series (page 90).

212. CONSTRUCTING THE BASIC GROWTH SERIES

The effect of environmental factors on diameter growth can be studied separately for each tree or from data compiled from several trees. Since the diameter growth of trees will be discussed as a general phenomenon in this study rather than concentrating on the differences between individual trees, the latter method was considered more suitable and adopted (cf. FRITTS 1959, 1960).

The simplest way of constructing a basic growth series is to use unweighted means. Each unit (day) is represented by the mean of the growth measurements made on the day, and the means are directly used in the series. However, unweighted means may introduce considerable errors into the series. It has been found that since the greater absolute variations receive more weight than the smaller ones, a few strongly reacting trees may mask any valuable information provided by several trees exhibiting weaker responses. Therefore, it has been recommended that growth series for individual trees be weighted by their standard deviations, and these standardized series be used to construct the ultimate basic growth series using unweighted means or means weighted by trial-and-error. As the standard deviation of each single tree growth series is given the same value, each tree will receive the same average weight in determining the basic growth series. This method also leads to a decrease of the differences due to variations of different magnitude, and the reliability of the growth analysis will increase.

The basic growth series used in this study were constructed from standardized growth series. For comparison, unweighted growth series were also used for the Metsä-Saramäki data. The data for the different years, the different tree species, and the two experimental stands were treated separately. To allow comparisons between the auxanographic and girth band measurements, the two sets of data were analysed separately. The following basic growth series were constructed for analytical work:

Stand	Year	Species	Measuring device	No. trees
Metsä-Saramäki	1964	pine	auxanograph	4[1]
» »	1964	»	girth band	21[1]
» »	1965	»	auxanograph	4[1]
» »	1966	»	»	4[1]
» »	1966	»	girth band	18[1]
» »	1967	»	auxanograph	4[1]
» »	1967	»	girth band	18[1]
Huikko	1966	spruce	auxanograph	2
»	1966	»	girth band	3
»	1966	pine	»	4
»	1966	birch	auxanograph	2
»	1966	»	girth band	7
»	1967	spruce	»	3
»	1967	pine	»	3
»	1967	birch	»	7

[1] Growth series have been computed using both unweighted and standardized means.

The length of the growing period to be used in the calculation processes was taken directly from tables 6 and 7, indicating the average period of measurable increment of the experimental trees. The number of days during the growing period will be the same as the number of replicas in the analysis.

The computing work was carried out, in constructing the basic growth series, by the IBM 1620 computer of the Computing Center of the University of Helsinki.

It is useful to keep in mind that the auxanograph series are based on measurements of the tree radius at one side, but the girth band measurements have been converted into mean radial values from measurements of the tree girth. The starting and ending points of the series used in computations were determined, as described in chapter III 14, from the cumulative diameter growth curves.

213. EXECUTION OF THE REGRESSION ANALYSIS

The following environmental factors were considered in the analytical work; they were selected according to the principles discussed in chapter II 3:

Environmental factor	Unit of measurement	Year	Site
Metsä-Saramäki			
(Days from the start of growing season ..	number	1964, –65, –66, –67)	
Total solar radiation	cal/sq. cm/day	1964, –66, –67	clearing
Air temperature, maximum	°C	1964, –65, –66, –67	crown lev.
» » minimum	»	1964, –65, –66, –67	» »
» » max.-min.	»	1964, –65, –66, –67	» »
» » degree-hours exc. ± 0°C	h × °C/2	1964, –65, –66, –67	» »
» » + 5°C	»	1964, –65, –66, –67	» »
» » » + 10°C	»	1964, –65, –66, –67	» »
Precipitation	mm	1964, –65, –66, –67	clearing
Rel. air humidity, minimum	%	1964, –65, –66, –67	crown lev.
Wind velocity	m/sec	1964	» »
Soil temperature, maximum	°C	1964, –65, –66, –67	10 cm depth
Huikko			
(Days from the start of growing season ..	number	1966, –67)	
Air temperature, maximum	°C	1966, –67	2 m level
» » minimum	»	1966, –67	»
» » max.-min.	»	1966, –67	»
» » degree-hours exc. ± 0°C	h × °C/2	1966, –67	»
» » » + 5°C	»	1966, –67	»
» » » + 10°C	»	1966, –67	»
Precipitation	mm	1966, –67	clearing
Rel. air humidity, minimum	%	1966, –67	2 m level
Soil temperature, maximum	°C	1966, –67	10 cm depth

Since the diameter growth was determined by the differences of the daily maxima in the auxanograph records, 7 a.m. was chosen for the beginning of the new day. This was also suitable for the girth band measurements, which were made at 8 a.m. in the morning (page 51).

Determining the regression relationship between growth and the individual environmental variables largely rested on assumptions. Theoretically, each growth factor works in about the following way: with an increase in the quantity of a factor, it first passes the low critical point (cardinal point) and it begins to affect the growth process. As the conditions improve for growth, the relative amount of growth for which the growth factor is responsible increases at first and then decreases, and an optimum point is reached where the growth is at a maximum. With increases of the growth factor from this point, growth decreases instead of increasing, and stops at the high critical point (cf. BILLINGS 1952, WENT 1957, DAUBENMIRE 1962, LEOPOLD 1964, and others). In some cases the growth rate may change very little within a considerable range above the growth factor optimum.

In northern Europe, the relationships between the growth of forest trees and the individual environmental factors have been studied from many points of view, but only indirect answers to the present question are available. However, numerous observations indicate that the probably most important factor, air temperature, is linearly correlated with growth in the range studied here (relationships with tree diameter growth, e.g. HUSTICH 1948, SIRÉN 1961, HEIKURAINEN and SEPPÄLÄ 1965, HUIKARI and PAARLAHTI 1967; relationships with height growth, e.g. MORK 1941, DAHL and MORK 1959, and GODSKE 1961), but applying these results directly in this study can still not be done without reservations. — Useful data concerning the other environmental factors are still more scarcely available.

Therefore, the simplest, linear relationship was only studied for all environmental factors. This naturally weakens the model (it should be kept in mind that a strictly linear relationship between an environmental factor and growth is an exception occurring within certain limits rather than a rule), but it is satisfactory in meeting the requirements of this study (cf. however e.g. FRITTS 1959, 1960).

The time relationship of the current increment is fairly well in accordance with the general model (e.g. SMITH 1939, LYR *et al.* 1967, p. 383—388):

$y = ab^{(x-c)^2}$, where a, b, and c are constants.

This model was, however, substituted in this analysis by the simpler parabolic model:

$y = c + bx + ax^2$, where a, b, and c are constants.

The early and late periods of gradually increasing and decreasing growth rates are lost (cf. figures 24—38), but computational work is considerably easier.

The computing work involved in the correlation and regression analyses was entirely carried out by the Elliott 503 computer of the State Computer Center in Helsinki. The programming was based on the principles discussed by RALSTON and WILF (1962).

The hypotheses providing the basis for the computing work were partly also provided by the preliminary study carried out in 1964—1966 on the data from Metsä-Saramäki for the years 1964 and 1965 (LEIKOLA 1966, unpublished).

The computing was carried out in several stages (cf. DRAPER and SMITH 1967, p. 234—242). The first stage was computing the simple correlation coefficients between the various environmental factors and growth. A number of possible combinations were selected of those environmental factors providing the best apparent explanation for growth, for regression models. The combinations were varied, as was also the number of independent variables, in an attempt to find the models explaining diameter growth as well as possible. This method also provided a test for the relative significance of the various environmental factors to diameter growth. The probabilities of individual variables were studied by the t-test (e.g. SNEDECOR 1956, p. 125—159, and others).

22. THE RELATIONSHIP BETWEEN VARIOUS ENVIRONMENTAL FACTORS AND THE DAILY DIAMETER GROWTH

221. SIMPLE CORRELATION ANALYSIS

The coefficients of correlation between the various environmental factors and daily diameter growth for the years 1964—1967 from the data for the experimental stand at Metsä-Saramäki are given in tables 13—16, and those for 1966—1967 for the data from Huikko in tables 17—19.

The following table summarizes the factors in direct correlation with the diameter growth of the same day ($growth_{day\ n}$) at a probability level of at least 95 %:

Diameter growth of trees →	Metsä-Saramäki							Huikko					
	1964		1965	1966		1967		1966			1967		
Environmental factor	au	gb	au	au	gb	au	gb	pi gb	sp gb	bi gb	pi gb	sp gb	bi gb
Max. air temp.	—	—**	+*	—	—	—	—	—	—	+**	—	—	—
Min. air temp.	—	—	+**	—	—	—	—	+**	—	—	+*	—	—
Air temp. diff.	—*	—***	—	—	—**	—	—	—*	—	—	—	—	
Degr. hours exc. ± 0°C	—	—*	+*	—	—	—	—	—	—	+**	—	—	—
Degr. hours exc. + 5°C	—	—*	+*	—	—	—	—	—	—	+**	—	—	—
Degr. hours exc. + 10°C	—	—*	+*	—	—	—	—	—	—	+**	—	—	—
Precipitation	+***	+***	—	+***	+***	+***	+***	+***	+***	—	+***	+***	+***
Rel. air humidity	+*	+***	—	—	+**	+*	+**	+**	—	—	+*	+*	—
Total solar radiation ..	—**	—***	..	—	—	—**	—***	..	..	..	..	..	..
Wind velocity	—	—	..	..	..	..	..	..	..	..	..	..	..
Soil temperature	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 13. Correlation coefficients between the daily diameter growth and the environmental factors. Metsä-Saramäki, 1964, (d.f. = 93).

Row	Day	Daily diam. growth		Max. air temp.	Min. air temp.	Diff. T max- T min.	Degr. hours > ± 0° C	Degr. hours > + 5° C	Degr. hours > + 10° C	Air humidity	Wind velocity	Solar radiation	Soil temper- ature	Precipita- tion
		Incr. meas. device	Method of basic series con- struction	1	2	3	4	5	6	7	8	9	10	11
1	n	Aux.	Arithm.	.001	.203*	−.228*	.046	.046	−.028	.262*	.184	−.301**	−.087	.504***
2	n	Aux.	Stand.	.003	.199	−.223*	.045	.044	.028	.260*	.176	−.302**	−.088	.503***
3	n	Girth bd.	Stand.	−.261**	.064	−.392***	−.219*	−.224*	−.258*	.368***	.254	−.381***	−.184	.691***
4	n + 1	Aux.	Arithm.	.039	−.038	.097	.081	.079	.084	−.333**	.209	.416***	−.031	−.156
5	n + 1	Aux.	Stand.	.032	−.048	.101	.070	.068	.074	−.311**	.199	.405***	−.039	−.127
6	n + 1	Girth bd.	Stand.	.195	.136	.078	.157	−.159	−.163	−.012	.232*	.146	−.170	−.161
7	n + 2	Aux.	Arithm.	−.048	−.137	.097	−.048	−.048	−.049	−.076	.085	.143	−.085	−.122
8	n + 2	Aux.	Stand.	−.071	−.145	.079	−.063	−.064	−.069	−.071	.092	.136	−.092	−.077
9	n + 2	Girth bd.	Stand.	−.155	−.168	.004	−.110	−.114	−.124	−.010	.166	.104	−.127	−.120

Table 14. Correlation coefficients between the daily diameter growth and the environmental factors. Metsä-Saramäki, 1965, (d.f. = 72).

Row	Day	Daily diam. growth		Max. air temp.	Min. air temp.	Diff. Tmax- Tmin.	Degr. hours > ± 0° C	Degr. hours > + 5° C	Degr. hours > + 10° C	Air humidity	Wind velocity	Precipi- tation
		Incr. meas. device	Method of basic series con- struction	1	2	3	4	5	6	7	8	9
1	n	Aux.	Arithm.	.200	.339**	−.075	.248*	.250*	.228	.200	−.001	.201
2	n	Aux.	Stand.	.248*	.357**	−.033	.291*	.293*	.272*	.156	.014	.180
3	n + 1	Aux.	Arithm.	.405***	.170	.336**	.394***	.400***	.406***	−.453***	.004	−.198
4	n + 1	Aux.	Stand.	.433***	.195	.346**	.429***	.435***	.440***	−.445***	.003	−.204
5	n + 2	Aux.	Arithm.	.243*	.088	.219	.221	.221	.235*	−.220	−.059	−.197
6	n + 2	Aux.	Stand.	.268*	.103	.237*	.245*	.245*	.262*	−.238*	−.069	−.208

Table 15. Correlation coefficients between the daily diameter growth and the environmental factors. Metsä-Saramäki, 1966, (d.f. = 85).

Row	Day	Daily diam. growth		Max. air temp.	Min. air temp.	Diff. Tmax- Tmin.	Degr. hours > ± 0° C	Degr. hours > + 5° C	Degr. hours > + 10° C	Air humidity	Solar radiation	Soil temper- ature	Precipita- tion
		Incr. meas. device	Method of basic series con- struction	1	2	3	4	5	6	7	8	9	10
1	n	Aux.	Arithm.	.108	.176	−.029	.105	.100	.106	.031	.096	−.071	.417***
2	n	Aux.	Stand.	.124	.160	.013	.108	.104	.112	−.006	.116	−.099	.407***
3	n	Girth bd.	Stand.	−.053	.182	−.321**	−.030	−.003	−.034	.360**	−.228	−.024	.530***
4	n + 1	Aux.	Arithm.	.203	.037	.265*	.183	.174	.172	−.409***	.348***	−.067	−.358***
5	n + 1	Aux.	Stand.	.213	.016	.306**	.181	.172	.182	−.465***	.387***	−.099	−.418***
6	n + 1	Girth bd.	Stand.	.287**	.127	.283*	.245**	.267*	.262*	−.384***	.369***	.041	−.281**
7	n + 2	Aux.	Arithm.	.208	−.085	.406***	.090	.104	.114	−.524***	.337**	−.113	−.262*
8	n + 2	Aux.	Stand.	.155	−.139	.382***	.038	.051	.069	−.481***	.270*	−.163	−.279*
9	n + 2	Girth bd.	Stand.	.221*	.165	.149	.223*	.249*	.246*	−.165	.194	.073	.083

Table 16. Correlation coefficients between the daily diameter growth and the environmental factors. Metsä-Saramäki, 1967, (d.f. = 81).

Row	Day	Daily diam. growth		Max. air temp.	Min. air temp.	Diff. Tmax- Tmin.	Degr. hours ± 0° C	Degr. hours + 5° C	Degr. hours + 10° C	Air humidity	Solar radiation	Soil temper- ature	Precipita- tion
		Incr. meas. device	Method of basic series con- struction	1	2	3	4	5	6	7	8	9	10
1	n	Aux.	Arithm.	.007	.082	−.129	−.000	.000	−.009	.302**	−.333**	−.030	.703***
2	n	Aux.	Stand.	.017	.074	−.100	.004	.005	−.005	.263*	−.312**	−.045	.683***
3	n	Girth bd.	Stand.	−.110	−.008	−.200	−.143	−.138	−.153	.353**	−.418***	−.010	.616***
4	n + 1	Aux.	Arithm.	.253*	.159	.168	.272*	.281**	.275*	−.431***	.287**	.064	−.159
5	n + 1	Aux.	Stand.	.253*	.136	.184	.268*	.278*	.274*	−.452***	.309**	.050	−.160
6	n + 1	Girth bd.	Stand.	.122	.165	−.056	.163	.166	.150	−.099	.054	.090	.177
7	n + 2	Aux.	Arithm.	.198	−.086	.215	.158	.159	.185	−.261*	.288**	.134	−.169
8	n + 2	Aux.	Stand.	.196	−.104	.231*	.140	.142	.169	−.263*	.286**	.114	−.166
9	n + 2	Girth bd.	Stand.	.188	.028	.169	.176	.178	.187	−.133	.122	.157	.057

Table 17. Correlation coefficients between the daily diameter growth and the environmental factors. Huikko, 1966, pine and spruce.

Row	Day	Daily diam. growth		Max. air temp.	Min. air temp.	Diff. Tmax-Tmin.	Degr. hours > ± 0° C	Degr. hours > + 5° C	Degr. hours > + 10° C	Air humidity	Soil temperature	Precipitation
		Incr. meas. device	Method of basic series construction	1	2	3	4	5	6	7	8	9
		Pine (d.f. = 87)										
1	n	Girth bd.	Stand.	−.038	.285**	−.238*	.053	.047	.023	.292**	097.	.533***
2	n + 1	Girth bd.	Stand.	.241*	.271*	.025	.290**	.288**	.300**	−.153	.081	.032
		Spruce (d.f. = 85)										
3	n	Aux.	Arithm.	.129	.168	−.023	.139	.141	.133	−.060	−.047	.403***
4	n	Girth bd.	Stand.	.030	.104	−.013	.105	.098	.105	.058	.069	.342**
5	n + 1	Aux.	Arithm.	.223*	−.085	.346**	.161	.187	.275*	−.407***	−.095	−.400***
6	n + 1	Girth bd.	Stand.	.347**	.169	.216*	.345**	.355***	.385***	−.367***	.032	−.075

Table 18. Correlation coefficients between the daily diameter growth and the environmental factors. Huikko 1966, birch, (d.f. = 57).

Row	Day	Daily diam. growth		Max. air temp.	Min. air temp.	Diff. Tmax-Tmin.	Degr. hours > ± 0° C	Degr. hours > + 5° C	Degr. hours > + 10° C	Air humidity	Soil temperature	Precipitation
		Incr. meas. device	Method of basic series construction	1	2	3	4	5	6	7	8	9
1	n	Aux.	Arithm.	.357**	.405**	−.021	.426***	.412***	.361**	−.169	.046	.024
2	n	Girth bd.	Stand.	.343**	.250	.110	.371**	.365**	.344**	−.181	−.017	.042
3	n + 1	Aux.	Arithm.	.439***	.183	.323*	.447***	.445***	.450***	−.486***	−.061	−.265*
4	n + 1	Girth bd.	Stand.	.406**	.161	.307*	.429***	.434***	.442***	−.445***	−.127	−.108

Table 19. Correlation coefficients between the daily diameter growth and the environmental factors. Huikko, 1967.

Row	Day	Daily diam. growth		Max. air temp.	Min. air temp.	Diff. Tmax-Tmin.	Degr. hours > ± 0° C	Degr. hours > + 5° C	Degr. hours > + 10° C	Air humidity	Soil temperature	Precipitation
		Incr. meas. device	Method of basic series construction	1	2	3	4	5	6	7	8	9
		Pine (d.f. = 70)										
1	n	Girth bd.	Stand.	.098	.263*	−.122	.074	.053	.009	.240*	.013	.585***
2	n + 1	Girth bd.	Stand.	.321**	.142	.178	.232*	.237*	.211	−.225	.010	.066
		Spruce (d.f. = 50)										
3	n	Girth bd.	Stand.	.059	.262	−.137	−.001	−.021	−.066	.336*	−.125	.729***
4	n + 1	Girth bd.	Stand.	.195	.255	.002	.225	.216	.165	−.205	−.093	.029
		Birch (d.f. = 49)										
5	n	Girth bd.	Stand.	.064	.082	−.017	−.042	−.042	−.075	.049	−.065	.550***
6	n + 1	Girth bd.	Stand.	.139	−.015	.133	.093	.088	.038	−.202	−.124	−.104

The most consistent feature of the table is the high positive correlation between the daily precipitation and growth in all cases except the auxanograph records for 1965 at Metsä-Saramäki and the girth band records for Huikko birch for 1966. Relative air humidity has also been positively correlated with growth in most years. The air temperature variables and the amount of total solar radiation have either been negatively correlated or exhibit no significant correlation. The only distinct exceptions are the observation series already mentioned, the Metsä-Saramäki 1965 auxanograph records and the 1966 Huikko girth band records for birch. In the individual correlations, the negative correlation between the maximum and minimum air temperature difference and diameter growth, occurring in several years, and the total lack of correlation between soil temperature and the diameter growth of trees, are also interesting.

Before further conclusions can be made about the results of correlation analysis, the mutual correlation coefficients for the various environmental factors in tables 20—25 should be examined. For the Huikko stand, only the conditions for the longest growing season, that of pine diameter growth, are given. Similar relationships were found for the shorter growing seasons of spruce and birch, and the values of the correlation coefficients exhibited small differences from those shown in the tables.

The total environment composed by various factors can be discussed for two combined factors, according to the results, the radiation-temperature factor and the humidity-precipitation factor. These factors have also been recognized elsewhere (cf. e.g. Geiger 1965, Mitscherlich *et al.* 1965 a, b, 1966, Kern 1966). E.g. the strong negative correlation between daily precipitation and maximum air temperature could be expressed simply by stating that the daily maximum temperatures are lower on rainy on than rainless sunny days.

In regression analysis, the network of mutual correlations between the independent variables in this analysis (multicollinearity) makes the interpretation of results difficult (cf. Riihinen 1962, p. 32—33, Mäkelä 1968, p. 39). Since it has the greatest effect when several variables are simultaneously considered, it will be further discussed on page 117.

The hydrostatic diameter changes discussed in chapter II 42242 should also be dealt with in connection with correlation analysis. All devices used for measuring tree diameter growth on top of the bark register diameter growth as well as the temporary, reversible diameter changes. Thus both have been introduced into the correlation analysis as a part of the same variable. Despite all the measures were taken to obtain true diameter readings, and although only the maximum daily hydrostatic values were considered in the analysis, a major part of the correlations found between the environmental factors and the diameter growth of the same day are probably due to the rapid hydrostatic diameter changes of the stem. A swelling of the stem exceeding normal hydrostatic values, within a few hours in heavy rain, has been recorded simultaneously as the

Table 20. The mutual correlation coefficients between the environmental factors during the growing season. Metsä-Saramäki, 1964, (d.f. = 93).

Environmental factor	1	2	3	4	5	6	7	8	9	10	11
1 Max. air temperature	1.000										
2 Min. air temperature	.628***	1.000									
3 Diff. T max. – T min.	.515***	–.319**	1.000								
4 Degr. hours > ± 0° C	.924***	–.790***	.259*	1.000							
5 Degr. hours > + 5° C	.926***	.780***	.272**	.999***	1.000						
6 Degr. hours > + 10° C	.925***	.711***	.146***	.976***	.981***	1.000					
7 Air humidity	–.442***	.038	–.564***	–.330**	–.338***	–.381***	1.000				
8 Wind velocity	–.022	.110	–.165	.028	.027	.001	–.027	1.000			
9 Solar radiation	.394***	–.065	.566***	.307**	.319**	.362***	–.768***	.160	1.000		
10 Soil temperature	.621***	.692***	.007	.650***	.640***	.586***	.003	–.108	.006	1.000	
11 Precipitation	–.259*	.089	–.408***	–.189	–.197	–.243*	.181	.104	–.309**	–.344***	1.000

Table 21. The mutual correlation coefficients between the environmental factors during the growing season. Metsä-Saramäki, 1965, (d.f. = 72).

Environmental factor	1	2	3	4	5	6	7	8	9
1 Max. air temperature	1.000								
2 Min. air temperature	.587***	1.000							
3 Diff. T max. – T min.	.669***	–.206	1.000						
4 Degr. hours > ± 0° C	.925***	.778***	.405***	1.000					
5 Degr. hours > + 5° C	.931***	.743***	.445***	.995***	1.000				
6 Degr. hours > + 10° C	.937***	.626***	.560***	.958***	.976	1.000			
7 Air humidity	–.534***	.155	–.789***	–.344*	–.374*	–.468***	1.000		
8 Soil temperature	.546***	.645***	.079	.618***	.591**	.499***	.145	1.000	
9 Precipitation	–.258*	.117	–.415***	–.211	–.236*	–.290*	.500***	.118	1.000

Table 22. The mutual correlation coefficients between the environmental factors during the growing season. Metsä-Saramäki, 1966, (d.f. = 86).

Environmental factor	1	2	3	4	5	6	7	8	9	10
1 Max. air temperature	1.000									
2 Min. air temperature	.773***	1.000								
3 Diff. T max. — T min.	.679***	.082	1.000							
4 Degr. hours > ± 0° C	.939***	.874***	.472***	1.000						
5 Degr. hours > + 5° C	.916***	.843***	.472***	.977***	1.000					
6 Degr. hours > + 10° C	.920***	.807***	.516***	.975***	.958***	1.000				
7 Air humidity	−.587***	−.113	−.794***	−.459***	−.458***	−.489***	1.000			
8 Solar radiation	.677***	.366***	.644***	.616***	.600***	.623***	−.795***	1.000		
9 Soil temperature	.676***	.795***	.165	.765***	.754***	.708***	−.060	.285**	1.000	
10 Precipitation	−.263*	.035	−.399***	−.234*	−.229*	−.273*	.496***	−.447***	.021	1.000

Table 23. The mutual correlation coefficients between the environmental factors during the growing season. Metsä-Saramäki, 1967, (d.f. = 81).

Environmental factor	1	2	3	4	5	6	7	8	9	10
1 Max. air temperature	1.000									
2 Min. air temperature	.686***	1.000								
3 Diff. T max. — T min.	.596***	−.116	1.000							
4 Degr. hours > ± 0° C	.931***	.831***	.358***	1.000						
5 Degr. hours > + 5° C	.930***	.830***	.357***	.999***	1.000					
6 Degr. hours > + 10° C	.912***	.812***	.344**	.989***	.991***	1.000				
7 Air humidity	−.505***	−.004	−.682***	−.382***	−.383***	−.392***	1.000			
8 Solar radiation	.514***	.014	.694***	.404***	.403***	.404***	−.806***	1.000		
9 Soil temperature	.765***	.664***	.305**	.785***	.787***	.767**	−.158	.340**	1.000	
10 Precipitation	−.179	.001	−.279*	−.193	−.194	−.213	.487***	−.510***	−.083	1.000

Table 24. The mutual correlation coefficients between the environmental factors during the growing season of pine. Huikko, 1966, (d.f. = 82).

Environmental factor	1	2	3	4	5	6	7	8	9
1 Max. air temperature	1.000								
2 Min. air temperature	.466***	1.000							
3 Diff. T max. — T min.	.425***	−.086	1.000						
4 Degr. hours > ± 0° C	.934***	.706***	.280**	1.000					
5 Degr. hours > + 5° C	.941***	.675***	.297**	.995***	1.000				
6 Degr. hours > + 10° C	.941***	.565***	.331**	.862***	.979***	1.000			
7 Air humidity	−.505***	.234*	−.362***	−.292**	−.328**	−.421***	1.000		
8 Soil temperature	.593***	.641***	.161	.713***	.690***	.604***	.244*	1.000	
9 Precipitation	−.262*	.185	−.136	−.164	−.173	−.239*	.424***	.092	1.000

Table 25. The mutual correlation coefficients between the environmental factors during the growing season of pine. Huikko, 1967, (d.f. = 70).

Environmental factor	1	2	3	4	5	6	7	8	9
1 Max. air temperature	1.000								
2 Min. air temperature	.336**	1.000							
3 Diff. T max. — T min.	.645***	−.494***	1.000						
4 Degr. hours > ± 0° C	.854***	.573***	.323**	1.000					
5 Degr. hours > + 5° C	.864***	.547***	.355**	.997***	1.000				
6 Degr. hours > + 10° C	.878***	.462***	.440***	.975***	.983***	1.000			
7 Air humidity	−.313**	.300**	−.532***	−.219	−.241*	−.292*	1.000		
8 Soil temperature	.615***	.519***	.135	.714***	.712***	.670***	.155	1.000	
9 Precipitation	−.067	.255*	−.278*	−.045	−.062	−.130	.467***	.131	1.000

variables representing the radiation-temperature factor, e.g. maximum air temperature, have exhibited unusually low values. A correlation results which has only apparent significance in relation to growth.

After it was found that the daily tree diameter changes during the growing season were probably greatly affected by hydrostatic changes, it was decided that the correlations between the environmental factors on a given day (day n) and growth on the following day (day n+1) will be computed. This computation thus provides no solution for a complete chronological analysis of the various environmental factors; rather, it is restricted to the relationship:

environmental $\text{factors}_{\text{day n}}$ / diameter $\text{growth}_{\text{day n+1}}$.

The following arguments are presented in favor of this method:

— Despite the possibility that the diameter growth of trees is directly related to prevailing environmental condititions, it is more natural to presume — especially in the case of full-size trees — that a time interval is necessary, considering e.g. the rate of cell division (cf. WILHELMI 1960, KOZLOWSKI *et al.* 1962).

— The hydrostatic effects of rain persisting after a day have only a small effect on tree diameter. This is especially so for the maximum daily diameter (e.g. MAC DOUGAL 1938, KERN 1961). However, e.g. HUIKARI and PAARLAHTI (1967) have found hydrostatic swelling persisting after 2—3 days.

The correlation coefficients obtained at this stage are also shown in tables 13—19. A summary presentation of the new correlations, constructed as the one on page 93, follows:

Diameter growth of trees →	Metsä-Saramäki							Huikko					
	1964		1965	1966		1967		1964			1965		
Environmental factor	au	gb	au	gb	au	au	gb	pi gb	sp gb	bi gb	pi gb	sp gb	bi gb
Max. air temperature ..	—	—	+***	+*	+**	+*	—	+*	+**	+**	+**	—	—
Min. air temperature ..	—	—	—	—	—	—	—	+*	—	—	—	—	—
Air temp. difference ..	—	—	+**	+**	+*	—	—	—	+*	+*	—	—	—
Degr. hours exc. ± 0°C	—	—	+***	—	+**	+*	—	+**	+**	+***	+*	—	—
Degr. hours exc. + 5°C	—	—	+***	—	+*	+*	—	+**	+***	+***	+*	—	—
Degr. hours exc. + 10°C	—	—	+***	—	+*	+*	—	+**	+***	+***	—	—	—
Precipitation	—	—	—	—***	—**	—	—	—	—	—	—	—	—
Rel. air humidity	—**	—	—***	—***	—***	—***	—	—	—***	—***	—	—	—
Total solar radiation ..	+***	+**	..	+***	+***	+**	—	..	..	..	..	..	..
Wind velocity	—	—	..	..	..	..	..	..	..	..	..	..	..
Soil temperature	—	—	—	—	—	—	—	—	—	—	—	—	—

The results differ considerably from those of the previous summarization. Now, maximum air temperature, the temperature sums computed using various threshold temperatures, and the amount of total solar radiation are highly and positively correlated with diameter growth in practically every year. Relative air humidity is in most years negatively correlated, and the daily amount of precipitation, which decisively determined growth responses in the previous summary, attains a significant, but negative, correlation only for the 1966 data from the Metsä-Saramäki stand. Wind velocity and soil temperature again show no correlation with diameter growth.

On the basis of a careful examination of the results, it was decided that

computing will be continued, using daily growth data and the values of the environmental factors for the preceding day. It was, however, decided to try out the relationship between daily diameter growth and the environmental conditions two days earlier (environmental $\text{factors}_{\text{day n}}$ / diameter $\text{growth}_{\text{day n+2}}$). The correlation coefficients for this are also shown in tables 13—16 for the Metsä-Saramäki stand. A summary presentation of the new correlations at a level of probability of at least 95 %, constructed as those on pages 93 and 102, follows:

Diameter growth of trees →	Metsä-Saramäki						
	1964		1965	1966		1967	
Environmental factor	au	gb	au	au	gb	au	gb
Max. air temperature	—	—	+*	—	+*	—	—
Min. air temperature	—	—	—	—	—	—	—
Air temp. difference	—	—	+*	+***	—	+*	—
Degr. hours exc. ± 0°C	—	—	+*	—	+*	—	—
Degr. hours exc. + 5°C	—	—	+*	—	+*	—	—
Degr. hours exc. + 10°C	—	—	+*	—	+*	—	—
Precipitation	—	—	—	—	—	—	—
Rel. air humidity	—	—	—*	—***	—	—*	—
Total solar radiation	—	—	..	+*	—	+**	—
Wind velocity	—	—	..	..	..	..	..
Soil temperature	—	—	—	—	—	—	—

The correlations are now distinctly lower than those between daily diameter growth and the environmental factor values of the preceding day. The general relationships are otherwise similar to the ones in the preceding summarization: the variables representing air temperature and solar radiation are positively, and those representing air humidity negatively correlated with growth.

The analytical stage led to the conclusion that a two-day lag will not offer the best explanations of the diameter growth-environment relationship (cf. FRITTS 1960, KOZLOWSKI *et al.* 1962). It was, however, decided that supplementary regression analysis will be carried out for the Metsä-Saramäki stand for the setup:

environmental $\text{factors}_{\text{day n}}$ / diameter $\text{growth}_{\text{day n + 2}}$.

222. MULTIPLE REGRESSION ANALYSIS

2221. The relationship between various environmental factors and diameter growth on the following day

The major results of regression analysis for the experimental stand at Metsä-Saramäki are shown in appendix 3 and the one at Huikko in appendix 4. Since the selection of environmental variables followed correlation analysis, the results of this work led to the choice of slightly different variable combinations for the various years and the different tree species.

In general, the results of the regression analyses are rather similar to those of correlation analyses. The reliability of the results has increased, however, with the use of several environmental variables instead of computing simple correlations. The effect of the mutual correlations between the independent variables of the analysis on the true significance of the analysis in pointing out the causal relationships of diameter growth, probably distorts the tables and has to be considered. Since the multicollinearity of the variables (cf. page 98) tends to increase the numerical value of the multiple correlation coefficient (R) especially, when the number of variables is large, this symbol has been repleaced by the less misleading coefficient of determination (R^2) (Ezekiel 1941, p. 210—213, and others). The numerical values of the regression coefficients have also been dropped from the tables, since they are of little value by themselves in growth studies of this kind, and their accuracy can be questioned on the basis of the reasons stated.

The independent variables will be discussed in the order they appear in the tables of appendices 3 and 4.

It is somewhat surprising that the parabolic function of the effect of the t i m e f a c t o r alone (number of days from the beginning of the growing season) in the Metsä-Saramäki stand provided a significant explanation for the diameter growth of pine for none of the four observation years, and the combined daily effect of the environmental factors masked it almost entirely. No explanation for pine diameter growth was provided by the number of days at Huikko, either, but the relationship was significant for spruce and birch in both years of observation. Several reasons can be given for the difference, a hereditary difference in the manner of growth probably being a major one. The rate of diameter growth expressed as mean daily diameter increment apparently has no effect on the phenomenon. The daily diameter increment of the pines studied at Huikko was larger than that of the spruces and birches in 1966 and 1967, as is shown by the following comparative summary of their mean growth:

Year	Tree species	Mean radial increment, μ/day	
		Girth bands	Auxanographs
1966	Pine	25.5	. .
1966	Spruce	22.3	30.3
1966	Birch	21.5	32.9
1967	Pine	24.1	. .
1967	Spruce	11.4	. .
1967	Birch	15.3	. .

Rather, it would be natural to presume that the daily deviations of diameter growth from the mean are significant in this respect. This can be seen in comparing the coefficients of variation of the diameter growth of the species:

Year	Tree species	The coefficient of variation (C) of the daily diameter growth	
		Girth bands	Auxanographs
1966	Pine	1.77	. .
1966	Spruce	1.35	1.47
1966	Birch	0.63	0.79
1967	Pine	1.53	. .
1967	Spruce	2.09	. .
1967	Birch	0.79	. .

It can also be said that since the effect of time alone on growth was insignificant at e.g. Metsä-Saramäki, as compared to daily variations, the value of the model including the environmental factors increases in explaining growth. Also the reservations introduced by the autoregression of diameter growth (cf. page 89) and its significance in the growth study can be dealt with more lightly.

As could be expected, m a x i m u m a i r t e m p e r a t u r e is one of the environmental factors exerting a strong effect on diameter growth. The only exceptions of this general result are the 1964 data and the 1967 girth band data from Metsä-Saramäki. It is, however, very difficult to find the reasons for these exceptions without additional study. Nothing indicates that the temperature conditions in 1964 were exceptional as compared with the other field years. This is also indicated by the mean temperature maxima of the growing seasons:

Year	Mean maximum temperature	Standard deviation (s)
1964	18.8° C	4.2° C
1965	16.6° C	4.4° C
1966	19.4° C	5.2° C
1967	19.3° C	4.3° C

M i n i m u m a i r t e m p e r a t u r e exhibits a much lower significance in the analysis than the daily maximum temperature. The greater role of this factor in explaining pine growth at Huikko in 1966 than of maximum air temperature is probably due rather to the poor maximum temperature correlation than the good minimum temperature correlation.

The reasons for the role of minimum air temperature in most growth analyses are probably found in the rather high correlation of the temperature extremes and the resulting indirect causal relationship. Still, other factors like connections with the physiology of tree growth and the daily energy balance may also be worth considering.

The significance of the difference between the daily temperature extremes was also tested, but it was low in almost all cases. It should be noted that according to correlation analysis, daily maximum temperature is practically the sole determinant of the difference between the extreme temperatures. However, since this factor is far from reaching the significance of the preceding factor, it is most certain to reach the same conclusions as for the minimum air temperature. It should still be mentioned that many research workers have in several connections emphasized the significance of temperature variations and an adequate temperature range to the growth of trees (e.g. Kramer 1957, Richardson 1964).

The effect of temperature on diameter growth was also studied by temperature sums, daily cumulative degree-hours computed using three different threshold temperatures. It is understandable that these variables provided regression relationships with higher levels of significance than the daily extreme temperatures or their difference. It is interesting to compare the threshold temperatures used in the computations. Figure 49 shows the per cent decrease in the daily total standard deviations of diameter growth due to the introduction of the degree hours computed by the different threshold temperatures. The + 10° C threshold is generally much less effective than the others. The only exceptions are the spruce and birch auxanographic records from Huikko in 1966, for which this is most effective, but even the girth band measurements in the same year do not support generalizations of the result. This detail may still have some significance, since the stand at Huikko is generally cooler than the one at Metsä-Saramäki and the temperature difference is most distinct in the daily temperature minima, as is seen in the following summary of the daily means of the air temperature variables:

Exp. stand	Year	T max., °C	T min., °C	Daily degree-hours, aver.		
				exc. ± 0° C	exc. + 5° C	exc. + 10° C
Metsä-Saramäki	1966	19.4	10.2	181.1	120.6	66.6
»	1967	19.3	10.2	178.9	119.1	63.4
Huikko	1966	18.8	6.3	160.3	102.8	53.2
»	1967	19.0	6.8	163.6	105.3	55.4

Although exactly the same periods of time are not shown for the two stands, the differences in the temperature conditions are still clear. Against this background, also the physiological differences between the tree species, especially the responses to low temperatures during the growing season, are important.

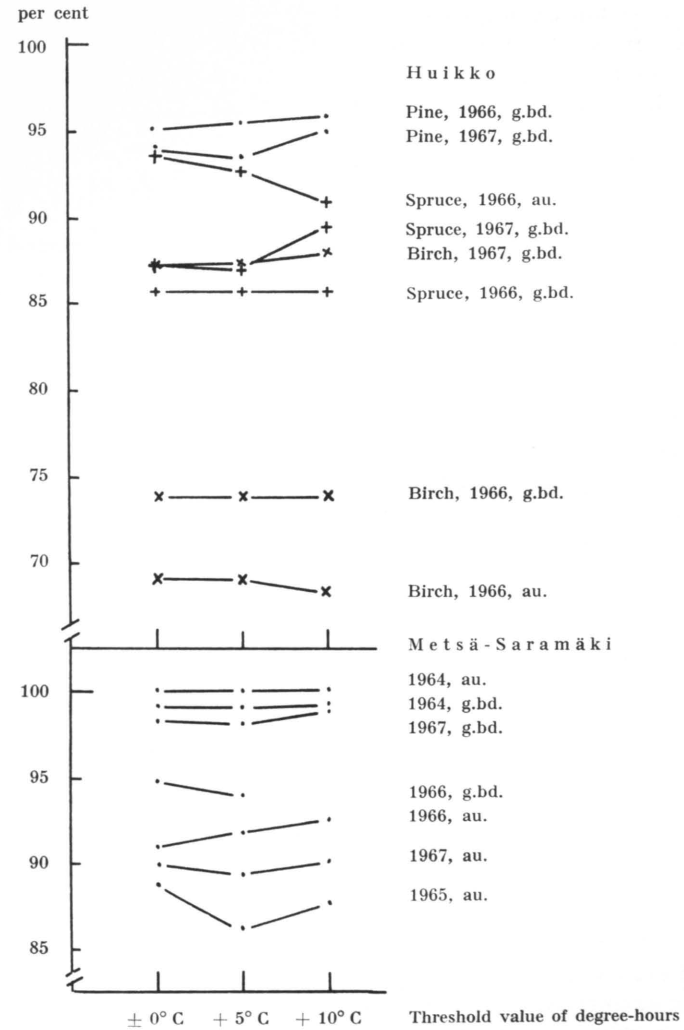

Figure 49. The decrease in the daily total standard deviation of diameter growth due to degree-hours computed by three different threshold temperatures. Relative values from the original standard deviations of growth.

It is more difficult to select the more useful of the two lower threshold temperatures. It seems that in the stand at Metsä-Saramäki the $+5°$ C threshold provides a better explanation for growth, while the two temperatures are about equal at Huikko. This result supports the earlier conclusion (page 64) that the threshold value of the temperature sum providing the best explanation falls between $\pm 0°$ C and $+5°$ C, closer to the latter.

S o l a r r a d i a t i o n was only measured in three years at Metsä-Saramäki. Attention is drawn by the fact that in 1964 this factor has explained a larger part of the growth variation in the regression analysis than any air-temperature variable. In the two other years (1966 and 1967), however, these factors have explained practically equal parts of the variation. Considering the fairly high correlation between air temperature and solar radiation, this result is not unexpected, but the degree of explanation provided by solar radiation is still higher in connection with the other environmental variables than would be expected on purely this basis.

In correlation analysis, s o i l t e m p e r a t u r e was found to have no effect on the daily diameter growth on the desired level of significance, and the factor also decreased the level of significance of regressions, when introduced after air temperature and total solar radiation, for the Metsä-Saramäki stand. This was also true for Huikko, except for the auxanographic records for birch in 1966 and the girth band measurements of pine in 1967. The effect on pine growth was, however, very small.

Several explanations are available for the low correlation of soil temperature with growth. The variation of soil temperature at a depth of 10 cm is, as is well known, rather small (e.g. Franssila 1961), and too many of the data fall within too narrow limits of variation. It is also quite possible that the daily soil temperature changes are not seen in tree growth on the following day, but the favorable or unfavorable environmental conditions of the roots are seen in the responses of the cambium layer of the stem after a long chain of reactions, much later.

W i n d v e l o c i t y was only measured in 1964 at Metsä-Saramäki. In correlation analysis, no significant growth relationships were discovered, but its addition to three regression equations, combined in different ways, decreased the residual variance of all of these. It is, however, difficult to find the actual role of this factor in determining growth (cf. chapter II 326). It is possible that wind is a nice-weather variable, indicated by the fact that of the other environmental variables it exhibits one of the highest correlations with solar radiation (table 20). It must be emphasized, however, that a high rate of air flow on foliar surfaces may affect photosynthesis and diameter growth.

In successive work, various environmental-factor combinations were introduced into multiple regression equations to find the best explanations for daily diameter growth. The selection of variables for these combinations must be done with utmost care. It can generally be said that the best combinations

provided a 25 % reduction in the residual variance, with the exception of the 1966 birch growth equations providing a 50 % reduction.

The best environmental factor combinations for the different years, experimental stands, measuring devices, and tree species are summarized here:

Metsä-Saramäki 1964, auxanographs:
day + day^2 + T_{max} + sol.rad. + d.h. $> \pm 0°$ C
Metsä-Saramäki 1964, girth bands:
day + day^2 + T_{max} + T_{diff} + sol.rad. + wind vel.
Metsä-Saramäki 1965, auxanographs:
day + day^2 + T_{diff} + d.h. $> \pm 0°$ C
Metsä-Saramäki 1966, auxanographs:
day + day^2 + sol.rad. + d.h. $> \pm 0°$ C
Metsä-Saramäki 1966, girth bands:
day + day^2 + sol.rad. + d.h. $> +5°$ C
Metsä-Saramäki 1967, auxanographs:
day + day^2 + T_{max} + sol.rad. + d.h. $> +5°$ C
Metsä-Saramäki 1967, girth bands:
day + day^2 + T_{max} + T_{diff} + sol.rad. + d.h. $> +5°$ C + T_{soil}
Huikko 1966, pine, girth bands:
day + day^2 + T_{max} + d.h. $> \pm 0°$ C
Huikko 1966, spruce, auxanographs:
day + day^2 + T_{max} + T_{diff} + d.h. $> +10°$ C
Huikko 1966, spruce, girth bands:
day + day^2 + T_{max} + T_{diff} + d.h. + $> 5°$ C + T_{soil}
Huikko 1966, birch, auxanographs:
day + day^2 + T_{max} + T_{min} + T_{diff}
Huikko 1966, birch, girth bands:
day + day^2 + T_{max} + T_{min} + T_{diff}
Huikko 1967, pine, girth bands:
day + day^2 + T_{max} + T_{diff}
Huikko 1967, spruce, girth bands:
day + day^2 + T_{max} + d.h. $> \pm 0°$ C
Huikko 1967, birch, girth bands:
day + day^2 + T_{max} + d.h. $> \pm 0°$ C

The maximum air temperature variable is naturally best represented, but also solar radiation and various temperature sums are found in most combinations. The frequencies of the minimum air temperature and the minimum-maximum temperature difference are surprisingly high, one of these occurs in eight combinations out of fifteen, in a few, both. Soil temperature and wind velocity have been determinants in a couple of combinations.

In comparisons of the measurement devices, the results based on auxanographic records from Metsä-Saramäki are better for each year than those based on the girth band measurements. Fewer data were available for the Huikko stand; there auxanographic results were inferior to girth band results for spruce, and superior for birch. It can be said, however, that the results indicate the general superiority of auxanographs for work of this type. In preliminary work, (LEIKOLA 1966, unpublished) girth band data exhibited higher correlations with the environmental factors. It should be kept in mind that these results were based on measurements made by the two types of devices in 1964 at Metsä-Saramäki only. — The different growth measurement methods have been discussed more thoroughly in chapter II 424.

2222. The relationship between various environmental factors and diameter growth on the second day after measurement

As stated on page 103, regression analysis was continued for the Metsä-Saramäki experimental stand by studying the relationship between diameter growth and the environmental factors measured two days earlier. The complete results are not, however, published here. In comparison to the results of correlation analysis (tables 13—19), the low degree of explanation offered by this alternative is clear. For 1964, the correlations found with every environmental factor combination tried were especially low. The 1966 regressions were the best, but still much inferior to those from the regressions for: environmental $\text{factors}_{\text{day n}}$ / diameter $\text{growth}_{\text{day n+1}}$. The best environmental factor combinations were composed of almost the same variables as in the preceding analyses.

It can be concluded that regression analysis confirmed the doubts about the weakness of this model in explaining daily diameter growth.

2223. The validity of the regression analysis during various parts of the growing season

Correlation and regression analyses only provide information of the average relationships between the diameter growth of trees and the various environmental variables during the growing season. For further information of the role of the time factor in the computing methods used, the daily deviations from the best-combination regressions were computed. Figures 50—59 show these deviations (cf. e.g. DRAPER and SMITH 1967, p. 88—90).

No consistent trend is seen in the deviations at Metsä-Saramäki (fig. 50—53); the deviations are rather evenly distributed throughout the growing season. When large positive deviations are compared to rainy periods, a clear relationship is seen. This confirms the presumtion that the hydrostatic diameter changes due to rainy and dry periods remain one of the largest sources of error in the attempts to explain tree growth by environmental measurements.

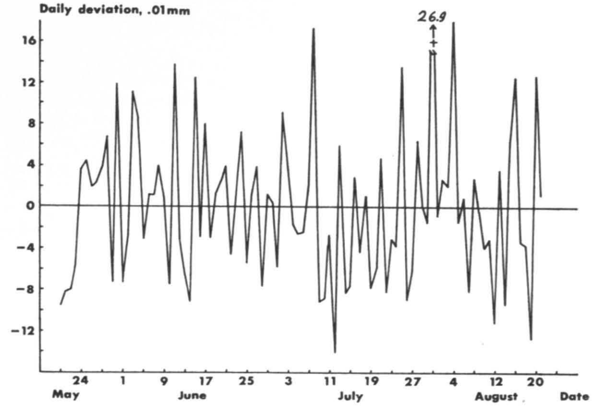

Figure 50. The daily deviations of the calculated diameter growth based on the best-combination regression from the recorded diameter growth. Metsä-Saramäki, auxanogr., 1964.

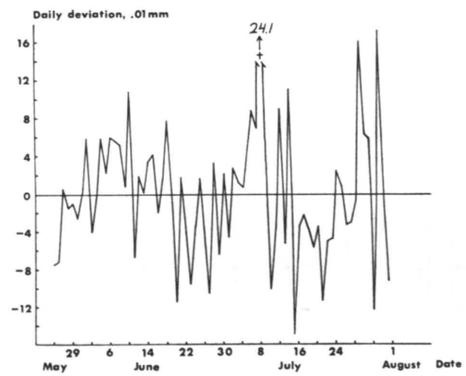

Figure 51. The daily deviations of the calculated diameter growth based on the best-combination regression from the recorded diameter growth. Metsä-Saramäki, auxanogr., 1965.

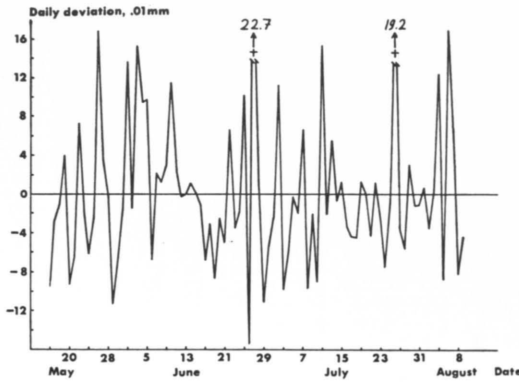

Figure 52. The daily deviations of the calculated diameter growth based on the best-combination regression from the recorded diameter growth. Metsä-Saramäki, auxanogr., 1966.

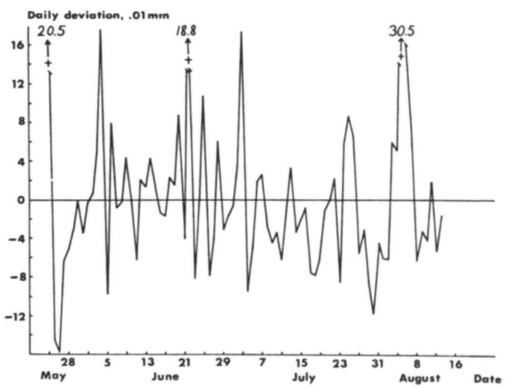

Figure 53. The daily deviations of the calculated diameter growth based on the best-combination regression from the recorded diameter growth. Metsä-Saramäki, auxanogr., 1967.

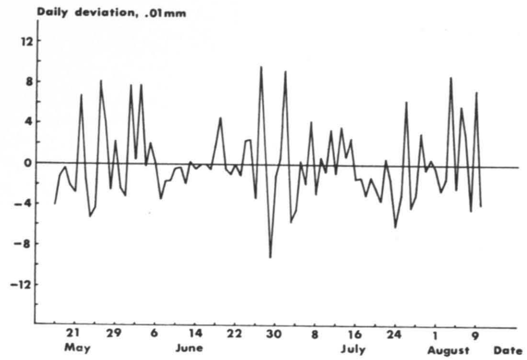

Figure 54. The daily deviations of the calculated diameter growth based on the best-combination regression from the recorded diameter growth. Huikko, spruce, auxanogr., 1966.

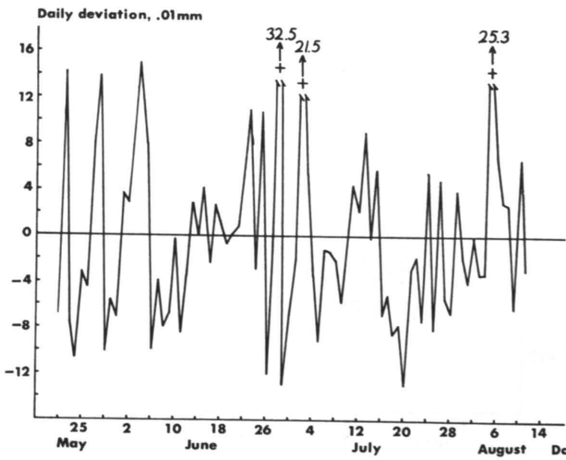

Figure 55. The daily deviations of the calculated diameter growth based on the best-combination regression from the recorded diameter growth. Huikko, pine, girth bd., 1966.

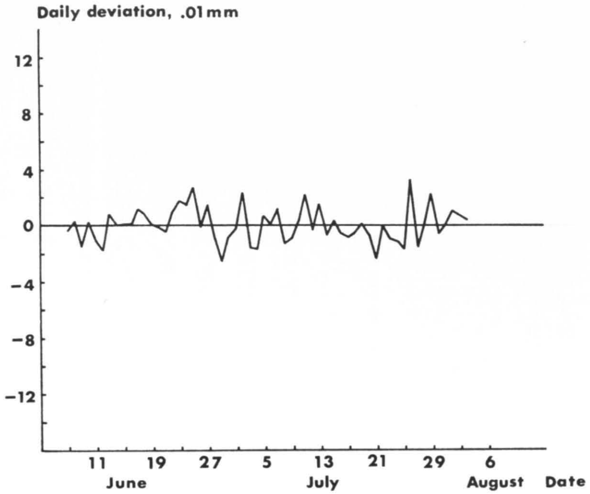

Figure 56. The daily deviations of the calculated diameter growth based on the best-combination regression from the recorded diameter growth. Huikko, birch, auxanogr., 1966.

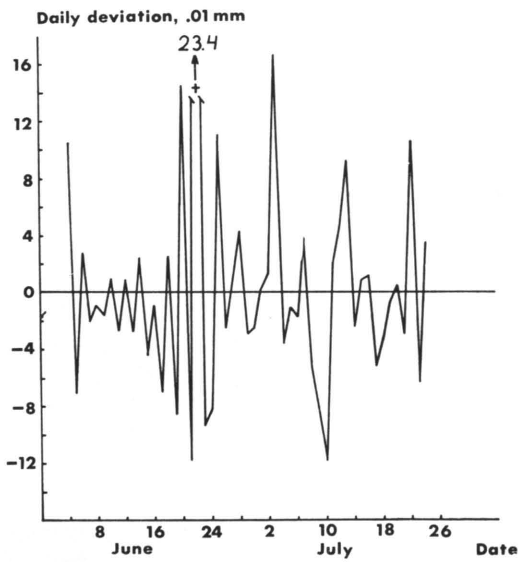

Figure 57. The daily deviations of the calculated diameter growth based on the best-combination regression from the recorded diameter growth. Huikko, spruce, girth bd., 1967.

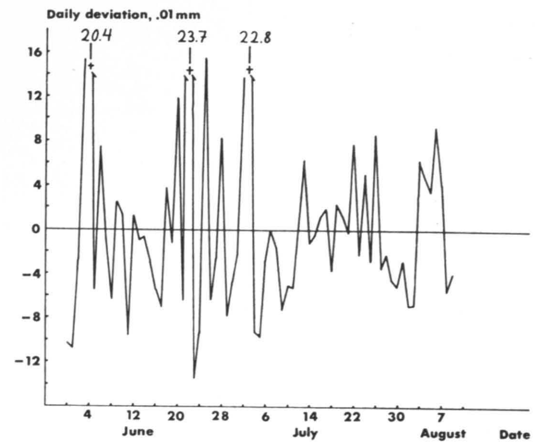

Figure 58. The daily deviations of the calculated diameter growth based on the best-combination regression from the recorded diameter growth. Huikko, pine, girth bd., 1967.

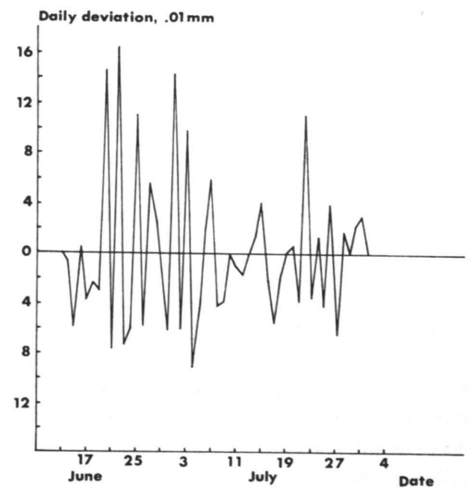

Figure 59. The daily deviations of the calculated diameter growth based on the best-combination regression from the recorded diameter growth. Huikko, birch, girth bd., 1967.

For Huikko (fig. 54—59), the deviations found for conifers resemble those discussed above, but birch exhibits relatively small deviations from the regression surface in 1966 and a clear diminishing trend in the deviations toward the end of the growing season in 1967. The regression model constructed for birch from the environmental factors was clearly better in late than early summer, improving steadily with time. An explanation is provided by the poor ability of tree diameter growth to respond to environmental factors in early summer, and the increasing sensitivity of the trees with time, as the rate of diameter growth increases and the leaf mass of the trees grows. Hydrostatic changes are apparently not responsible in early summer, since they are small in birch at this time.

The closest comparative material to these results is offered by the studies dealing with the growing season of trees in parts. The validity of such a mechanical method in presenting irregular weather periods will not be discussed. Mitscherlich *et al.* (1966) emphasize the greater significance of early-season temperatures than late-season ones to Douglas-fir growth in South Germany. Similar results have been published by Kozlowski *et al.* (1962) of studies concerning the diameter growth of northern pin oak (*Quercus ellipsoidalis* Hill) in three-week periods in the Lake States, USA. Wilhelmi (1960) has also reached similar conclusions in growth measurements in North Germany. Many other students, on the basis of more superficial study, refer to the changing mutual relationships of the various climatic factors and growth during the growing season (e.g. Gaertner 1964, Bassett 1966).

The results of this study do not support the direct applications of such models in research. The usual environmental factor combination with air temperature and solar radiation variables should have provided an explanation weakening toward the end of the summer, if other factors, e.g. soil moisture, had gained in importance. In Finnish climatic conditions, the role of the different growth factors is apparently of the same maginitude during the entire growing season except during accidental periods that can already be considered abnormal. This fact simplifies the computing model considerably and also supports the analysis in view of the reservations discussed on page 89 concerning the general use of a time series in growth analysis.

23. DISCUSSION OF THE RESULTS OF THE ANALYSIS

The effect of climatic factors on the diameter growth of forest trees has been studied by annual ring analysis for over fifty years in northern Europe. All research workers have consistently found the highest correlations between the temperature prevailing during the growing season and the width of the annual ring formed in the same year (e.g. Erlandson 1936, Ording 1941, Mikola 1950, Eklund 1954). It has been found that the other main climatic factor, moisture and rainfall has an effect on diameter growth only in the driest sites, and the response has only been seen in unusually dry years (Mikola 1950). The diameter growth is closest correlated with temperature at the northern timber line, where correlations as high as $+ 0.84 \pm .05$ have been found between the best climatic indexes and annual ring width (Sirén 1961, also Hustich 1948). Towards the south, precipitation starts to compete with temperature on an equal level even in normal conditions in South Sweden and Denmark (Holmsgaard 1955, Hedemann-Gade 1965). In conditions corresponding to Central European lowlands, temperature usually regulates growth only in the spring, and precipitation is more important than temperature in mid- and late summer (Friedrich 1897, Trendelenburg and Mayer-Wegelin 1955, Kern 1966, Mitscherlich *et al.* 1966). In North America, the same shift of weight from one group of environmental factors to another is seen from the northern parts of the continent to the south (Mac Dougal 1938, Fraser 1952).

It is of interest to compare this outline of factors affecting the diameter growth of trees to the one found on the basis of the results of this study concerning daily measurements of growth. In general, the results are quite similar. The role of the solar radiation and air temperature variables is considerable also in the model dealing with daily growth. The results obtained are, however, lower in their level of significance than the ones generally available for annual ring analysis in Finland and Scandinavia. Nothing was found indicating that the mutual causal relationship between tree growth and the environmental variables affecting it is different for the total growing season and its individual parts. Many factors, however, decrease the significance of daily analysis. The technical difficulties of measuring daily growth are much greater and the uncertainty factors connected with these are more serious than in annual ring analysis. These aspects were throughly discussed in chapter II 3. Serious attention should also be paid to the view that the linear regression relationship between the individual environmental factors and diameter growth, on which the present computations were based, is probably not the closest one to be found. E.g. Fritts, who used primarily purely linear equation models in the growth analysis he published in 1958, used only transformed curvilinear models in successive work (1960), the results of which he considers better.

A possibility to improve the computational results from growth analysis is the use of factor analysis in solving regression problems. This method has the following advantages (cf. Vahervuo and Ahmavaara 1958, Mäkelä, 1968):

— As the independent variables are combined into factors, the regression model is simplified,

— The difficulties due to the multicollinearity of the independent variables are lessened, and the possibilities to interpret and use the regression coefficients are improved.

Factor analysis is still a fairly laborious method, requiring considerable information about the relationships of the various factors for successful results. In analyses of much more easily measured processes like height growth, factor analysis is already useful.

Although it is necessary to emphasize that deducting similarities from correlations and forming them into causally significant rules, as done above, is always based on numerous assumptions, it is nevertheless tempting to outline a picture of the mechanism regulating tree diameter growth and how it works. That the variables representing solar radiation and maximum air temperature provided the best explanation for growth points to the significance of the overall current energy balance of trees (cf. Polster 1950, Went 1957). In numerous laboratory experiments, it has been found that the daily photosynthesis/respiration ratio and the amount of photosynthetic products which it regulates affects the growth of tree seedlings (e.g. Kramer 1957, Hellmers 1962, Lyr *et al.* 1967, p. 344—349). It is also known that the rate of flow of photosynthetic products and the growth hormone transported, from the leaves and through the phloem toward the roots, ranges from 0.5 to 1.5 m/h (Huber 1956, Zimmermann 1958). The distance between the green crown of the sample trees and the auxanometrs at breast height is suitable at this rate. The height growth of trees mostly uses energy from the immediate neighborhood of the shoot; in Scandinavian climatic conditions, it has been found to follow temperature changes rather closely, but after a ca. six-hour lag (Mork 1941, Godske 1961). If a similar, though less exact and more hypothetic time table is constructed for the diameter growth of trees, the lag in cambial activity would be ca. 20—24 hours.

It is, however, apparent that daily diameter growth is also affected by the conditions of other days than the one preceding growth. Although quite small significance could be assigned to the conditions prevailing two days before growth on the basis of this study (cf. Wilhelmi 1960, Kozlowski *et al.* 1962, Kern 1966), it is not impossible that the weather conditions of the time of growth were partly responsible for the rate of organic matter production. The effect of the immediate environmental conditions are unfortunately so heavily masked by temporary hydrostatic changes that this question remained unanswered in this study.

The significance of constant water supply to undisturbed tree growth has been emphasized in several connections (e.g. Mac Dougal 1938, Kramer 1962, Kozlowski 1964), and many research workers have found that this factor is responsible for a large part of the diameter growth responses. It is unfortunate that this factor remained essentially unexplained at Metsä-Saramäki. In the experimental stand at Huikko, adequate soil moisture was guaranteed for the entire growing season. Including accurate soil moisture measurements in the analysis would naturally have increased its significance. It is doubtful, however, whether this would have resulted in a considerable change in the results.

IV. SUMMARY

The influence of various environmental factors on the diameter growth of trees has been studied. The study is based on data recorded through the growing season on the daily diameter increment of trees and various environmental factors. The field work was carried out in two experimental stands in southern Finland in 1964—1967.

The following main results were obtained in the study:

— The temperature sums preceding the beginning of diameter growth were of the same magnitude in the years studied, indicating a dependence relationship.

— The part of a pine stem subjected to warmer conditions did not exhibit an earlier beginning of growth than the rest of the stem.

— The formation of new xylem cells took place in the pine stem ca. every third day during the period of most active diameter growth.

— No summer growth inhibition was detected in diameter growth.

— None of the cumulative temperature sums tried determined the time of cessation of diameter growth. In several cases, a positive correlation was found between the length of the growing season and the width of the annual ring formed.

— The walls of the formed xylem cells had not thickened sufficiently before the end of July to enable drawing a definite limit between carlywood and latewood. A decrease in vacuole size was, on the contrary, seen already from the end of June.

— In studying the relationships between the diameter increment and the environmental factors of the same day, it was found that the diameter increment was totally masked in the records by the hydrostatic changes of the tree stem.

— In studying the relationships between the diameter increment and the environmental factors of the preceding day, it was found that the variables representing solar radiation and air temperature were closest correlated with growth.

— The relationships between the diameter increment and the environmental factors of the second day preceding growth were found to be poor.

— In studying the deviations of the recorded daily increments from the regression surface, no clear general trend was seen for pine and spruce, but a clear diminishing trend towards the end of the growing season could be seen for birch in 1967.

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Appendix 1

Principal stand data for the Metsä-Saramäki experimental stand. The DBH values are the means of the largest and the smallest diameter. The sites and the crown projections of the trees are shown in figure 3. The sample trees in the stand are described in table 2. Measurements in 1964.

Symbol and number of tree	DBH, cm	Height, m	Bottom of canopy, m	Canopy class
1	26	17.5	8.5	I
2	22	16.0	7.5	I
3	24	16.5	8.0	I
4	29	17.0	7.0	I
5	19	14.5	7.0	II
6	22	17.0	6.5	I
7	20	17.0	8.0	I
8	15	13.0	6.5	II
9	17	14.5	7.0	I
10	16	13.5	7.5	II
11	21	15.5	7.0	I
12	22	15.5	8.5	I
13	19	15.0	7.0	I
14	15	14.0	7.5	II
15	26	18.0	8.0	I
16	16	13.5	6.0	II
17	18	14.5	6.0	II
18	14	11.5	5.0	II
19	16	13.0	6.0	II
20	16	11.0	6.5	II
21	16	14.0	7.0	II
22	15	13.5	6.0	III
23	15	13.0	6.0	III
24	16	15.0	6.0	I
25	27	17.5	5.5	I
26	18	15.0	7.0	II
27	22	16.5	6.0	I
28a	25	17.5	6.5	I
28b	19	17.0	7.0	I
29	24	16.5	7.5	I
30	24	16.5	6.0	I
31	14	13.5	5.0	II
32	16	15.0	7.0	I
33	15	15.5	7.5	I
34	12	13 0	5.5	II
35	20	16.0	6 5	I
36	18	15.0	6.0	I
37	18	14.5	6.5	I
38	15	13.5	5.5	II
39	12	11.0	5.0	III
40	13	12.0	5.5	II
41	17	14.5	5.5	I

Symbol and number of tree	DBH, cm	Height, m	Bottom of canopy, m	Canopy class
42	23	16.5	7.0	I
43	18	14.5	7.0	I
44	19	15.5	6.0	I
45	15	14.0	6.0	II
46	14	11.5	5.0	III
47	12	11.0	5.0	III
48	24	17.0	6.0	I
49	16	14.5	5.5	I
50	18	16.0	6.0	I
51	16	15.0	6.0	II
52	21	17.0	6.5	I
53	20	17.0	6.5	I
54	19	15.5	7.0	I
55	17	16.0	6.0	I
56	17	15.5	6.0	I
57	13	14.0	5.0	II
58	19	16.0	5.5	I
59	16	14.5	5.0	II
60	14	12.5	5.0	II
Sf – 1	19	16.5	7.0	I
Sf – 2	15	14.5	5.5	II
Sf – 3	15	13.0	5.5	II
Sf – 4	23	16.5	6.0	I
Sf – 5	14	13.0	6.0	II
Sf – 6	18	16.0	6.5	I
Sf – 7	17	16.0	6.0	I

Appendix 2

Principal stand data for the Huikko experimental stand. The DBH values are the means of the largest and the smallest diameter. The sites and crown projections of the trees are shown in figure 5. The sample trees in the stand are described in table 4. Measurements 1967.

Number of tree	Tree species	DBH, cm	Height, m	Bottom of canopy, m	Canopy class
1	Birch	14	11.0	7.0	III
2	»	16	14.0	7.0	II
3	»	15	16.0	7.0	I
4	»	19	15.5	8.0	I
5	Spruce	21	16.0	2.0	I
6	Birch	18	16.0	7.0	I
7	»	16	16.5	7.0	I
8	Pine	16	15.0	10.0	II
9	Spruce	14	14.0	1.0	III
10	Pine	22	17.0	8.0	I
11	Birch	17	15.0	8.0	I
12	»	17	16.5	8.0	I
13	Spruce	26	18.5	6.5	I
14	Birch	15	15.5	7.0	I
15	»	18	14.5	9.0	II
16	»	13	13.5	8.0	III
17	Spruce	21	16.0	6.0	I
18	Birch	20	16.0	8.0	I
19	Pine	14	14.0	9.0	II
20	»	17	16.0	6.0	I
21	»	22	17.0	9.0	I
22	Spruce	12	11.0	2.0	III
23	Pine	15	13.5	7.0	II
24	Birch	15	16.5	8.0	I
25	»	14	16.5	9.5	I
26	»	13	14.0	8.5	II
27	»	15	14.0	8.5	II
28	Pine	12	13.0	9.5	III
29	Birch	16	15.5	8.0	I
30	Spruce	13	12.0	1.0	III
31	Birch	12	12.5	7.0	III
32	Pine	19	17.0	10.0	I
33	Birch	13	13.0	7.0	III
34	Spruce	14	14.0	1.0	II
35	Pine	10	10.1	7.0	III
36	Birch	19	15.5	7.0	I
37	»	13	14.0	7.0	II
38	Spruce	20	17.0	2.0	I
39	»	16	17.0	2.0	I
40	Pine	15	15.0	10.0	II

Appendix 3

Table 1. The combinations of environmental factors best correlated with daily diameter growth. Metsä-Saramäki, 1964, auxanographs and girth bands, standardized means, envir. fact. day n/diam. growth day n + 1.

Row	Combination of environmental factors	Growth measur. device	d.f.	R^2	S[1]	t-values of importance
1	day + day^2	aux.	91	△	8.519	day = .00, day^2 = .32
		girth bd.	91	.011	7.394	day = .19, day^2 = .63
2	day + day^2 + T max.	aux.	90	△	8.550	T max. = .58
		girth bd.	90	.032	7.313	T max. = 1.73
3	day + day^2 + T diff.	aux.	90	△	8.544	T diff. = .69
		girth bd.	90	.016	7.376	T diff. = 1.19
4	day + day^2 + d.h. > ± 0° C	aux.	90	△	8.513	d.h. > ± 0° C = 1.06
		girth bd.	90	.024	7.368	d.h. > ± 0° C = 1.28
5	day + day^2 + d.h. > + 5° C	aux.	90	△	8.517	d.h. > + 5° C = 1.02
		girth bd.	90	.019	7.364	d.h. > + 5° C = 1.31
6	day + day^2 + d.h. > + 10° C	aux.	90	△	8.520	d.h. > + 10° C = .99
		girth bd.	90	.022	7.354	d.h. > + 10° C = 1.40
7	day + day^2 + s.rad.	aux.	90	.138	7.890	s.rad. = 3.99***
		girth bd.	90	.008	7.403	s.rad. = .87
8	day + day^2 + T max. + d.h. > ± 0° C	aux.	89	△	8.527	d.h. > ± 0° C = 1.32
		girth bd.	89	.026	7.335	d.h. > + 0° C = .74
9	day + day^2 + T max. + d.h. > + 5° C	aux.	89	△	8.514	d.h. > + 5° C = 1.22
		girth bd.	89	.027	7.331	d.h. > + 5° C = .67
10	day + day^2 + T max. + s.rad.	aux.	89	.151	7.832	T max. = 1.56
		girth bd.	89	.065	7.187	T max. = 2.54*
11	day + day^2 + T max. + T diff.	aux.	89	△	8.590	T max. = .17, T diff. = .41
		girth bd.	89	.022	7.354	T max. = 1.24, T diff. = .09
12	day + day^2 + T diff. + s.rad.	aux.	89	.116	7.807	T diff. = 1.74
		girth bd.	89	.042	7.278	T diff. = 2.03
13	day + day^2 + s.rad. + d.h. > ± 0° C	aux.	89	.131	7.923	d.h. > ± 0° C = .59
		girth bd.	89	.034	7.307	d.h. > ± 0° C = 1.84
14	day + day^2 + s.rad. + d.h. > + 5° C	aux.	89	.132	7.918	d.h. > + 5° C = .68
		girth bd.	89	.036	7.299	d.h. > + 5° C = 1.89
15	day + day^2 + s.rad. + d.h. > + 10° C	aux.	89	.135	7.908	d.h. > + 10° C = .82
		girth bd.	89	.042	7.277	d.h. > + 10° C = 1.71
16	day + day^2 + Tmax. + s.rad. + d.h. > ± 0° C	aux.	88	.173	7.730	
		girth bd.	88	.063	7.193	
17	day + day^2 + T max. + s.rad. + d.h. > + 5° C	aux.	88	.166	7.761	
		girth bd.	88	.062	7.201	
18	day + day^2 + T max. + s.rad. + T diff.	aux.	88	.153	7.825	
		girth bd.	88	.062	7.199	
19	day + day^2 + T max. + d.h. > ± 0° C + w.vel.	aux.	88	.008	8.466	
		girth bd.	88	.047	7.257	
20	day + day^2 + T max. + T diff. + s.rad. + w.vel.	aux.	87	.158	7.800	
		girth bd.	87	.076	7.148	
21	day + day^2 + T max. + T diff. + s.rad. + d.h. > ± 0° C	aux.	87	.157	7.806	
		girth bd.	87	.053	7.236	
22	day + day^2 + T max. + s.rad. + d.h. > + 5 °C + T soil	aux.	87	.159	7.794	
		girth bd.	87	.052	7.238	
23	day + day^2 + T max. + T diff. + s.rad. + d.h. > ± 0° C + T soil	aux.	86	.151	7.839	
		girth bd.	86	.043	7.275	
24	day + day^2 + T max. + T diff. + s.rad. + d.h. > + 5° C + w.vel.	aux.	86	.166	7.764	
		girth bd.	86	.067	7.178	

[1] s diam. gr., aux. = 8.501, girth bd. = 7.435.

Table 2. The combinations of environmental factors best correlated with daily diameter growth. Metsä-Saramäki, 1965, auxanographs, standardized means, envir. fact. day n/diam. growth day n + 1.

Row	Combination of environmental factors	d.f.	R^2	S[1]	t-values of importance
1	day + day^2	69	.033	8.277	day = .24, day^2 = .29
2	day + day^2 + T max.	68	.236	7.355	T max. = 4.40***
3	day + day^2 + T diff.	68	.109	7.947	T diff. = 2.61*
4	day + day^2 + d.h. > ± 0° C	68	.263	7.226	d.h. > ± 0° C = 4.75***
5	day + day^2 + d.h. > + 5° C	68	.256	7.260	d.h. > + 5° C = 4.65***
6	day + day^2 + d.h. > + 10° C	68	.228	7.391	d.h. > + 10° C = 4.30***
7	day + day^2 + T max. + d.h. > ± 0° C	67	.252	7.276	d.h. > ± 0° C = 1.57
8	day + day^2 + T max. + d.h. > + 5° C	67	.247	7.307	d.h. > + 5° C = 1.37
9	day + day^2 + T max. + d.h. > + 10° C	67	.229	7.391	d.h. > + 10° C = .57
10	day + day^2 + T max. + T diff.	67	.228	7.392	T max. = 3.41, T diff. = .57
11	day + day^2 + T diff. + d.h. > ± 0° C	67	.257	7.257	d.h. > ± 0° C = 3.81***
12	day + day^2 + T diff. + d.h. > + 5° C	67	.248	7.298	d.h. > + 5° C = 3.69***
13	day + day^2 + T diff. + d.h. > + 10° C	67	.219	7.441	d.h. > + 10° C = 3.25**
14	day + day^2 + T diff. + d.h. > + 5° C + T max.	66	.237	7.352	
15	day + day^2 + T diff. + d.h. > + 5° C + T soil	66	.245	7.315	

[1] s diam. gr. = 8.419

Table 3. The combinations of environmental factors best correlated with daily diameter growth. Metsä-Saramäki, 1966, auxanographs and girth bands, standardized means, envir.fact. day n/diam. growth day n + 1.

Row	Combination of environmental factors	Growth measur. device	d.f.	R^2	S[1]	t-values of importance
1	day + day^2	aux.	83	.071	8.385	day = .42, day^2 = .31
		girth bd.	77	△	8.131	day = .05, day^2 = .19
2	day + day^2 + T max.	aux.	82	.164	7.957	T max. = 3.19**
		girth bd.	76	.119	7.594	T max. = 3.50***
3	day + day^2 + T diff.	aux.	82	.133	8.101	T diff. = 2.63*
		girth bd.	76	.055	7.863	T diff. = 2.52*
4	day + day^2 + d.h. > ± 0° C	aux.	82	.172	7.916	d.h. > ± 0° C = 3.34**
		girth bd.	76	.104	7.659	d.h. > ± 0° C = 3.28**
5	day + day^2 + d.h. > + 5° C	aux.	82	.158	7.982	d.h. > + 5° C = 3.10**
		girth bd.	76	.116	7.604	d.h. > + 5° C = 3.47***
6	day + day^2 + d.h. > + 10° C	aux.	82	.147	8.037	d.h. > + 10° C = 2.89**
		girth bd.	76	.147	8.037	
7	day + day^2 + s.rad.	aux.	82	.194	7.807	s.rad. = 2.14*
		girth bd.	76	.127	7.557	s.rad. = 3.63***
8	day + day^2 + s.rad. +	aux.	81	.198	7.793	d.h. > ± 0° C = 1.14
	d.h. > ± 0° C	girth bd.	75	.135	7.527	d.h. > ± 0° C = 1.27
9	day + day^2 + s.rad. +	aux.	81	.194	7.812	d.h. > + 5° C = .95
	d.h. + 5° C	girth bd.	75	.144	7.483	d.h. > + 5° C = 1.58
10	day + day^2 + s.rad. +	aux.	81	.189	7.833	d.h. > + 10° C = .68
	d.h. > + 10° C	girth bd.	75	.130	7.544	d.h. > + 10° C = 1.12
11	day + day^2 + s.rad. + T max.	aux.	81	.192	7.822	T max. = .83
		girth bd.	75	.139	7.508	T max. = 1.41
12	day + day^2 + s.rad. + T diff.	aux.	81	. .	. .	. .
		girth bd.	75	.118	7.598	T diff. = .43
13	day + day^2 + T max. + T diff.	aux.	81	.154	8.001	T max. = 1.75, T diff. = .33
		girth bd.	75	.107	7.643	T max. = 2.33*, T diff. = .17
14	day + day^2 + T max. + s.rad. +	aux.	80	.188	7.837	
	d.h. > ± 0° C	girth bd.	74	.127	7.557	
15	day + day^2 + T max. + s.rad. +	aux.	80	.184	7.861	
	d.h. > + 5° C	girth bd.	74	.134	7.530	
16	day + day^2 + T max. + s.rad. +	aux.	80	.181	7.871	
	d.h. > + 10° C	girth bd.	74	.127	7.558	
17	day + day^2 + T max. + s.rad. +	aux.	80	.181	7.871	
	T diff.	girth bd.	74	.130	7.544	
18	day + day^2 + T diff. + s.rad. +	aux.	80	.188	7.840	
	h.d. > ± 0° C	girth bd.	74	.123	7.577	
19	day + day^2 + T diff. + s.rad. +	aux.	80	.184	7.859	
	d.h. > + 5° C	girth bd.	74	.133	7.553	
20	day + day^2 + T max. + T diff. +	aux.	79	.174	7.909	
	d.h. > + 5° C	girth bd.	73	.122	7.579	
21	day + day^2 + T max. + T diff. +	aux.	79	.139	8.073	
	d.h. > + 5° C + T soil	girth bd.	73	.093	7.706	

[1] s diam. gr., aux. = 8.702, girth bd. = 8.091

Table 4. The combinations of environmental factors best correlated with the daily diameter growth. Metsä-Saramäki, 1967, auxanographs and girth bands, standardized means, envir.fact. day n/diam. growth day n + 1.

Row	Combination of environmental factors	Growth measur. device	d.f.	R^2	S[1]	t-values of importance
1	day + day^2	aux.	79	.022	9.164	day = 1.03 day^2 = .60
		girth bd.	79	△	9.012	day = .41, day^2 = .18
2	day + day^2 + T max.	aux.	78	.150	8.537	T max. = 3.61***
		girth bd.	78	.007	8.918	T max. = 1.63
3	day + day^2 + T min.	aux.	78	.106	8.758	T min. = 2.91**
		girth bd.	78	.055	8.700	T min. = 2.60**
4	day + day^2 + T diff.	aux.	78	.046	9.049	T diff. = 1.73
		girth bd.	78	△	9.052	T diff. = .56
5	day + day^2 + d.h. > ± 0° C	aux.	78	.192	8.330	d.h. > ± 0° C = 4.19***
		girth bd.	78	.036	8.792	d.h. > ± 0° C = 2.24*
6	day + day^2 + d.h. > + 5° C	aux.	78	.201	8.275	d.h. > + 5° C = 4.34***
		girth bd.	78	.037	8.781	d.h. > + 5° C = 2.28*
7	day + day^2 + d.h. > + 10° C	aux.	78	.188	8.346	d.h. > +10° C = 4.15***
		girth bd.	78	.026	8.834	d.h.> + 10° C = 2.05*
8	day + day^2 + s.rad.	aux.	78	.144	8.567	s.rad. = 3.52***
		girth bd.	78	△	9.050	s.rad. = .59
9	day + day^2 + s.rad. + d.h. > ± 0° C	aux.	77	.208	8.243	d.h. > ± 0° C = 2.69**
		girth bd.	77	.029	8.820	d.h. > ± 0° C = 2.26*
10	day + day^2 + s.rad. + d.h. > + 5° C	aux.	77	.216	8.201	d.h. > + 5° C = 2.85**
		girth bd.	77	.032	8.806	d.h. > + 5° C = 2.32*
11	day + day^2 + s.rad. + d.h. > + 10° C	aux.	77	.206	8.254	d.h. > + 10° C = 2.65**
		girth bd.	77	.017	8.872	d.h. > + 10° C = 2.04*
12	day + day^2 + s.rad. + T max.	aux.	77	.170	8.442	T max. = 1.82
		girth bd.	77	△	8.960	T max. = 1.60
13	day + day^2 + s.rad. + T diff.	aux.	77	.139	8.593	T diff. = .73
		girth bd.	77	△	9.010	T diff. = 1.30
14	day + day^2 + s.rad. + T min.	aux.	77	.204	8.264	T min. = 2.62*
		girth bd.	77	.044	8.753	T min. = 2.52*
15	day + day^2 + T max. + T diff.	aux.	77	.153	8.528	T max. = 3.29**, T diff. = 1.08
		girth bd.	77	.074	8.612	T max. = 3.03**, T diff. = 2.58*
16	day + day^2 + s.rad. + T max.	aux.	76	.211	8.230	
	+ d.h. > ± 0° C	girth bd.	76	.024	8.840	
17	day + day^2 + s.rad. +	aux.	76	.225	8.151	
	T max. + d.h. > + 5° C	girth bd.	76	.029	8.817	
18	day + day^2 + s.rad. +	aux.	76	.201	8.279	
	T max. + d.h. > + 10° C	girth bd.	76	.005	8.927	
19	day + day^2 + s.rad. +	aux.	76	.201	8.283	
	T max. + T diff.	girth bd.	76	.066	8.649	

Row	Combination of environmental factors	Growth measur. device	d.f.	R^2	S[1]	t-values of importance
20	day + day^2 + T max. + T diff. + d.h. > + 5° C	aux.	76	.187	8.350	
		girth bd.	76	.065	8.655	
21	day + day^2 + s.rad. + T max. + T diff. + d.h. > + 5° C	aux.	75	.218	8.190	
		girth bd.	75	.557	8.699	
22	day + day^2 + s.rad. + T max. + T diff. + d.h. > + 5° C + T soil	aux.	74	.211	8.230	
		girth bd.	74	.089		

[1] s diam. gr. aux. = 9.264, girth bd. = 8.951

Appendix 4

Table 1. The combinations of environmental factors best correlated with daily diameter growth. Huikko, pine, 1966, girth bands, standardized means, envir.fact. day n/diam. growth day n + 1.

Row	Combination of environmental factors	d.f.	R^2	S[1]	t-values of importance
1	day + day^2	79	Δ	9.133	day = .87, day^2 = 1.02
2	day + day^2 + T max.	78	.040	8.911	T max. = 2.23*
3	day + day^2 + T min.	78	.098	8.636	T min. = 3.32**
4	day + day^2 + T diff.	78	Δ	9.189	T diff. = .21
5	day + day^2 + d.h. > ± 0° C	78	.095	8.652	d.h. > + 0° C = 3.17**
6	day + day^2 + d.h. > + 5° C	78	.087	8.689	d.h. > + 5° C = 3.05**
7	day + day^2 + d.h. > + 10° C	78	.081	8.718	d.h. > + 10° C = 2.95**
8	day + day^2 + d.h. > ± 0° C + T max.	77	.122	8.572	d.h. > ± 0° C = 2.70**
9	day + day^2 + d.h. > + 5° C + T max.	77	.097	8.639	d.h. > + 5° C = 2.45
10	day + day^2 + d.h. > + 10° C + T max.	77	.083	8.707	d.h. > + 10° C = 2.16*
11	day + day^2 + d.h. > + 5° C + T diff.	77	.090	8.674	d.h. > + 5° C = 3.24 T diff. = .77
12	day + day^2 + d.h. > + 5° C + T max. + T diff.	76	.080	8.694	
13	day + day^2 + d.h. > + 5° C + T max. + T diff. + T soil.	75	.079	8.723	
14	day + day^2 + T max. + T min. + T diff.	76	.096	8.646	

[1] s diam. gr. = 9 093

Table 2. The combinations of environmental factors best correlated with daily diameter growth. Huikko, spruce, 1966, auxanographs, means, girth bands, standardized means, envir. fact. day n/diam. growth day n + 1.

Row	Combination of environmental factors	Growth measur. device	d.f.	R^2	S[1]	t-values of importance
1	day + day^2	aux.	83	.085	4.272	day = 1.30, day^2 = 1.97
		girth bd.	83	.126	7.937	day = 2.48**, day^2 = 3.11**
2	day + day^2 + T max.	aux.	82	.135	4.153	T max. = 2.41**
		girth bd.	82	.230	7.451	T max. = 3.49***
3	day + day^2 + T diff.	aux.	82	.148	4.121	T diff. = 2.68**
		girth bd.	82	.131	7.916	T diff. = 1.20
4	day + day^2 + d.h. > ± 0° C	aux.	82	.127	4.171	d.h. > ± 0° C = 2.24*
		girth bd.	82	.265	7.279	d.h. > ± 0° C = 4.08***
5	day + day^2 + d.h. > + 5° C	aux.	82	.137	4.147	d.h. > + 5° C = 2.46**
		girth bd.	82	.266	7.275	d.h. > + 5° C = 4.10***
6	day + day^2 + d.h. > + 10° C	aux.	82	.174	4.059	d.h. > + 10° C = 3.15**
		girth bd.	82	.264	7.281	d.h. > + 10° C = 4.08***
7	day + day^2 + d.h. > ± 0° C + T max.	aux.	81	.125	4.189	d.h. > ± 0° C = .705
		girth bd.	81	.259	7.307	d.h. > ± 0° C = .21
8	day + day^2 + d.h. > + 5° C + T max.	aux.	81	.128	4.170	d.h. > + 5° C = .58
		girth bd.	81	.261	7.299	d.h. > + 5° C = 2.11*
9	day + day^2 + d.h. > + 10° C + T max.	aux.	81	.178	4.048	d.h. > + 10° C = 2.30*
		girth bd.	81	.258	7.313	d.h. > + 10° C = 2.03*
10	day + day^2 + T diff. + T max.	aux.	81	.142	4.136	T diff. = 1.30
		girth bd.	81	.259	7.308	T diff. = 2.05*
11	day + day^2 + T diff. + d.h. > ± 0° C	aux.	81	.149	4.119	T diff. = 1.76
		girth bd.	81	.264	7.285	T diff. = .93
12	day + day^2 + T max. + T min + T diff.	aux.	80	.154	4.108	
		girth bd.	80	.250	7.353	
13	day + day^2 + d.h. < ± 0° C + T max. + T diff.	aux.	80	.155	4.102	
		girth bd.	80	.256	7.234	
14	day + day^2 + d.h. > + 5° C + T max. + T diff.	aux.	80	.167	4.073	
		girth bd.	80	.260	7.306	
15	day + day^2 + d.h. > + 10° C + T max. + T diff.	aux.	80	.214	3.957	
		girth bd.	80	.269	7.255	
16	day + day^2 + d.h. > + 5° C + T max. + T diff. + T soil	aux.	79	.158	4.098	
		girth bd.	79	.280	7.206	

[1] s diam. gr., aux. = 4.466, girth bd. = 8.492

Table 3. The combinations of environmental factors best correlated with daily diameter growth. Huikko, birch, 1966, auxanographs, means, girth bands, standardized means, envir. fact. day n/diam. growth day n + 1.

Row	Combination of environmental factors	Growth measur. device	d.f.	R^2	S[1]	t-values of importance
1	day + day²	aux.	55	.351	1.568	day = 2.59*, day² = 3.77***
		girth bd.	55	.281	5.364	day = .99, day² = 2.21*
2	day + day² + T max.	aux.	54	.521	1.348	T max. = 4.52***
		girth bd.	54	.413	4.921	T max. = 3.37**
3	day + day² + T min.	aux.	54	.416	1.488	T min. = 2.67**
		girth bd.	54	.396	4.995	T min. = 3.07**
4	day + day² + T diff.	aux.	54	.457	1.436	T diff. = 3.41**
		girth bd.	54	.337	5.229	T diff. = 1.97
5	day + day² + d.h. > ± 0° C	aux.	54	.524	1.344	d.h. > ± 0° C = 4.57***
		girth bd.	54	.456	4.739	d.h. > ± 0° C = 4.06***
6	day + day² + d.h. > + 5° C	aux.	54	.524	1.344	d.h. > + 5° C = 4.57***
		girth bd.	54	.457	4.737	d.h. > + 5° C = 4.06***
7	day + day² + d.h. > + 10° C	aux.	54	.534	1.330	d.h. > + 10° C = 4.74***
		girth bd.	54	.457	4.738	d.h. > + 10° C = 4.06***
8	day + day² + d.h. > ± 0° C	aux.	53	.521	1.348	d.h. > ± 0° C = 1.00
	+ T max.	girth bd.	53	.450	4.764	d.h. > ± 0° C = 2.15*
9	day + day² + d.h. > + 5° C	aux.	53	.521	1.348	d.h. > + 5° C = .99
	+ T max.	girth bd.	53	.451	4.761	d.h. > + 5° C = 2.16*
10	day + day² + d.h. > + 10° C	aux.	53	.526	1.341	d.h. > + 10° C = 1.25
	+ T max.	girth bd.	53	.527	4.737	d.h. > + 10° C = 2.29*
11	day + day² + T diff. + T max.	aux.	53	.515	1.356	T diff. = .64
		girth bd.	53	.404	4.960	T diff. = .39
12	day + day² + T diff. +	aux.	53	.542	1.319	T diff. = 1.75
	d.h. > ± 0° C	girth bd.	53	.447	4.778	T diff. = .32
13	day + day² + T max. +	aux.	52	.588	1.249	
	T min. + T diff.	girth bd.	52	.484	4.614	
14	day + day² + d.h. > ± 0° C	aux.	52	.543	1.318	
	+ T max. + T diff.	girth bd.	52	.462	4.709	
15	day + day² + d.h. > + 5° C	aux.	52	.540	1.322	
	+ T max. + T diff.	girth bd.	52	.461	4.718	
16	day + day² + d.h. > + 10° C	aux.	52	.534	1.330	
	+ T max. + T diff.	girth bd.	52	.451	4.759	
17	day + day² + d.h. > + 5° C	aux.	51	.549	1.309	
	+ T max. + T diff. + T soil	girth bd.	51	.477	4.651	

[1] s diam. gr., aux. = 1.948, girth bd. = 6.428

Table 4. The combinations of environmental factors best correlated with daily diameter growth, Huikko, pine, 1967, girth bands, standardized means, envir. fact. day n/diam. growth day n+1.

Row	Combination of environmental factors	d.f.	R^2	S[1]	t-values of importance
1	day + day²	68	△	9.140	day = .73, day² = .48
2	day + day² + T max.	67	.174	8.272	T max. = 4.00***
3	day + day² + T min.	67	.025	8.986	T min. = 1.83
4	day + day² + d.h. > ± 0° C	67	.121	8.532	d.h. > ± 0° C = 3.32**
5	day + day² + d.h. > + 5° C	67	.127	8.507	d.h. > + 5° C = 3.39**
6	day + day² + d.h. > + 10° C	67	.095	8.658	d.h. > + 10° C = 2.96**
7	day + day² + d.h. > ± 0° C + T max.	66	1.63	8.328	d.h. > ± 0° C = .31
8	day + day² + d.h. > + 5° C + T max.	66	.163	8.328	d.h. > + 5° C = .34
9	day + day² + T diff. + T max.	66	.185	8.218	T diff. = 1.37
10	day + day² + d.h. > + 5° C + T max. + T diff.	65	.174	8.275	
11	day + day² + d.h. > + 5° C + T max. + T diff. + T soil	64	.175	8.265	
12	day + day² + T max. + T min. + T diff.	65	.172	8.281	

[1] s diam. gr. = 9 103

Table 5. The combinations of environmental factors best correlated with daily diameter growth. Huikko, spruce, 1967, girth bands, standardized means, envir. fact. day n/diam. growth day n +1.

Row	Combination of environmental factors	d.f.	R^2	S[1]	t-values of importance
1	day + day²	48	.053	8.220	day = .22, day² = .32
2	day + day² + T max.	47	.222	7.454	T max. = 3.37**
3	day + day² + T min.	47	.103	8.002	T min. = 1.91
4	day + day² + T diff.	47	.067	8.159	T diff. = 1.31
5	day + day² + d.h. > ± 0° C	47	.241	7.362	d.h. > ± 0° C = 3.58***
6	day + day² + d.h. > + 5° C	47	.243	7.353	d.h. > + 5° C = 3.60***
7	day + day² + d.h. > + 10° C	47	.196	7.575	d.h. > + 10° C = 3.08**
8	day + day² + d.h. > ± 0° C + T max.	46	.244	7.345	d.h. > ± 0° C = 1.55
9	day + day² + d.h. > + 5° C + T max.	46	.244	7.345	d.h. > + 5° C = 1.55
10	day + day² + T diff. + T max.	46	.223	7.488	T max. = 3.22**, T diff. = 1.04
11	day + day² + T diff. + d.h. > ± 0° C	46	.227	7.425	d.h. ± 0° C = 3.27** T diff.
12	day + day² + T max. + T diff. + d.h. > + 5° C	45	.232	7.405	
13	day > day² + T max. + T diff. + d.h. > + 5° C + T soil	44	.216	7.483	
14	day + day² + T max. + T min. + T diff.	45	.206	7.528	

[1] s diam. gr. = 8 451

Table 6. The combinations of environmental factors best correlated with daily diameter growth. Huikko, birch, 1967, girth bands, standardized means, envir. fact. day n/diam. growth day n+1.

Row	Combination of environmental factors	d.f.	R^2	S[1]	t-values of importance
1	day + day²	47	.163	6.625	day = 1.9, day² = 2.53*
2	day + day² + T max.	46	.250	6.272	T max. = 2.53*
3	day + day² + T min.	46	.154	6.659	T imn. = .72
4	day + day² + T diff.	46	.172	6.589	T diff. = 1.23
5	day + day² + d.h. > ± 0° C	46	.240	6.311	d.h. > ± 0° C = 2.40*
6	day + day² + d.h. > + 5° C	46	.240	6.312	d.h. > + 5° C = 2.40*
7	day + day² + d.h. > + 10° C	46	.224	6.381	d.h. > + 10° C = 2.16*
8	day + day² + T max. + d.h. > ± 0° C	45	.246	6.288	d.h. > ± 0° C = .87
9	day + day² + T max. + d.h. > + 5° C	45	.246	6.293	d.h. > + 5° C = .83
10	day + day² + T max. + d.h. > + 10° C	45	.236	6.330	d.h. > + 10° C = .40
11	day + day² + T max. + T diff.	45	.233	6.340	T diff. = .13
12	day + day² + d.h. > + 5° C + T diff.	45	.247	6.282	
13	day + day² + T max. + T diff. + d.h. > ± 0° C	44	.233	6.342	
14	day + day² + T max. + T diff. + d.h. > + 5° C	44	.230	6.352	
15	day + day² + T max. + T diff. + d.h. > + 10° C	44	.218	6.401	
16	day + day² + T max. + T min. + + T diff.	44	.217	6.407	

[1] s diam. gr. = 7.242

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