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Studies of the increment rhythm of Scots pine and Norway spruce plants

Studier av tall- och granplantors tillväxtrytm

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Abstract

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The report gives simultaneous measurements of leading-shoot length, stem diameter and meteorological factors. The height and stem increment in pines is described during two growing seasons in the field at 67° N and during two months in climate chamber (pine and spruce plants).

The daily increment rhythm, which was regular during fair weather days, varied during the season. The stem increment of the pines in the field started at almost the same time during the day (at noon and early in the morning during early and late growing seasons respectively). The continued growth was individual.

Changes in the weather resulted in changes in the daily increment rhythm as well as regards the total diurnal growth.

Stem-diameter variations, typical of hydration changes, have not been registered and the influence of dead tissue was inconsiderable.

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1 Introduction

The increment of forest trees is determined by factors within the trees and in their environment. Observations of the daily course of the increment are, for that reason, of value in the study of tree growth itself as well as its dependence on external factors.

Growth can be defined in different ways (*Lyr, Polster* and *Fiedler,* 1967). It is determined by cell-division, cell-extension and cell-differentiation. The methods used here in order to measure increment defines height and stem-diameter growth or increment as the irreversible increase in leading-shoot length and stem diameter, respectively.

However, it is not only the growth that is registered when measuring the height and size of the stem. Other factors, especially the water balance of the trees, affect the measurement.

The growth is primarily determined by the net assimilation. *Polster* (1950) points out the necessity of keeping the formation of assimilate and its consumption, in the form of increment, separate. He is of the opinion that the assimilate after trans-localization is used up directly as increment at higher temperatures but is stored at lower (indigenous tree species). Stored assimilation products can later on, for example during the following vegetation period, be consumed as growth through compound transformations. The rhythm in height and stem-diameter increment during the day would in this way primarily be determined by the assimilation intensity, by the speed at which the assimilate is transported and by the compound transformation (*Lyr* et al., 1967). These processes, regarded separately or as a continuous sequence of processes, are affected by the periodical twenty-four-hour variation of external factors, chiefly radiation and temperature. The growth rhythm is also modified by other factors, such as water supply and soil temperature.

There are many investigations dealing with the variation during the season in height increment of trees and tree plants. *Kozlowski* (1964) has compiled the extensive literature on the subject. The daily increment rhythm has been studied less and the reports on the daily rhythm are contradictory. *Mork* (1941) measured in the field the largest increment in the evening and night on Norway spruce. There was growth stop in the day between 6 a.m. and 12 noon. Also in Pinus radiata (*Fielding* 1955), Pinus silvestris and Pseudotsuga taxifolia (*Lyr* et al., 1967, Figure X/21), the largest increment was measured in the evening and at night. However, *Lyr, Erdmann, Hoffman* and *Köhler* (1968) report on registrations of Pinus silvestris, in which the maximum increment took place during daytime between 9 a.m. and 3 p.m. *Danilov* (1954) found that trees such as ash, oak and Siberian larch had larger shoot increment in the day than during the night.

Ever since the end of the nineteenth century (*Friedrich*, 1897) and down to the present time the daily variation in stem increment on large trees has been studied. It has been found that the study of the growth rhythm during day and night has been complicated by the simultaneous variations in stem depending on hydrostatic diameter changes or hydration changes. *Kramer* and *Kozlowski* (1960), *Kozlowski* (1964) and *Leikola* (1969), and others, have discussed this phenomena. A development of tensions in the stems occurs when the transpiration from the leafy network exceeds the water absorption through the root system. In connection with this, there is a decrease of cell volume which is registered as a contraction of the tree stem. These hydration changes are the cause of the typical daily changes in stem diameter which have been much discussed in the literature, see e.g. *Kern* (1965) and *Leikola* (1969 a and b). Immediately after sunrise, the stem diameter decreases and continues to decrease until the transpiration ceases, owing to the closing of stomata, or until the water-conveying cells reach their minimum size. The stems increase in diameter during the night when the transpiration is at a minimum. As a rule, the maximum stem diameter is observed just before sunrise. The weather has a great influence on the stem-diameter changes which are caused by hydration changes. Cold and cloudy weather cause a considerably smaller contraction of the stem than warm and dry weather.

According to investigations made by *Ninokata* and *Miyazato* (1959) and *Kozlowski* (1967) the daily stem-diameter variation of the young trees is the same as in full-grown trees. The firstmentioned authors made registrations of the stem diameter on a number of broad-leaved trees and bushes. *Kozlowski* made the registration in greenhouse of Acer negundo L. and Pinus resinosa Ait. He points out how great the importance of the soil humidity is to the daily stem diameter change.

The aim of the present investigation has been to study the growth rhythm during the day. Comparisons have also been made, however, between the annual course of the height and stem-diameter increments and their relationship to different weather conditions. The new equipment, constructed by *Openshaw* and described by *Odin* and *Openshaw* (1971), permits meticulous measurements of the plant increment in field conditions.

The field investigation was in the main carried out in the summers of 1968 and 1969. This report forms part of a more extensive investigation at the plant nursery of the Royal College of Forestry at Vidsel in 1968—1971 about the relationship of the increment to ecological factors. This work is carried out by a team at the Department of Reforestation.

2 Material and methods

The measurements of growth were carried out by means of electro-mechanical instruments, described by *Odin* and *Openshaw* (1971). The best measurement accuracy, when the leading shoot length was measured, was ±0.05 mm. For the stem diameter measurements, an instrument designed as a circumference gauge was used. All the primary data have been converted into stem diameter (mm or μm) and adjusted to one and the same temperature, +20° C. The measurement accuracy was ±0.5 μm.

2.1 Phytotron experiments

The purpose of the investigation in the phytotron of the Royal College of Forestry was chiefly of a technical nature; namely, to study the temperature dependence of the leading shoot- and stem-increment instruments. While this work was going on, some registrations chiefly of the stem-increment variation were obtained.

The locality available for the test measurement was a climatically adjusted greenhouse. The day was divided into two periods: Twenty hours of light (24,000 lux, Sylvania Gro Lux W.S. armature) with an air temperature of 20° C and four hours of darkness and 15° C. The relative air humidity was constant, 75 %.

Measurements were carried out on two potted spruce plants (*Picea abies L.* Karst., about 50 cm high) and one pine plant (*Pinus silvestris L.*, about 35 cm high). The stem diameters of the plants were about 8 mm (at a height of 5 cm above the substratum surface). They were of Central European provenance.

After having been kept in a cold-storage room (a minimum of 0° C and darkness), the plants were exposed during one week to 8 hours light per day at a temperature of +10° C (8 h, +10° C). During the following week i.e. up to the beginning of the experiment, they received 24 h, +20° C. The spruces had earlier had three, and the pine two, vegetation periods in the phytotron.

The forcing in the growth chamber caused the plants to develop weak leading shoots and soft stems. After the stem-increment instruments had been dismantled, it could be observed that the stems had been strangulated through the pressure of the measuring devices.

The tree plants were watered to field capacity of the soil continuously by means of drip and also manually once a day, half-an-hour to one hour before the beginning of the dark period.

At the same time as the increment measurement was made, the radiation was registered by a pyranometer, constructed by *Bringman* and *Rodskjer* (1968) and the temperature in the air by means of small thermocouples (0.1 mm in diameter). The pyranometer and the thermometer in the air were placed at the same level as the top of the pine. The meteorological instruments and the increment meters were connected to one and the same digital data logger equipment. From the twentyeighth day of the experiment the test cart was moved to a corner of the room and was at the same time lowered 35 cm. This change resulted in a reduction of radiation, by 45 % or from 0.22 to 0.12 cal. cm^{-2} min^{-1}.

2.2 Field experiments

The test area, Linalompolo, was situated on latitude 67°15′ N and longitude 20°30′ E, 14.8 km northwest of Gällivare (railway station). In the summer of 1967, instrument prototypes for increment measurement were tested here. During the two following summers, the leading-shoot length and the stem

Table 1. Survey of the pine material studied at Linalompolo in 1968 and 1969.

Pine No.	Height cm	Stem, cm		Leading shoot increment, cm			Height of stem instrument above ground cm	Notes
	1969	1968	1969	1968	1969	1970		
1	69	1.2	1.3	9	4	13	9.5	
2	38	1.2	—	4	5	18	12	Damaged leading shoot 1968
3	34	1.1	1.2	4	1	d	5.5	In forest, potted
4	26	1.3	—	d	d	d	6.5	Dry plant
5	127		4.2	15	4	26	10	Damaged leading shoot 1969
6	48		—	10	5	11	—	
7	63		1.7	—	10	26	14.5	
8	64		1.7	—	3	6	10	
9	175		3.2	—	11	22	16	
10	400		4.3	—	15	30	11	In forest

d=dead plant

diameter of some pines were measured at least once an hour, often at shorter intervals.

As in the test in the phytotron, strangulations round the stems were observed in the field after the measuring bands had been dismantled. Half of the plants showed visible signs of strangulation which disappeared later in the autumn.

The pines, which were naturally regenerated (except No. 3), were of different sizes (Table 1) and 5 to 10 years old. They were standing partly on a clear-felled area and partly in sparse fjeld forest, predommantly pine. The test area was situated near the forest limit at a height of 475 m above sea level. This involved great strain on instruments and vegetation, of which the great mortality in the pine reforestation of the clear-felled area is an indication.

One of the pines was dead (No. 4 in Table 1). Measurements of this plant should give an idea of how the dead tissues of the tree stem, for example in the wood or in the bark, can affect the daily and annual variation of the stem diameter.

The measurement periods include days with slight increment before and after the main growth season. Hydration changes ought to appear on living plants during these days on the assumption that there is a pronounced daily course in transpiration.

The leading-shoot length and the stem diameter have, together with meteorological elements, such as radiation, temperature, humidity and wind, been registered on one and the same data logger equipment system (Solartron make). The global radiation (cal. cm^{-2}), daily or by the hour, the air temperature at a height of 50 cm above ground (daily mean value or value each hour) and the rainfall (daily or by the hour) will be given in the following sections. The global radiation constitutes the direct solar radiation and diffuse sky radiation which falls upon a horizontal surface.

The global radiation energy was measured by means of an instrument, type Moll-Gorczynski (Solarimeter, Kipp & Zonen), and the air temperature by means of resistance wire thermometers (Pt RT 100, Heraus) which were placed in electrically ventilated shields against radiation. The rainfall was registered on a clockwork driven month gauge (Lambrecht). The stem-increment instruments were equipped with radiation shields, semi-cylinders of fine glossy light metal plate. The temperature of the cover of the electric component was measured by means of thermocouples. The output and the compilation have been done manually, after the punched tapes have been listed on computers.

3 Results

3.1 Stem-diameter changes without correlation to the growth process

The stems of forest trees, like all other substances, are subject to volume changes, which are due to changes in the temperature of the material. Wood has, moreover, hygroscopic properties, i.e. the capability of absorbing and evaporating water, which causes swellings and contractions.

3.1.1 *Studies of a dead pine plant*

In order to investigate the magnitude of the stem-diameter changes in the field that are due to the physical properties of the tree, measurements on a dead plant were carried out in the summer of 1968. The plant (No. 4) died in the late winter and the bark and the grey-brown needles remained during the measurement.

The dead stem gradually decreased in diameter in the course of the summer (Figure 5), probably owing to desiccation. In the middle of August the contraction ceased and the stem diameter was thereafter about constant.

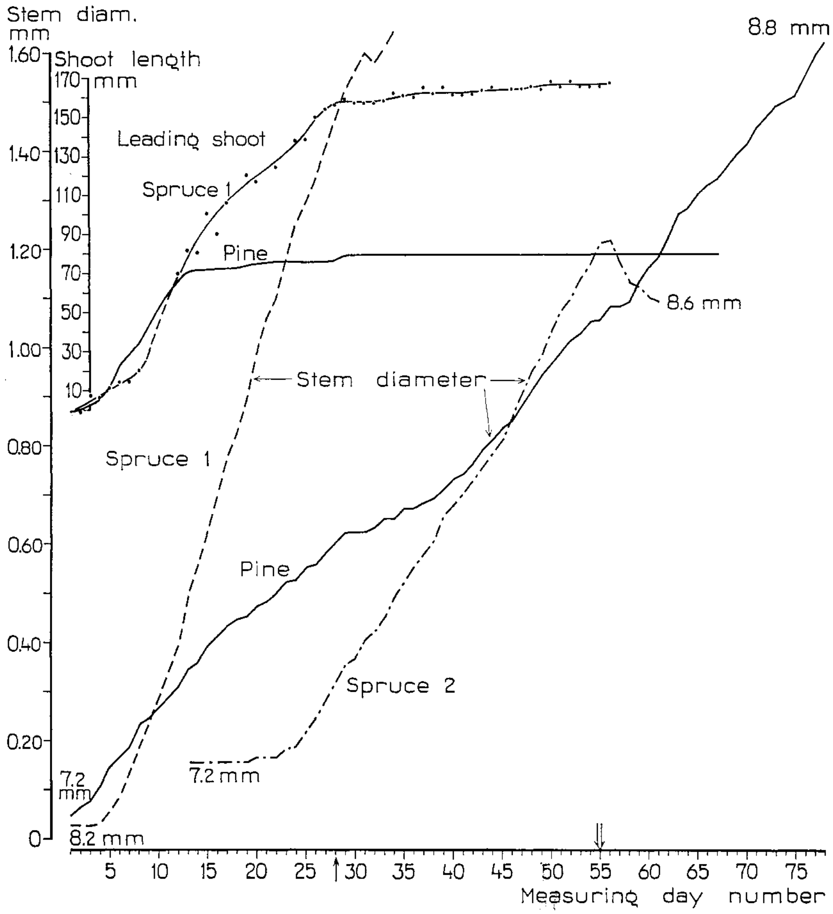
The daily variation in diameter was small with a minimum in the morning and a weak maximum in the day during the fairweather day (Figure 11). The result of the measurement showed that the influence of the dead tissues, as the bark and the wood, on the daily rhythm of the stem-diameter variation was insignificant.

Supposing that the whole stem (13 mm in diameter) has one and the same temperature and that this temperature is equal to the one that was measured on the cover of the stem increment instrument, a daily stem variation, as is shown by the thin continuous curve in Figure 11, plant 4, is obtained. The temperature coefficient of expansion of the stem has here been put at $3 \cdot 10^{-5}$° C^{-1}. On these suppositions the temperature during the 3rd July caused a stem-diameter variation of about 5 μm. Simultaneously with this variation a desiccation was going on. This desiccation had no variation during the day. This last factor resulted in a decrease of the stem of about 15 μm in four days. The rain which fell during the period 2—5.7 or at other times in the summer (Figure 5) did not affect the stem diameter of the dead pine plant.

3.1.2 *Studies of non-growing pine plants*

In the investigation in the phytotron (section 3.2) and from the measurements in the field (3.4 and 3.5), a daily variation in stem diameter was obtained which differed from the daily rhythm that the hydration changes account for. An explanation of this situation might be that the registered daily rhythm has been dominated by the daily course of the increment. This does not necessarily mean that the errors on account of hydrostatical diameter changes were slight. The assumption here has been that magnitudes on hydration changes appear during days of small increment, but with a pronounced course in transpiration. This ought to be the case during days with large daily temperature- and radiation-amplitude immediately after the beginning of the increment and directly before its end.

The plants 3 and 8 started the stem increment during the period 21—24.6 1969, Figure 10. The figure shows that the stem diameter of plant 3, which had been marked with an accuracy of 1 μm, had no daily variation. In the curve for plant 8, a weak daily rhythm in stem diameter did not appear (the 22nd and 23rd of June) until the values had been marked, with an accuracy of 0.1 μm. The maximum took place in the evening (the 22nd) and the minimum in the morning about 8 a.m. The amplitude was smaller than in the curve which is obtained



Phytotron experiments.

↑ the day of radiation reduction (to 0.12 cal $cm^{-2}min^{-1}$)

⇓ the day of watering stop of spruce

Figure 1 The leading-shoot length and the stem diameter at growth in fluorecent light (20h, 0.22 cal $cm^{-2}min^{-1}$ per cycle) and darkness (4h per cycle) at +20° C and +15° C respectively.

by solely temperature expansion (Figure 11).

Provided that there was a daily variation in the transpiration, the June measurement shows that the errors owing to hydration changes were small and probably neutralized each other by stem-diameter changes due to temperature expansions. Nor at the end of the increment period, the 6th to the 10th of July 1969 (Figure 12), were there any changes in the stem diameter of the plants 3 and 8 registered, in spite of heavy rain on the 8th of July.

3.2 The leading shoot and stem-diameter growth in phytotron experiments

The shoot elongation was going on when the measurements started. Figure 1 shows the cumulative growth of the pine and the spruces. The curves indicate the measuring values of the fourth hour after the start of the light period each day. The height growth of the pine was already greatly reduced during the 13th day of the measurement. Five days after this reduction, the stem-

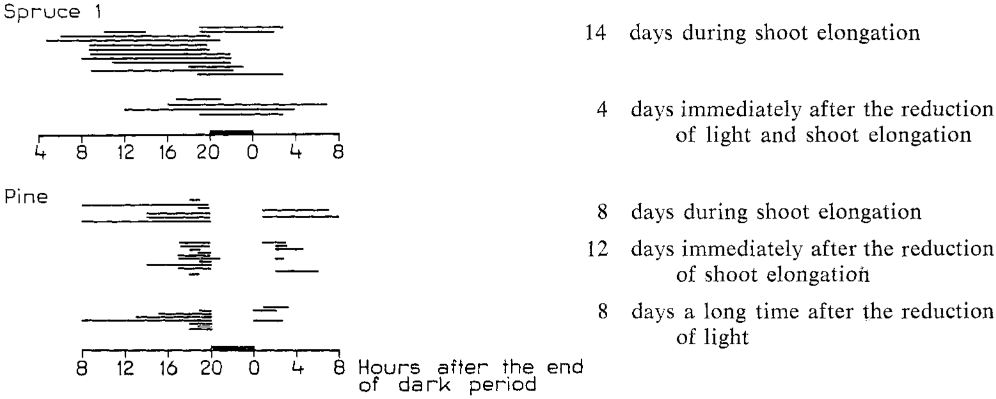


Figure 2 Distribution of the daily stem-diameter increase. The same experiment as in Figure 1.

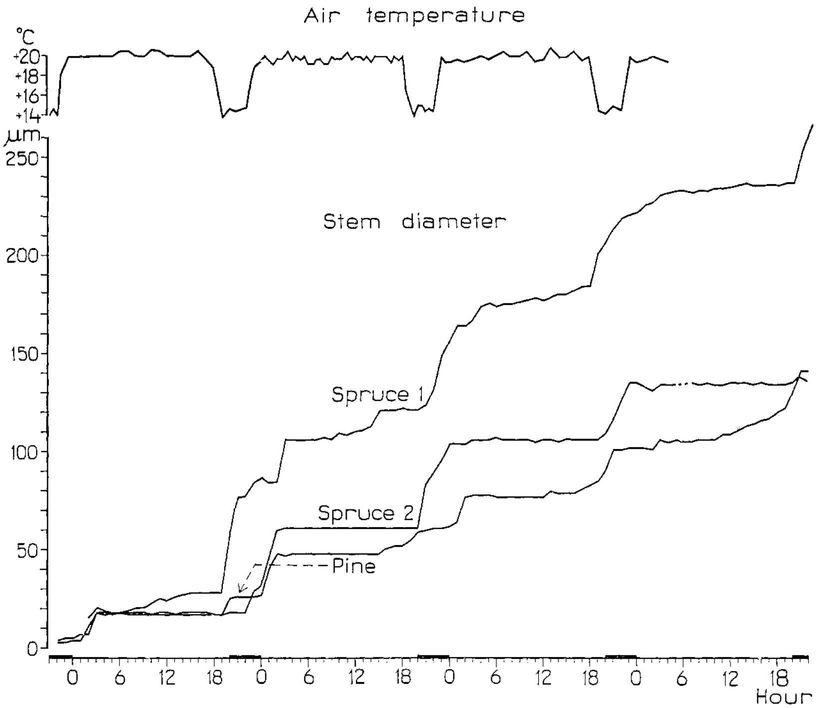


Figure 3 The daily variation in air temperature and stem diameter during periods of light and darkness in phytotron, during the 22nd—26th measuring day for spruce 1 and the 46th—50th day for spruce 2 and the pine.

diameter growth decreased from 0.025 mm per day to 0.015 mm per day.

At the same time as the radiation decreased, day 28, the height growth of the pine ceased completely, and that of the spruce was greatly reduced. The stem-diameter growth in the pine also declined and came to be 0.01 mm per day during the following ten days.

Did the change in height growth or the change in radiation energy affect the stem growth rhythm during the day? This is probably the case since the stem-increment period per day of the pine became short after the height-growth reduction (day 13, Figure 2), and the period with stem increment of the spruce took place later in the day after the amount of radiation energy and the height increment had decreased (day 28, Figure 2).

On further study of the stem-diameter variation during the day, it can be noted that the stems (spruce No. 1 and the pine) increased in thickness mostly during the later part of the light period, Figure 2. Periods with stem increases were followed by constant diameter, Figure 3. Stem-diameter decreases were rare and small, which is believed to be due to the fact that the substrate was well watered. It is interesting to observe that the pine stem stopped increasing in diameter during darkness, Figures 2 and 3, while the stem diameters of the spruces increased in light as well as in darkness.

As from the 55th measuring day, spruce No. 2 was allowed to dry, Figure 1. The stem diameter still increased a little the first day without watering, but afterwards contracted—0.13 mm in five days.

3.3 **Observations of the seasonal growth rhythm in field experiments**

This section deals with the height and stem-diameter increment from day to day, during different phases of the growth course. For each day the measurement value at 6 p.m. or a mean value about 6 p.m. has been indicated in the curves for leading-shoot length and stem diameter, Figures 4—7. As will be shown later, the plants did not have periods of increment at the same time of day and, furthermore, displacements of the growth rhythm occurred. Consequently when comparing the increment of the different plants from day to day, fictitious differences may arise, owing to the fact that the increment value for one plant has been marked in on one day, whereas the corresponding value for another plant may be wholly or partially marked in on the following day.

The growing season is short at Linalompolo on account of the northerly location.

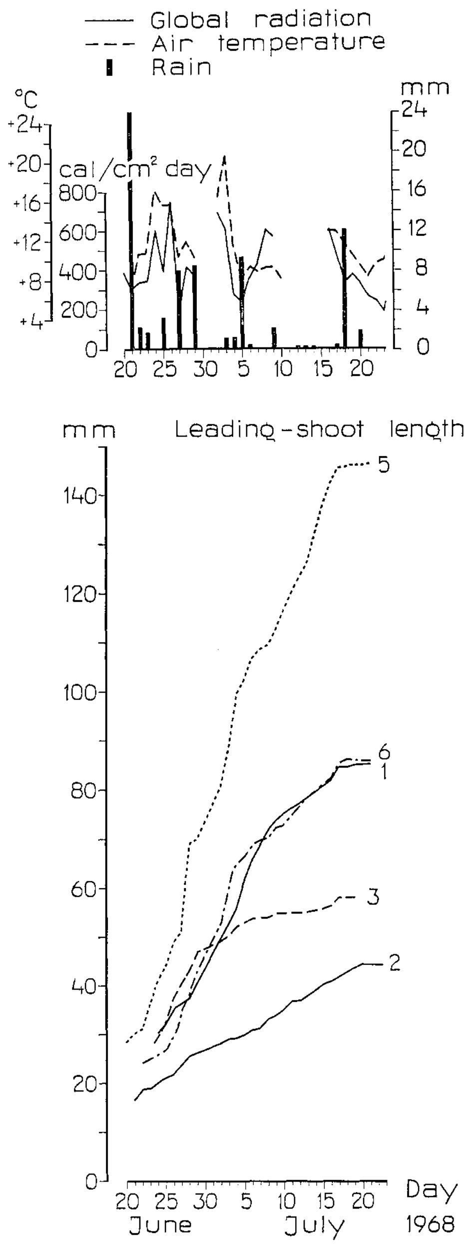


Figure 4 The leading-shoot length of five pine plants and the daily global radiation, temperature and rainfall during June—July 1968.

Growth takes place during the period with extended daylight—the main part at the time of the midnight sun. Growth often starts late in the year because of the late melting of snow. In mountainous regions there may still be snow and frozen soil in

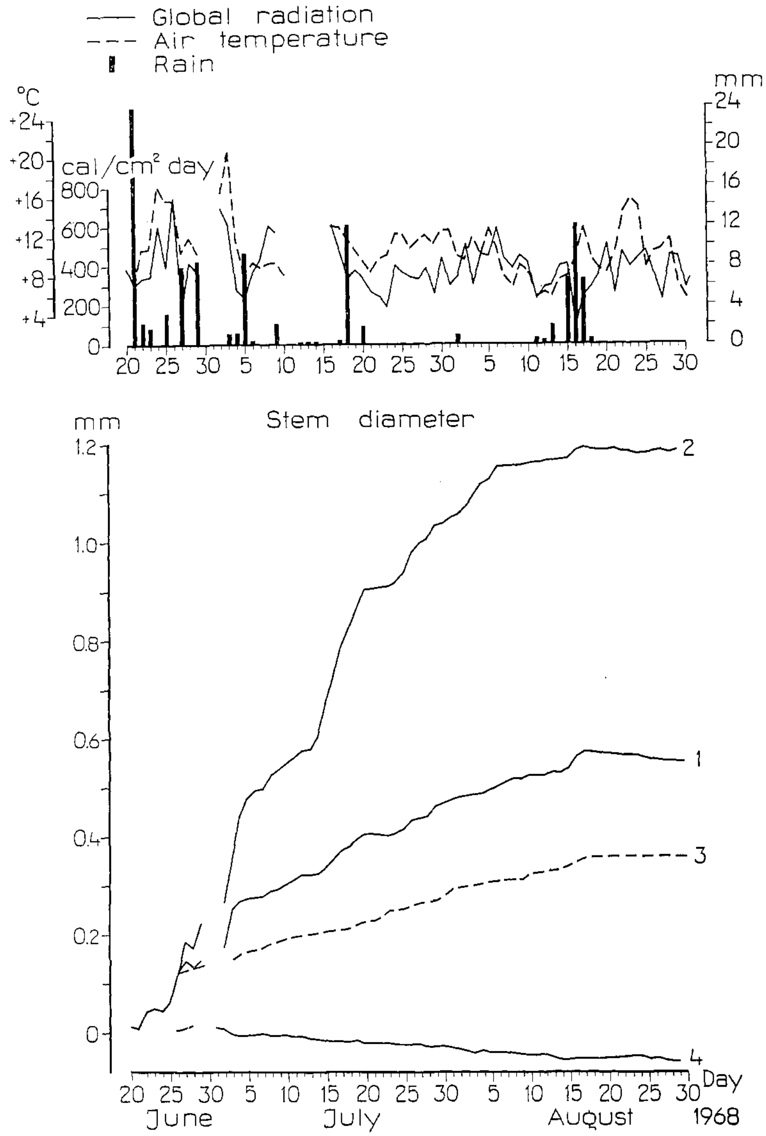


Figure 5 The stem diameter of four pine plants and the daily global radiation, air temperature and rainfall June—August 1968.

June. This was the case in 1968 and 1969. In Figure 6 it can be observed that the shoots had started increasing in length before the 10th June 1969. Snow was then still lying in hollows and the soil was partially frozen.

The continued cumulative increase in leading-shoot length and stem diameter is shown in the Figures 4—7. More or less pronounced stages between periods with different growth speeds can be distinguished in the increment curves of the figures. By means of these stages, the height and stem-diameter growth has been divided into four periods or phases which have been arranged in chronological order according to the following:

1. small daily growth changes in shoot length and stem diameter

2. large height and stem-diameter growth
3. small height but large stem-diameter growth
4. small, gradually decreasing stem-diameter growth and no height increment

1. The first growth phase of the leading shoots started, as mentioned, shortly after or during the melting of snow. The height increment was smaller than 0.7 mm per day from the start of the measurement to the 15th of June 1969 (Figure 6).

2. During the second growth phase the early wood is formed and, at the same time, almost the whole height increment takes place. The phase started 1969 in the middle of June (Figures 6 and 7). The start in the shoots and stems took place almost at the same time. In June 1968 the phase began about five days later, but the start was missed in the registration (the test area was impossible to reach owing to servere melting of the snow and thawing of the frozen soil).

All the trees did not start the rapid growth at the same time. Some pines which started about a week later than more active pine plants also showed a smaller total growth. Examples of pine plants with delayed start are pine Nos. 3 and 5 in leading-shoot increment in Figure 6, and Nos. 3 and 8 in stem-diameter increment, Figure 7.

There was a greater variation between the trees at the end of the second phase than at its start. Plants, which had a large increment during the season, ended the phase with rapid increase later than plants with small increment. In 1969 the rapid growth of the leading shoots ended as early as at the end of June or, for plants with large height increment, during the first week of July.

The second growth phase was ended earlier in 1969 than in 1968 (Figures 4, 5 and 6, 7). For that reason the period of 1969 became shorter in spite of the earlier start. The summer of 1969 was 1.8° C warmer than normally (1931—1960), whereas the summer of 1968 was 0.9° C colder (SMHI, 1968 and 1969). The warm period in 1969 during the second phase (the later part of June) resulted in a rapid increment. The period of warm weather caused a quick development of the leading shoots, of which the total length was determined by the previous cold summer of 1968.

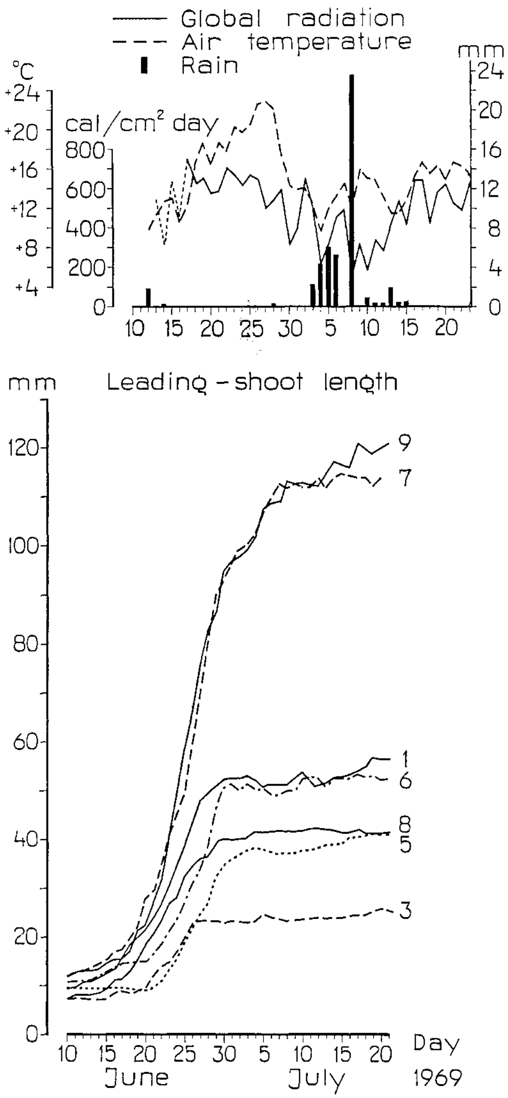


Figure 6 The leading-shoot length of seven pines and the daily global radiation, air temperature and rainfall during June—July 1969.

3. Investigations by *Romell* (1925) and *Jonsson* (1969) show that the main shoot elongation of the pine ends at the middle of the stem-diameter increment period. This point of time constitutes the limit between the second and the third phase of growth.

During the third phase, lower daily stem growth than during the second phase was

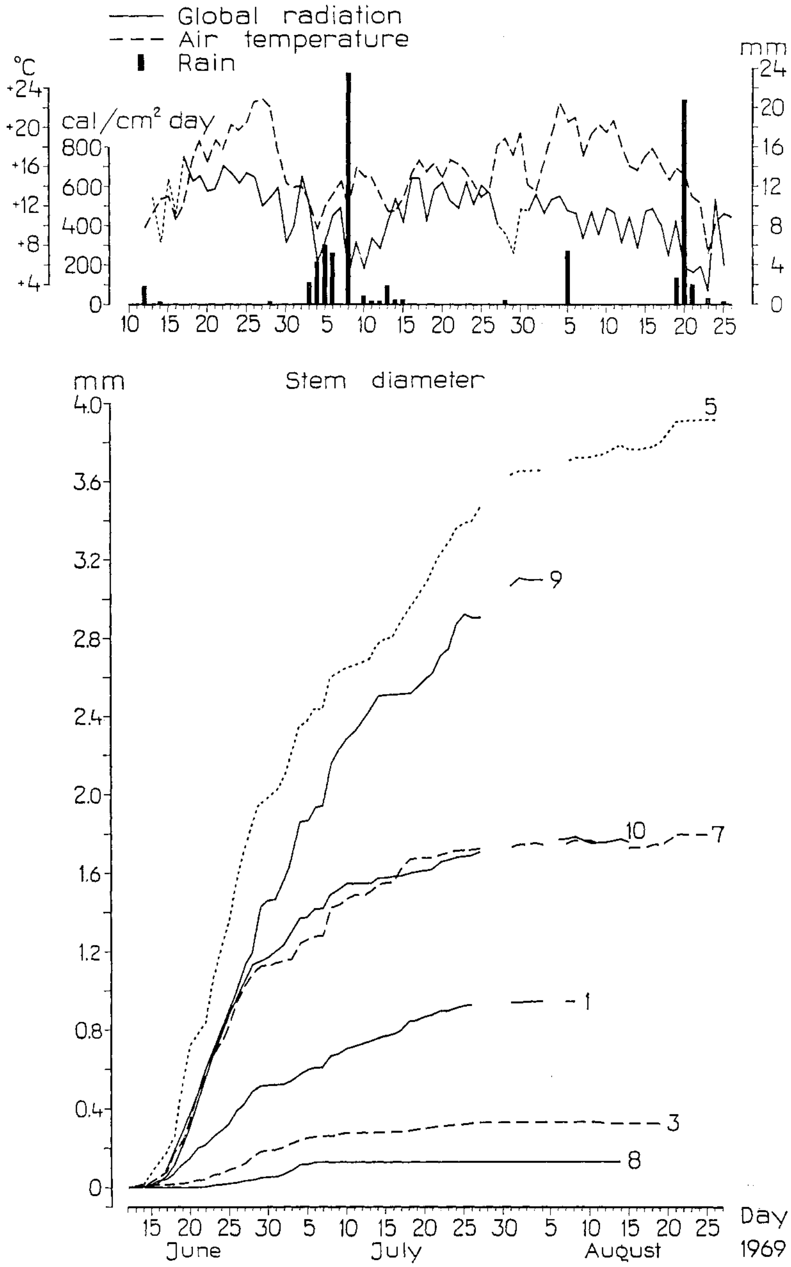


Figure 7 The stem diameter of seven pines and the daily global radiation, air temperature and rainfall during June—August 1969.

obtained (Figures 5 and 7). The increment was comparatively constant during the third phase. It was ended round about the 7th of August 1968 and 25th of July 1969.

4. The fourth growth phase is characterized by a gradually decreasing small daily stem-diameter increment. The exact point of time for the end of the increment cannot be stated, according to *Andersson* (1953). Under Swedish conditions, however, he found that the forming of the growth ring is completed on an average in the middle

of August. The point of time varied greatly from year to year.

In the Figures 4—7 one can see that there were great individual differences in total growth between the pines. The stem growth in plant 8 was inconsiderable and had already ended about the 5th of July 1969 (plant 4, 1968, was dead). The leading-shoot length in the plants 2 (1968) and 5 (1969) was probably impeded since these leading shoots, compared with other shoots on the same tree, appeared to be strongly stunted. Plant 2 had, furthermore, lost the leading side shoots. This probably resulted in increased stem growth. These two plants had in fact the greatest stem-diameter increment in respective years (Figures 5 and 7).

The two summers of 1968 and 1969 differed from one another in mean temperature as well as in total increment. The summer (June-August) of 1968 was colder than 1969. By comparing the Figures 5 and 7 and 4 and 6 respectively, it will be seen that the stem-diameter increase was greater in 1969 than in 1968, while the height increment was smaller in 1969. The height increment of 1968 and 1969 was determined by the summer temperature of 1967 (warmer than normally) and 1968, respectively.

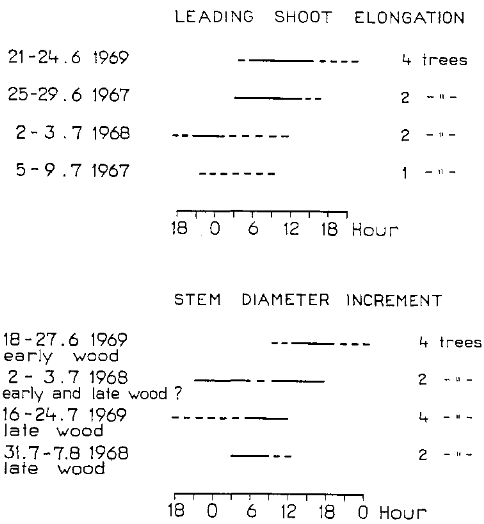


Figure 8 Periods during the day with increment in mainly clear weather. Broken line refers to observations of one pine only.

3.4 The increment rhythm by day, during different phases of the growing season. Field experiments

The daily rhythm of the increment has been studied during different periods of mainly fair weather. All these periods have a great daily amplitude in radiation and air temperature but can differ from one another, both regarding the size of the amplitude and the mean values of the radiation energy and the temperature.

There is midnight sun at Linalompolo from the beginning of June to the middle of July and global radiation consequently occurred during nights at this time. The amount of incoming radiation energy was, however, very small between 10 p.m. and 2 a.m. as the test area was then in the shade (Figure 10). During the periods of light nights, especially when the sky was clear, there was probably net assimilation, since the amount of light was sufficient for photosynthesis (*Lehtonen,* unpublished data) and the respiration was low (because of low temperature).

In Figure 8 the periods during the day when the leading-shoot length and stem diameter increased have been marked with lines. The line is continuous when the increment concerns two or more plants. It can be observed in the figure that the increment had a daily course (except the period 2—3.7 1968 in stem growth), but also that the daily rhythm was not constant during the growing season. During the earlier part of the second growth phase (in June) leading shoots, as well as stems, increased during the day, the height increment mostly in the morning and the stem-diameter increment in the afternoon. Later on, during phase (2—3.7 and 5—9.7), when approximately three-quarters of the leading-shoot elongation was completed, a displacement of the daily growth rhythm has taken place with height increment mainly during the night and in the morning, whereas it is not possible to distinguish a marked rhythm (2—3.7) in the stems. During the third growth phase, i.e. when the shoot elongation has almost ceased for the season and late wood probably is formed in the stems, the stem-diameter increment mostly took place in the morning.

Accordingly, the pines at Linalompolo had the largest increment during the day early in the season. If the point of time (2 a.m.), when the temperature started to rise rapidly, is chosen as a reference point in time, the height increment began 1 to 4 hours after the start of the temperature increase, and the stem-diameter increment 7 to 10 hours after that. The major part of the leading shoots ended the daily increment already before the highest temperature had been reached, and three of the stems as early as 5 hours afterwards.

Later on, during the shoot elongation period, the height increment started about 19 hours after the rise in air temperature.

The start of the stem-diameter increment occurred about 24 (one plant, 14) hours after the rise in temperature during the third growth phase. The displacement between the maximum of the increment and the temperature was about 15 hours (9 hours).

3.4.1 *Comments on the stem-diameter increment of the individual trees*

In order to study the growth rhythm of the stem diameter more closely, the size of the stem-diameter change was calculated every third hour from the measurements once an hour or more frequently during the whole increment period. In Figure 9, periods per day have been marked, when the stem-diameter increase during three hours (continuous lines) has been ≥ 0.4 % of the total growth during the summer. Periods of mainly clear weather have been marked with vertical lines at the date indication to the left. Mean start- and mean ending-time points per tree have been marked with crosses and circles for respective periods. These periods correspond to three of the periods in Figure 8. Consenquently the days 18—27.6 came during the shoot-elongation period (second phase) and the days 16—24.7 and 31.7—7.8 during the period of solely stem-diameter growth (third phase).

From the Figures 5 and 7 showing the daily total of the radiation and mean values of the air temperature, it can be observed that the two later periods had less radiation and, above all, lower temperature than the June period. This situation may have had an influence on the fact that, according to Figure 9, there were longer periods of stem-diameter increase in mainly fair weather days during the second growth phase than during the third one. This is still more evident, when the demand on the size of the increment is intensified (the dashed lines for plant 5 and 7). There are, however, great differences in the structure of the cells during early and late increment phases with early and late wood respectively.

By studying the daily rhythm it can be observed that all the pine plants and the trees, except the withered plant 3 (1969), had a more or less pronounced daily rhythm in stem-diameter increment.

During the second growth phase, the stem-diameter increment took place by day, starting in the morning or in the middle of the day (9 a.m.—12 noon), Figure 9. The pines started their increment almost at the same time, but ended it at different points of time. The smaller pine plants (1 and 7) ended the stem-diameter increase in the afternoon or in the evening, but the larger plant (5) and the four-metre pine (10) did not do this until late in the evening or during the night.

During the third growth phase, both in 1968 and 1969, the stems increased in the early morning and later in the morning, starting at dawn, on an average 3 a.m.—6 a.m. Also during the third growth phase, differences occurred between the pines at the end of the increment, which took place on an average between 6 a.m. and 12 noon. Plant No. 5 (1969), which had a damaged leading shoot, differed from the rest by starting the daily increment about 5 p.m. in the evening and ending it around 2 a.m.

The period of stem-diameter growth consequently took place at different times, when early and late growth phases are compared. The time displacement varied in scale from tree to tree. The difference between the second and the third phase in growth-start was on an

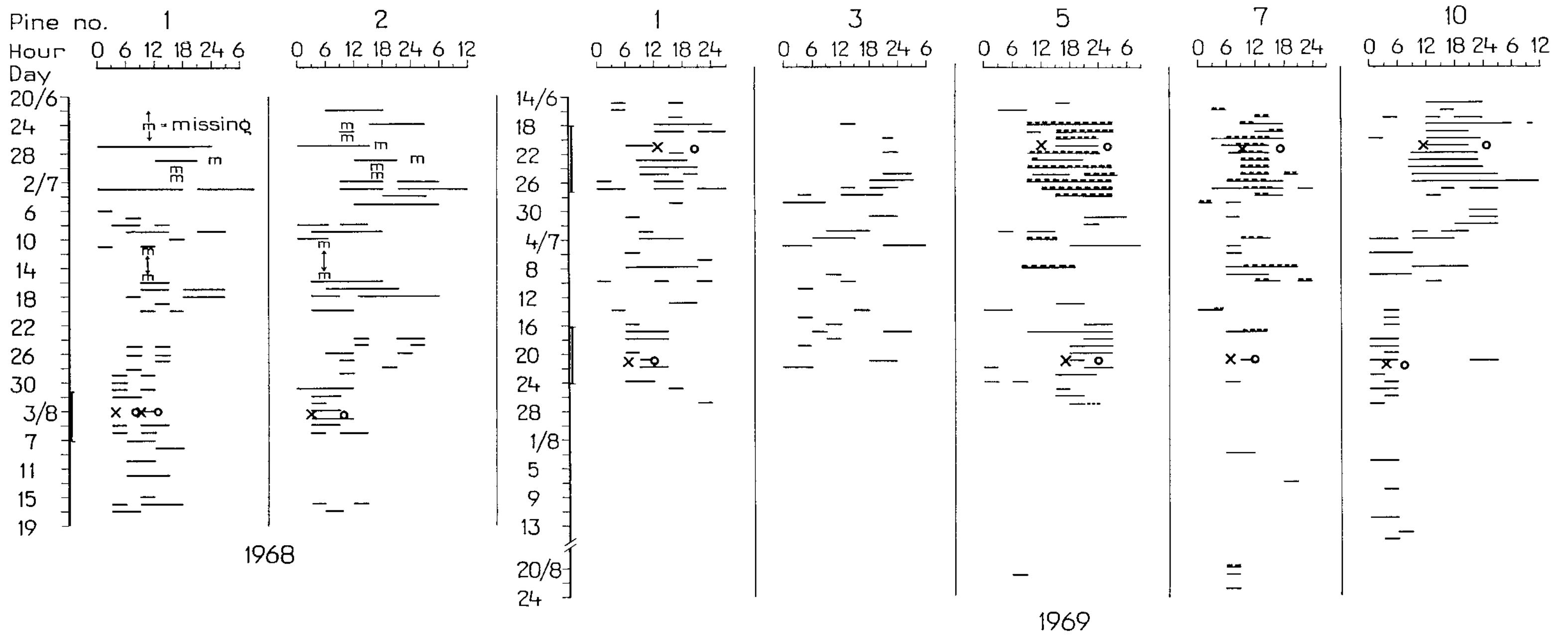


Figure 9 Periods during the day when the stem-diameter increase during three hours has been ≥ 0.4 % of the total growth of the season, continuous lines. Dashed lines mark when the increase during three hours has been ≥ 2.7 % and ≥ 1.9 % of the total growth [pine 5 and 7 respectively].

average 15 hours calculated ahead in time (from 12 noon to 3 a.m.) for the four-metre pine (10), and 18 and 21 hours for the plants 1 and 7 respectively. The displacement for plant 5 was only 6 hours.

3.5 **Growth and the weather**

The variations in the weather are reflected as irregularities in the increment curves, Figures 4—7. Warm and sunny days were followed by larger increment than cold and overcast days. Low temperature, which often was combined with small incident radiation, reduced the increment of the leading shoots 27.6 and 6—8.7 1968 and also 1.7, 3.7 and 6—7.7 1969. Seventeen out of twenty investigated cases (1968 and 1969) of small or no stem-diameter growth occurred during, or were preceded by, days with relatively low temperature.

Changes in the weather are presumed to have a great influence on the increment. One example will be shown here. In connection with the fact that the temperature fell from about 22° to 17° C at unchanged high insolation on the 28th to the 29th of June 1969 (Figure 7), the stem-diameter increment ceased or decreased already as from the 29th (from the morning and the middle of the morning), in spite of the relatively favourable temperature and radiation conditions still prevailing on the 29th.

During a period of bad weather, on the other hand, days with relatively low temperature and small insolation but with an improvement in weather, can be followed by a considerable increment. An exemple of this latter case is the increment of the 8th of July 1969, which followed after two days of variable cloudiness and a mean temperature about 14° C.

Days *with rain and the extent of the* rainfall is also shown in the Figures 4—7. During the increment periods of 1968 and 1969, changes owing to rain in leading-shoot length and stem diameter, are not possible to observe unambiguously. The stem diameters increased, however, probably because of swelling by rain on the 13th to the 17th of August 1968 and on the 19th to the 21st of August 1969 (plants 5 and 7), after the main increment was ended. Both these periods of rain followed a long spell of dry weather.

3.5.1 *The diurnal growth rhythm*

Section 3.4 dealt with the growth rhythm in mainly clear weather. The discussion in this section partially deals with the same periods. The first one (21—24.6 1969) comprises days with regular and great amplitude in air temperature and global radiation. During the second period (2—5.7 1968), a transition from warm to cold weather has been studied and during the third (6—10.7 1969), the increment in changeable but cold weather. The shoot elongation took place during the first two periods, but had ended during the third one.

Fair weather, early in the growing season

The spell of fair weather 21—24.6 came about a week after the start of the second increment phase in the major part of the plants. Plants 3 and 8, however, did not start until during the actual period, which resulted in a weakly developed daily stem growth rhythm, Figure 10. In the curves showing leading-shoot length and stem diameter, it is possible to distinguish an almost constant rhythm from day to day in the pines which had large increment. The height- and stem-variation had a similar course, with increment start in the early morning or later in the morning. The increment period of the leading shoot in the large plant (5) took place later in the day than in the smaller plants (6 and 8). The pines started the period with the largest stem-diameter increase almost at the same time, 9 a.m., but there were great differences in the course of the increment as from the afternoon.

In spite of the short and light night (incident radiation all the day) there was a great difference between day and night in global radiation and air temperature (Figure 10). The time lag of the highest temperature compared with that of the global radiation, typical of fair

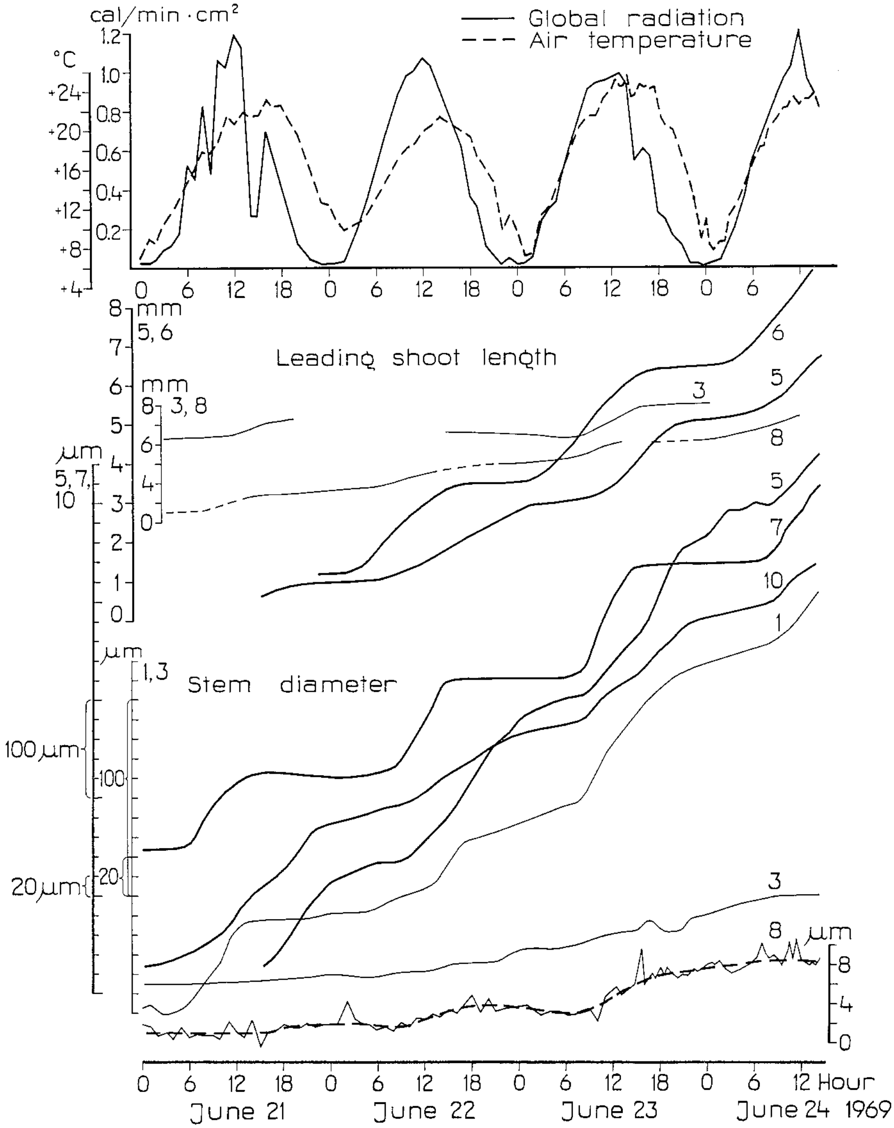


Figure 10 The daily variation in global radiation, air temperature, leading-shoot length and stem diameter 21—24 June 1969.

weather and summer, is evident. The temperature rose quickly from 1 a.m.—2 a.m. at the same time as the clear-felled area was lit up by the sun. It had been in the shade since 10 p.m.

Differences between the plants in starting and ending the height increment were observed. Consequently the plants (6 and 8) started and ended the height increment earlier in the day than the larger plant (5), of which the leading shoots later appeared to have been damaged. Plant (3), which was weak, had a short increment period with a late start and an early end. The increment cessation of the leading shoots, which took place in the evening and during the night, lasted (except pine 3) 9 to 10 hours.

In spite of disparities in height, age and locality in the pines, the increment of the stems started almost at the same time of the day, about 9 a.m. Pine No. 1 had, however, a more irregular daily rhythm than the fast-growing trees. The last two days it also started at about 9 a.m. (please note that the stem-diameter scale in Figure 10 is enlarged for plant 1 and 3 and greatly enlarged for No. 8). In the pines with

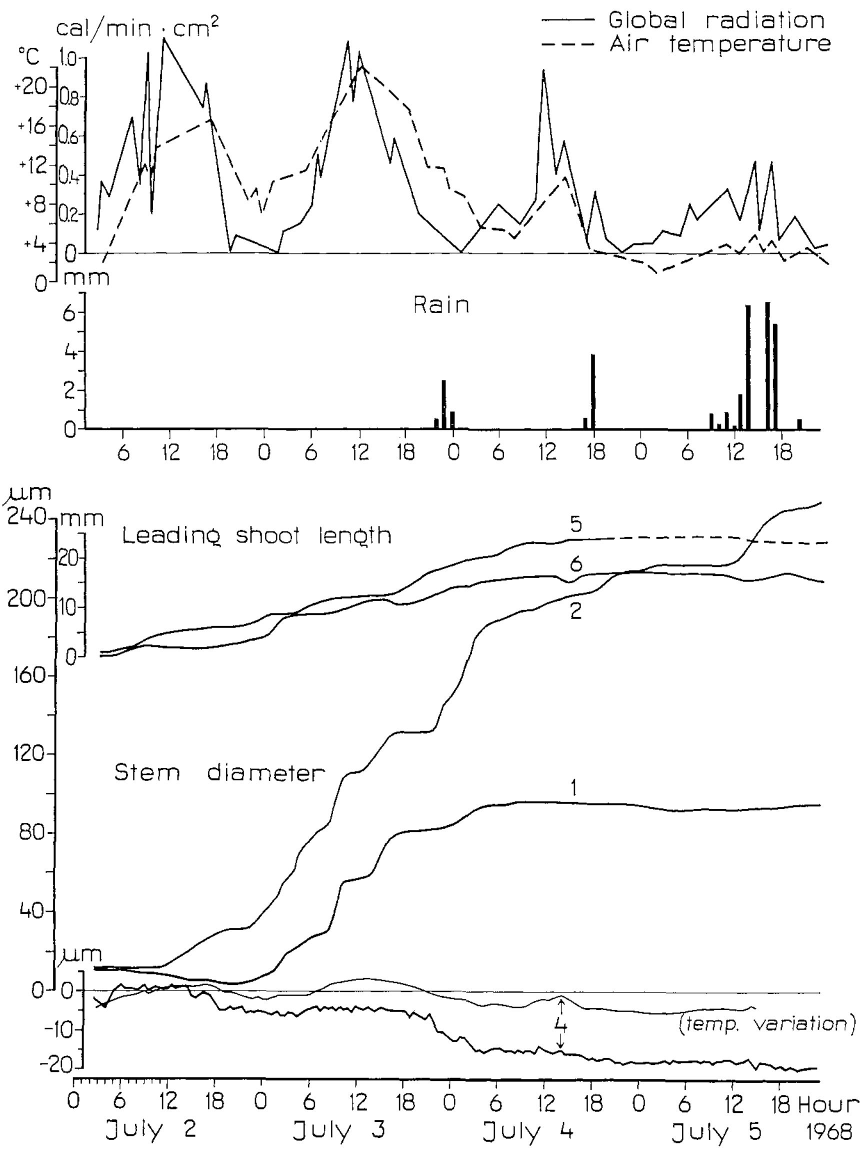


Figure 11 The daily variation in global radiation, air temperature, rainfall, leading-shoot length and stem diameter 2—5 July 1968. The thin line, 4, is the stem-diameter variation calculated from temperature measurements. The thick line, 4, is the real stem diameter of the dead plant.

the largest daily increment, Nos. 5 and 10, it can be discerned that the increment speed decreased about 2 p.m. which probably is an effect of hydration changes. The four-metre pine (10) increased in stem-diameter throughout the day. The small pine plants (1 and 7) had no or very small increment most of the day (from the afternoon to the following morning), while the big plant (5) had large increment and short periods of rest.

A change from warm to cold weather during the later part of shoot-elongation period

During the second period 2—5.7 1968, Figure 11, a cold front passed in the night preceding the 4th of July. Cold and cloudy weather followed the front passage. As the weather deteriorated the height and stem-

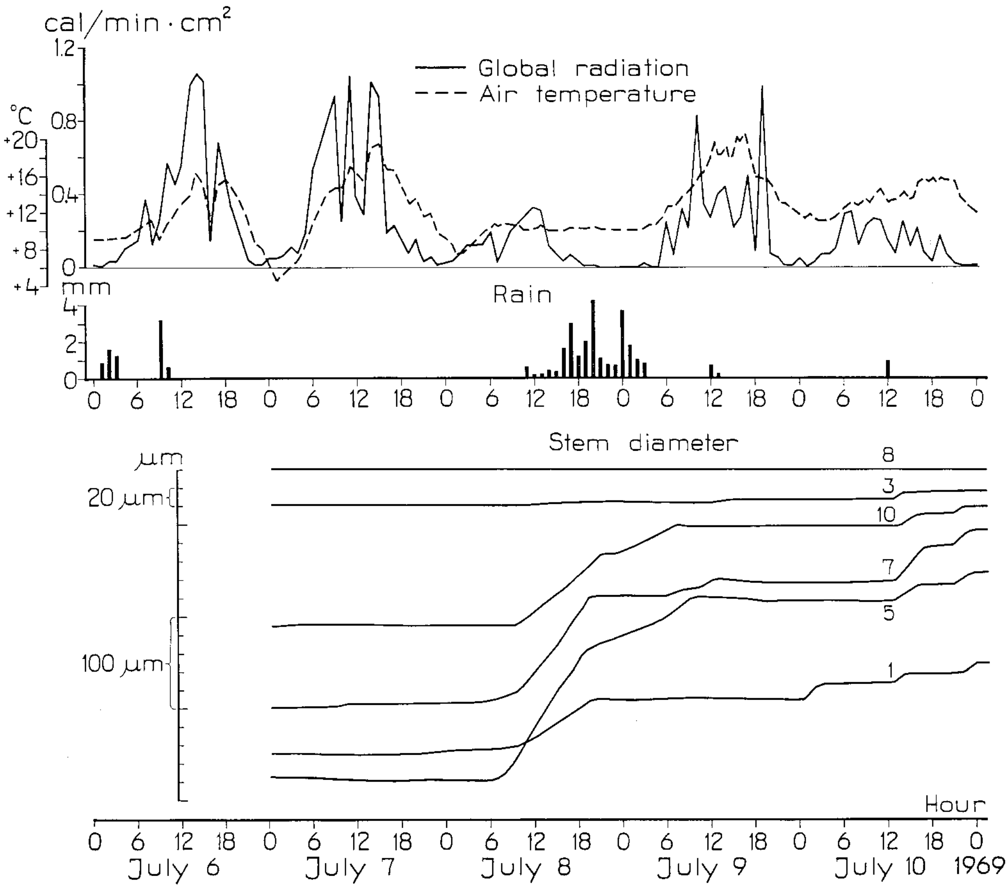


Figure 12 The daily variation in global radiation, air temperature, rainfall and stem diameter 7—10 July 1969.

diameter increment ceased or decreased as from the morning (4 a.m.—9 a.m.) of the 4th of July. The same quick reaction to changes in the weather was obtained at the fall of temperature on the 29th of June 1969 (section 3.5). During the 5th of July there was still no further increment registered from the leading shoots, nor from the stem to plant 1. Plant 2, on the other hand, slowly increased in stem diameter until the morning of the 5th and also grew rapidly during the afternoon of the same day.

The second period (2—5.7 1968) started with warm and mainly clear weather (Figure 11). The daily variation in the height increment during fair weather was not as pronounced as during the period 21—24.6. In the curves it is possible to distinguish a slight tendency to two increment periods in the leading shoots, one in the morning and the middle of the morning and one in the evening and night.

The stem diameter increased considerably in the two live plants on the 3rd July. The start, which in the slowly growing plant was preceded by contraction, took place during the night. Several interruptions occurred in the rapid stem-diameter increase. It is interesting to observe that the periods with different increment speed took place at the same points of time in both plants.

The rain which fell during the period may possibly have contributed to the stem-diameter increase in plant (2) (the night before the 4th and 6 p.m.—8 p.m. the same day and also in the afternoon on the 5th). The stem of plant (1) and the leading shoots do not seem to have been affected.

Variable but cold weather, late in the growing season

The daily variation of the stem-diameter increment was regular in fair weather during the third increment phase (section 3.4.1). The increment then started early in the morning, about 3 a.m., with a displacement of approximately 24 hours (except plant 3) in relation to the temperature. The difference between the maximum of the increment and the temperature was about 15 hours.

The shoot elongation had ended for the season 6—10th of July 1969 and also the stem increment in plant 8 and almost for plant 3, Figure 12. The figure shows that periods with irregular course in incident radiation and temperature seem to result in irregular daily rhythm in increment. Accordingly, there was no increment on the 7th of July, whereas the stem-diameter increase was large on the 8th, starting at 7 a.m. to 9 a.m., before the rain started. The next period with increment took place during the afternoon and night of the 10th of July. In contrast to the previous example, when the shoot extension was still going on, the stem increment in this example reacted slowly to the weather. The displacement of the maximum of the increment in relation to the maximum temperature was of the magnitude 24 hours (8.7 and 10.7 1969).

During the third period (Figure 12) the weather was variable but mostly with a great deal of cloudiness and low temperature. The weather on the 6th and 7th of July, however, involved an improvement compared with that of the 4th and 5th. The pines did not increase in diameter on the 7th of July in spite of sun and a maximum temperature of 15 to 16° C during the 6th and 7th. Not until the 8th, when it was overcast and a low even temperature all day did a considerable stem-diameter increment take place. Probably the rain did not affect the large increment of the 8th July, since the increment started before the rain started and there was probably also a high humidity in the soil after the rain on the 3—6th of July. There was an increment stop again as from the morning of the following day and it was not until the 10th that the stem diameters increased, only this time it took place in the afternoon and early night. One or two days running without any increment whatsoever is not unusual. In Figure 9, which was described in section 3.4.1, days with bad weather have irregular indication lines for increment or no indication at all.

4. Discussion

Errors. As soon as living organisms, e.g. plant individuals, have measuring devices attached to them their behaviour is more or less disturbed. The extent of the disturbance is sometimes possible to estimate by using different methods in order to measure one and the same factor. The assumption is here that the *daily growth rhythm* of the trees was not at all or only slightly affected by the measuring instruments, and this for two reasons: First the leading shoots and stems, which were measured by independent methods (different instruments) had similar growth rhythm. Secondly, the different trees showed approximately the same increment pattern despite differences in the placing and exposure of the instruments. On the other hand, the strangulation which was caused by stem-increment instruments affected the *total seasonal stem-diameter growth.*

Observations of the course of the stem growth during the day have hitherto not been stated in the literature on account of errors, which are due to hydrostatic stem size changes. *Kozlowski* gives in 1967 an account of results from stem-diameter registrations on small trees. In one of his partial tests in greenhouse, the stem diameter of four plants (Acer negundo L.), which were standing in well-watered substrate, was measured. A daily variation of the stem diameter in Kozlowski's tests could be distinguished in July, with a decrease (contraction) in the day and an increase (expansion) at night, caused by hydration changes. The growth in the cambium layer could not be determined, as the relationship between the growth and expansions-contractions was too small.

In the phytotron experiment, where the substrate was also very well-watered, but the change in the environment from light to darkness was considerably smaller, the growth seems to dominate over variations caused by hydration changes (Figures 2 and 3). The manual irrigation, immediately before the beginning of the dark period, may have contributed to the rapid part of the stem-diameter increase through expansion in Figure 3, but attention must be paid to the fact that the increase for one of the spruces and for the pine had already started before the irrigation. Moreover the plants were continuously irrigated by drip.

The pine plants and the pine in field have probably not been suffering from shortage of water, since the stems increased in diameter at rain on only a few occasions and contractions were very seldom registered. At the investigation in the summer of 1968, however, measurements were also made on plants in plastic pots, which were standing on the clear-felled area. The daily variation in stem diameter in these plants was irregular, probably because of hydration changes. Contractions were usual.

According to *Kozlowski* (1964, 1967), and for big trees *Leikola* (1969, a and b) and others, the low transpiration during darkness causes the stems to swell. At the phytotron test and during the early growth period in field, the pines reacted in different ways, i.e. the stems stopped increasing in diameter or decreased the growth speed during darkness or twilight. The spruces in phytotron, on the other hand, may have increased in diameter through swellings during the dark periods. It must be observed, however, that the stem diameter also for these trees was able to increase considerably during the light periods as well.

Consequently, our measurements showed a daily course in stem diameter which differed a great deal from the variations due to hydration changes. As mentioned, one of the reasons for this can be that there was plenty of water in the substrate and the soil. Another reason, combined with the former, can be the low tree-heights: The energy, (i.e. power multiplied by length), required for transporting water up through the stem, is probably lower for a plant or small tree than for a full-grown tree. By reason of this it is possible that the tendency towards development of tensions in stems and the connected decrease of cell volumes will be less for the small trees. Finally, a third reason may be that the cells might have been deformed by the pressure of the measuring band, since some stems were strangulated. The variations in the volume of the cells, which are caused by changes in water content, can possibly, by the pressure of the measuring band, mainly have taken place in directions along the stem, whereas variations perpendicularly to the longitudinal direction have been impeded.

The seasonal growth rhythm. According to *Mikola* (1950 and 1962), the size of the height increment and the quantity of early wood is determined by the conditions in the environment during the summer that precedes the growth period, in Scandinavia and Finland by the temperature. *Kozlowski* and *Winget* (1964) found that four-fifths of the shoot increment in Pinus resinosa took place with stored compounds which had been translocated from old needles.

Rutter (1957) observed that while the leading-shoot elongation in Pinus silvestris was going on, the owendry weight of the old needles went down approximately as much as the growing shoots gained in weight.

It is not unlikely that also the stem-diameter increment during the early stage of the increment, by analogy with the shoot elongation, to some extent takes place by means of stored assimilates.

In the phytotron investigation, lower daily stem diameter in the pine was observed from the point of time when the rapid shoot extension ceased. In spite of irregularities owing to variable weather, the same observations may be made in the field as well. This is most evident during 1969 and for plants on which both leading-shoot length and stem diameter were measured.

Gordon's and *Larson's* (1968) studies of Pinus resinosa indicate that the production of xylem cells with thick walls, usually combined with late wood, bear a physiological relation to the maturity of the needles formed during the current season. The shoot elongation was already effected to 90 % when the rapid growth of the new needles started, in *Gordon's* and *Larson's* investigation.

There was a great variation in the total growth of the pines. Trees with early increment-start ended the increment late. The two plants with impeded leading-shoot elongation had the largest stem-diameter increment. It seems as if compounds, which normally would have been used for increment at a certain point, by damage can be used in other parts of the plant.

The daily growth rhythm. Mork (1941) carried out height increment measurements at Hirkjölen's fjeld area on latitude 61°30′. There he found that the increment of the spruce was largest about 8 p.m. and that there was increment stop in the day between 6 a.m. and 12 noon. The maximum of the growth took place six hours after temperature was at its highest. *Mork* (1941, pp. 18—21) is of the opinion that the displacement of the height increment curve in relation to the temperature curve is an indication of how rapidly the assimilation products are transported from the needles to the places of consumption. The increment stop between 6 a.m. and 12 noon is explained by the fact that the major part of the added compounds are used up by 6 a.m. (no new production during the night) and that the increment does not start again until the daily assimilates are available (at noon).

Lyr et al. (1968) are of the opinion that the temperature in combination with the support of reserve nutrition and the apparent assimilation determines the increment course. Moreover, the authors state that when there is a good reserve nutrition support and high assimilation, the increment can take place the whole day, although somewhat reduced during the night, probably on account of low temperature. The height increment may not take place during the night for plants with small carbohydrate reserves.

Both the measurements in the field and in the phytotron show that the daily growth rhythm was not constant with the time. The contradictory results in the literature (section 1) on the daily rhythm of the height increment may be explained by the fact that the measurements have been carried out at varying points of time after the start of the leading-shoot elongation. The increment reaction of the pines to external factors (temperature and radiation) during the late growth period was considerably slower than that stated by *Mork* (1941) and *Lyr* et al. (1967) for the height increment.

The age of the pines varied between five and about ten years in the field investigation. According to *Lyr* et al. (1967) the daily growth rhythm changes with the age of the trees. Plants which develop juvenile wood, can consequently have another daily rhythm than that observed in elder plants. The pines (Nos. 5 and 10) with the thickest stems (4.2 and 4.3 cm) registered the greatest time difference in growth rhythm between the early and late growth periods (Figure 9).

The increment rhythm in stems and leading shoots was similar. But there was a tendency in the leading shoots to start and end the increment earlier in the day than the stems did. This was the case immediately after the start of the season and when the daily increment was very large. The longer distance for translocation to the stem measurement point than to the leading shoot is probably reflected here. In the investigation it has not been possible to distinguish disparities in increment rhythm between the pine plants due to varying distances between the needle masses of the bransches and the stem measurement points.

There was probably great variation in the ages and genetic qualities of the pines. The conditions in the ground had also changed considerably owing to the inhomogeneity of the soil. In spite of this the daily stem-diameter increase started at almost the same time of day. This indicates that the increment start is determined by external factors. The continued increment course during the day, in which the end of the increment is included, was individual.

A constant periodicity in external factors caused constant growth rhythm. The change in the course of the growth during the day, which has been observed between the different phases both in the leading shoots and in the stems, is probably primarily determined by physiological factors, e.g. the maturity of the new needles and shoots. Attention should here also be paid to the fact that there is a difference between the increment phases in the structure of the cells, early and late wood.

Furthermore, according to the scientists reported in this discussion, mainly stored assimilation products are utilized, during the early growth phase, whereas assimilates of recent formation are mainly used for increment during later growth stage. It was also to be observed that the dry substance increment can be large despite small volume increment.

The weather and the growth rhythm. The increment during a season is affected by the weather during the actual growth course as well as during earlier periods. *Jonsson* (1969) points out the influence different kinds of weather have on the annual ring width, not only during the increment period, but also during its preceding seasons. According to many investigations, the air temperature is the most important external factor affecting the increment of the forest trees in the north of Europe (*Mork* 1941, *Wielgolaski* 1966 and others in height growth, and *Mikola* 1950, *Eklund* 1954 and others in the annual ring width). The closer the northern forest limit one gets, the stronger the correlation will be (*Mork* 1941 in height increment and *Sirén* 1961 in annual ring width).

One of those who have made studies of the size of day-by-day increment is *Mork* (1941), who obtained high correlation between the height increment in spruce and the six hottest hours of the day and *Dahl* and *Mork* (1959) between height increment and the respiration (a function of the temperature). The relationships may be applicable during the middle of the growth period, equivalent to 60 % of the total shoot elongation. By introducing a dynamic model, *Hari*, *Leikola* and *Räsänen* (1970) have been able to eliminate this limitation and consequently to determine the daily height increment during almost the whole increment period. A corresponding model displaying the relationship between ecological factors and radial growth has been elaborated by *Hari* and *Sirén* (1972).

The stem-diameter growth from day to day has been investigated by *Leikola* (1969 a), in the south of Finland. He found that in the case of large trees, the stem-diameter increase was most strongly correlated with the solar radiation and the air temperature during the day that precedes the increment. The correlation to external factors was weak two days before the increment.

Irregularities in the daily course of the external factors, which are due to the weather, seem to result in an irregular daily rhythm in increment. It is worth noticing that in this case the actual change in weather can be of great importance. A cooling down of the air to a temperature still comparatively high, may, according to our observations, result in increment stop. The same "low" temperature in a different meteorological situation may result in considerable daily increment. The increment was affected simultaneously in all the trees when the temperature or the radiation changed. The increment of the pine plants and the pine reacted more quickly to changes in the weather during early increment phase than during late. This observation is consistent with the fact that the displacement in increment (in relation to the air temperature) was smaller during early than during late increment phase.

Summary

Leading-shoot length and stem diameter have been registered together with meteorological factors such as radiation, air temperature and rainfall. The measurements have been carried out in a climate chamber, the phytotron of the Royal College of Forestry and at a notherly situated locality in the field.

Height and stem growth or increment is here defined as the irreversible increase in leading-shoot length and stem diameter respectively.

In the phytotron test, with twenty hours of light and an air temperature of +20° C and four hours of darkness and +15° C, a reduction in the height-increment speed of a pine plant (Pinus silvestris L.) was followed by reduced stem-diameter increase and probably by a change in the increment rhythm of the stem during "the day". When the radiation energy (the light) was reduced by 45 %, the height increment in the pine ceased and was considerably decreased in a spruce (Picea abies L. Karst.). In addition, the stem increment of the pine decreased and the daily growth rhythm of the spruce stem was displaced. The stem diameter of the pine was constant during the periods of darkness.

The study in the field was carried out in the summers of 1968 and 1969 at a latitude of 67° N. Measurements were made on pine plants of varying ages, 5 to about 10 years old, and on a pine 4 metres high. The total increment during the season varied greatly. The trees which started the increment early, ended it late. Two plants with impeded leading-shoot elongation had the largest stem-diameter increment.

The daily rhythm of the increment was similar for leading shoots and stems. The daily course in external factors, such as solar radiation and air temperature, probably determined the starting point of time of the increment during the day. The continued increment and the end of the increment was individual. During the early growth phase, when the leading shoot and the stems greatly increased from day to day, the increment took place in the day — the height increment mainly in morning and the stem-diameter increment in the afternoon. During the later part of the shoot elongation, the leadingshoot length increased in the night and in the morning. After the end of the main shoot-elongation and after the development of the new needles was finished, the stem increment (late wood) took place in the early morning and later in the morning, with the exception of one plant which registered increment during the evening and night.

An irregular course during the day, principally in the air temperature, resulted in irregular increment rhythm. Changes in the weather affected the daily rhythm as well as the total amount. The increment in the pines reacted rapidly to changes in the weather during early growth phase, but slower (stem) during late phase. Days with low air temperature and/or small incident radiation were followed by growth stop or decreased increment speed. Rain did probably not affect the leading-shoot length and the stem diameter.

The daily variation in stem diameter was inconsiderable in pine plants which did not grow and also in a dead pine plant. The latter gradually decreased in diameter during the course of the summer. Observations of stem contraction were rare on plants in well watered substrate in climate chamber and on the naturally regenerated pine plants in the field.

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Sources and references

Andersson, S.-O. 1953. Om tidpunkten för den årliga diametertillväxtens avslutande hos tall och gran. (On the date of completion of annual diameter growth in pine and spruce). — Medd. Statens Skogsforskn. inst., 43 (5), 1—27.

Bringman, M. & Rodskjer, N. 1968. A small thermoelectric pyranometer for measurements of solar radiation in field crops. — Arch. Met. Geoph. Biokl., ser B, 16, 418—433.

Dahl, E. & Mork, E. 1959. Om sambandet mellom temperatur, åndning og vekst hos gran (Picea abies L. Karst.). (On the relationship between temperature, respiration and growth in Norway spruce (Picea abies L. Karst.). — Meddr. norske skogsfors. ves. 16.

Danilov, M. D. 1954. Diurnal periodity in the growth of shoots of some tree and shrub species. — Doklady Adad. Nauk. S.S.S.R. 96, 205—208.

Eklund, B. 1954. Årsringsbreddens klimatiskt betingade variation hos tall och gran inom norra Sverige åren 1900—1944. (Variation in the widths of the annual rings in pine and spruce due to climatic conditions in northern Sweden during the years 1900—1944). — Medd. Statens Skogsforskn. inst. 44.8.

Fielding, J. M. 1955. The seasonal and daily elongation of the shoots of Monterey pine and the daily elongation of the roots. — Forestry & Timber Bur. Australia, Lft 75.

Friedrich, J. 1897. Über den Einfluss der Witterung auf den Baumzuwachs. — Mitt. Forstl. Versuchw. Österr. 22.

Gordon, J. C. & Larson, Ph. R. 1968. Seasonal Course of Photosynthesis Respiration, and Distribution of ^{14}C in Young Pinus resinosa Trees as Related to Wood Formation. — Plant Physiol., 43, 1617—1624.

Hari, P., Leikola, M. & Räsänen, P. 1970. A dynamic model of the daily height increment of plants. — Ann. bot. fenn. 7, 375—378.

Hari, P. & Sirén, G. 1972. Model of radial growth of timber line pine defined by degree of physiological development and some ecological factors (Manuscript).

Jonsson, B. 1969. Studier över den av väderleken orsakade variationen i årsringsbredderna hos tall och gran i Sverige. (Studies of variation in the widths of annual rings in Scots pine and Norway spruce due to weather conditions in Sweden). — Skogshögskolan, Inst. f. Skogsprod., Rapp. och Upps. 16.

Kern, K. G. 1965. Beiträge zur Frage des Stärkenablaufs innerhalb einer Vegetationsperiode. — Schriftenr. Forstl. Abt. Alb. Ludv. Univ. 4, 124—141.

Kozlowski, T. T. 1964. Shoot growth in woody plants. — The Bot. Review, 30 (3), 335—392.

— 1964. Water Metabolism in Plants. — Harper & Row. Publ. New York—Evanston—London.

— 1967. Diurnal variation in stem diameters of small trees. — Bot. Gaz. 123 (1), 60—68.

Kozlowski, T. T. & Winget, C. H. 1964. Diurnal and seasonal variation in radii of tree stems. — Ecology 45, 149—155.

Kramer, P. J. & Kozlowski, T. T. 1960. Physiology of Trees. — Mc Graw-Hill Book Co., New York—Toronto—London.

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

— 1969 b. The effect of some climate factors on the daily hydrostatic variations on the stem thickness of Scots pine. — Ann. bot. fenn. 174—181.

Lyr, H., Erdmann, A., Hoffman, G. & Köhler, S. 1968. Über den diurnalen Wachstumsrhythmus von Gehölzen. — Flora, Abt. B, Bd. 157, 615—624.

Lyr, H., Polster, H. & Fiedler, H. J. 1967. Gehölzphysiologie. — Veb. Gustav Fisher Verl., Jena.

Mikola, P. 1950. Puiden kasvun vaihteluista ja niiden merkityksestä kasvututkimuksina. (On variations in tree growth and their significance to growth studies). — Comm. inst. for. Fenn. 38.5.

— 1962. Temperature and tree growth near the northern timber line. — Tree Growth by Kozlowski, T. T. Chapt. 16. Ronald Press. New York, N.Y.

Mork, E. 1941. Om sambandet mellom temperatur og vekst. (Über den Zusammenhang zwischen Temperatur und Wachstum). — Meddl. fr. Norske Skogsf.v., 27, 1—89.

Ninokata, K. & Miyazato, M. 1959. Measurement of daily variation of trunks by electrical strain gauge. — Bull. Fac. Agric. Kogoshima Univ., 8, 76—99 (på japanska).

Odin, H. & Openshaw, A. 1971. Eletrical methods for measuring changes in shoot length and stem diameter. — Inst. f. skogsföryngr. Rapp. o. Upps. 29.

Polster, H. 1950. Die physiologischen Grundlagen der Stofferzeugung im Walde. — Verl. GMPH, München.

Romell, L.-G. 1925. Växttidsundersökningar å tall och gran. (Recherches sur la marche de l'accroisement chez la pin et l'epicéa durant la periode de végétation.) — Medd. Statens Skogsforskn. inst. 22, 45—124.

Rutter, A. J. 1957. Studies in the growth of young plants of Pinus sylvestris L. I. The annual cycle of assimilation and growth. — Ann. Bot. 21, 399—425.

Sirén, G. 1961. Skogsgränstallen som indikator för klimatfluktuationer i norra Fennoskandien under historisk tid. — Comm. inst. for Fenn. 54.2.

SMHI 1968, 1969. Sveriges meteorologiska och hydrologiska institut. — Årsbok del 1 Vol. 50 (1968): 1 & 51 (1969): 1.

Wielgolaski, F. E. 1966. The influence of air temperature on plant growth and development during the period of maximal stem elongation. — Oikos 17, 121—141.

Sammanfattning

Toppskottlängd och stamdiameter har registrerats tillsammans med meteorologiska faktorer såsom strålning, lufttemperatur och regnmängd. Mätningarna har utförts i klimatkammare, Skogshögskolans fytotron, och på en nordligt belägen lokal i fält.

Höjd- och stamtillväxt definieras här som den irreversibla ökningen i toppskottlängd respektive stamdiameter.

Vid fytotronförsöket, med 20 timmars ljus och lufttemperaturen +20° C och 4 timmars mörker och +15° C, åtföljdes en reduktion i en tallplantas (Pinus silvestris L.) höjdtillväxthastighet av minskad daglig stamdiameterökning och sannolikt av att stammens tillväxtrytm under "dygnet" ändrades. Då strålningsenergin (ljuset) reducerades med 45 % upphörde höjdtillväxten hos tallen och minskades betydligt hos en gran (Picea abies L.). Strålningsminskningen medförde också att tallens dagliga stamdiametertillväxt avtog och att granstammens tillväxtrytm förskjöts. Tallens stamdiameter var konstant under mörkerperioderna.

Fältstudien genomfördes under sommaren 1968 och 1969 på ett höjdläge på 67° N. Mätningar gjordes på tallplantor av varierande ålder 5—10 år samt på en fyra meter hög tall. Den totala tillväxten under säsongen varierade betydligt. De träd, som startade tillväxten tidigt avslutade den sent. Två plantor som hade hämmad toppskottsträckning hade största stamdiametertillväxten.

Tillväxtens dygnsrytm var likartad för toppskott och stammar. Den dagliga gången i yttre faktorer såsom solstrålning och lufttemperatur bestämde sannolikt tillväxtens starttidpunkt under dygnet. Den fortsatta tillväxten och tillväxtens slut var individuell. Under tidigt tillväxtskede, då toppskottlängden och stammen ökade med stora belopp från dag till dag ägde tillväxten rum på dagen — höjdtillväxten huvudsakligen på förmiddagen och stamdiametertillväxten på eftermiddagen. Under skottsträckningens senare del ökade toppskottlängden under natten och morgonen. Efter den huvudsakliga skottsträckningens slut och sedan nya barr färdigbildats, ägde stamtillväxten rum (sommarved) under tidig morgon och förmiddag utom för en planta som hade tillväxt under kvällen och natten.

Oregelbunden gång under dygnet i främst lufttemperaturen medförde oregelbunden tillväxtrytm. Väderleksförändringar påverkade såväl dygnsrytm som tillväxtbelopp. Tallarna svarade snabbt med tillväxtändring på väderleksomslag under tidigt tillväxtskede men långsammare (stam) under sent skede: Dagar med låg lufttemperatur och/eller liten instrålning åtföljes av tillväxtstopp eller minskad tillväxthastighet. Regn påverkade sannolikt inte toppskottlängden och stamdiametern.

Den dagliga variationen i stamdiameter var obetydlig hos tallplantor som inte växte och likaså hos en död tallplanta. Den senare minskade gradvis i diameter under sommarens lopp. Observationer, då stammarna krympte, var sällsynta på plantor i väl uppvattnat substrat i klimatkammare och på de naturligt föryngrade tallplantorna i fält.