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THE PERIODICITY OF WOOD FORMATION

BY

KJELD LADEFOGED

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i kommission hos Ejnar Munksgaard

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I. Introduction.

Knowledge of the growth periodicity of the various species of trees is of importance for the understanding of their nature and growth reaction to different external conditions.

In Denmark the time of foliation, flowering, and defoliation is known from observations made in the field as well as from phenologic investigations carried out by LANGE (1873, 1879, and 1884) and BRUUN (1889 and 1919). The time of the extension growth of the roots has been investigated by O. G. PETERSEN (1898 and 1903) and LADEFOGED (1939).

On the other hand we have no certain knowledge of the periodicity of wood formation in this country. From observations of the rising of the sap and when the bark 'slips' we know in practice the approximate time of the beginning of wood formation in spring and its termination in autumn. But beyond this our knowledge of its periodicity and dependence on external conditions is pretty insufficient.

If we want to form an opinion in this direction it may be done on the basis of the many, and often very valuable, investigations carried out abroad, chiefly in Central Europe, England, and U.S.A.

Owing to the often considerable climatic differences the results of these investigations cannot directly be transferred to conditions in Denmark. To this comes that the results frequently differ to a certain extent, and chiefly apply to species of trees of a rather peripheric interest to Danish forestry.

From the desire to obtain a more satisfactory basis for the determination of the periodicity of wood formation in our forest trees I have from the time from March 1944 till November 1945 watched cambial activity and wood formation in the following species of trees:

Conifers:

- Pinus silvestris* L. Scotch pine.
- Larix decidua* MILL. Larch.
- Picea abies* L. KARST. Norway spruce.
- Picea sitchensis* (BONG.) CARR. Sitka spruce.
- Abies alba* MILL. European silver fir.
- Pseudotsuga taxifolia* (PORR.) Britt. Douglas fir.

Hardwoods:

Betula pendula ROTH. Birch.
Alnus glutinosa (L.) GAERT. Alder.
Corylus avellana L. Hazel.
Carpinus betulus L. Hornbeam.
Fagus silvatica L. Beech.
Quercus robur L. Common oak.
Ulmus glabra HUDS. Elm.
Tilia cordata MILL. Lime.
Aesculus hippocastanum L. Horse-chestnut.
Acer pseudoplatanus L. Maple.
Prunus avium (L.) MOENCH. Wild cherry.
Sorbus aucuparia L. Mountain ash.
Fraxinus excelsior L. Ash.

Through our examinations it has in the first line been our aim to throw light on:

1. The time of the beginning and termination of cambial activity in branches, stem, and roots.
2. The process of wood formation in the most important species of trees.
3. The time of the beginning of summer wood formation, and the difference between spring and summer wood.

Further, investigations have been carried out concerning the duration of the shoot extension period and water transportation at breast height.

II. Literature.

Some of the first investigations of the periodicity of wood formation were undertaken by TH. HARTIG (1857 and 1863a). In Germany he i. a. watched the wood formation in 16-year-old *Pinus silvestris*, *Larix decidua*, *Quercus robur* and *Acer pseudoplatanus* all through a summer.

He found that cambial activity began first in the young branches, then it started in the stem, and last in the roots. Between the time it began in the branches and in the roots a period of $1\frac{1}{2}$ to $2\frac{1}{2}$ months elapsed.

In *Pinus silvestris* and *Quercus robur* cambial activity began in the branches as well as in the stem before May 5th. He did not notice the same growth condition till June 7th in *Larix decidua* and *Acer pseudoplatanus*.

In autumn cambial activity terminated in the same succession as it began in spring, 2 to 3 weeks later in the roots than in the stem.

SCHRÖDER (1879) in Russia measured the thickness of the stem at a week's interval in young ($3\frac{1}{2}$ — $4\frac{1}{2}$ m high) *Quercus robur*, *Populus tremuloides* and *Picea abies* var. *sibirica*.

In *Picea abies* the wood formation was liveliest in May; in the *Quercus robur* and *Populus* in the middle of June. In all three trees it ceased in the middle of August.

RUSSOW (1884) found in contradistinction to TH. HARTIG that only a few days elapsed between the beginning of cambial activity in the stem and in the roots.

GULBE (1888a and b) has in Russia examined the periodicity of wood formation in seventeen different species of hardwoods and conifers. In conformity with TH. HARTIG and RUSSOW he found that cambial activity started in the branches, while it began later in stem and roots. Between the time of its inception in the young branches and roots a period of 4 to 5 weeks elapsed.

In autumn it ceased in the same succession—two months later in the roots than in the branches.

CHRISTISON (1889) through eight years at short intervals measured the increase in circumference in nineteen different species of trees in a botanical garden at Edinburgh.

In *Quercus robur* and evergreen conifers the growth in thickness began earlier—in the other species of trees¹ not until some time after bud break.

In May and June wood formation was livelier in conifers than in hardwoods. Averagely 54 % of the new annual ring was formed by July 1st in conifers against 35 % only in hardwoods.

MISCHKE (1890) examined in Germany the process of wood formation in *Pinus silvestris* and *Picea abies* by cutting sections from the stem nine times in the course of a summer and counting how many new cells had formed radially.

In *Pinus silvestris* wood formation began in May. It progressed slowly till the end of June when it completely ceased—probably owing to drought. In August it started again, and for a short time it was very lively.

In *Picea abies* wood formation began at the end of April. It was most lively during the time from the middle of May till the middle of June as well as in August.

R. HARTIG (1882b and 1891, pp. 161—164) has in various places in Germany examined the inception of cambial activity in trees in different growth localities.

He found that it started earlier in spring in sun-exposed than in shaded stems.

The branches are more quickly warmed up in spring than the stem and roots. Therefore cambial activity starts first in the branches.

MER (1892a) found under investigations of the time for the inception of cambial activity in *Quercus*, *Fagus*, *Carpinus*, *Tilia*, *Populus* and *Picea* that 10 to 15 days passed between its inception in the stem and the roots.

JOST (1892) through a period of two years regularly measured the increase of the circumference of the stem with a steel band in 16 different species of trees at the botanical garden in Strassburg. In 10 species of trees he further watched the growth in thickness by measuring their diameters with a "Fuhlhebel".

The growth in thickness began in May and reached maximum in June or July. Hereafter it quickly decreased and ceased in September or October.

¹ Of ring porous trees only *Quercus robur* was measured.

The growth in thickness in the branches all the time preceded that in the stem.

He found a still lively cambial activity at the base of one- and two-year-old branches after the leaves and buds were fully developed. From this he concludes that there is no connection between the development of the leaves and the growth in thickness of the branches.

REUSS (1893) constructed a dendrograph by means of which he through a period of two years followed the growth in thickness of the stem of a 15-year-old open-grown *Tilia*.

The growth in thickness began in May after foliation.

The first year it already ceased at the beginning of July, the second year not until the end of August.

FRIEDRICH (1897) constructed a "Zuwachs-Autograph" which might be placed on the stem and automatically recorded the changes in its circumference. With a series of such instruments he through a period of 5 years watched the growth in thickness from day to day at breast height in i. a., older *Fagus sylvatica*, *Acer pseudo-platanus*, *Tilia cordata*, *Picea abies* and *Pinus silvestris* at the botanical garden at Mariabrunn.

The growth in thickness on the whole began simultaneously with foliation. It did not, however, really gather speed till after the leaves were completely developed. In several of the species of trees there were two annual maxima: one at the end of May, and another towards the middle of July.

The growth in thickness ceased within the period between the middle of August and the beginning of October.

REICHE (1897) found that in Chile the growth in thickness began after bud break.

WALTER (1898) all through a summer watched the wood formation in the stems of four 100—200-year-old *Fagus sylvatica* standards in the neighbourhood of Giessen. At intervals he extracted cores with a borer from 1.5 m height, and under the microscope he then counted how many new cells had formed radially.

The opening of the buds began slowly on April 21st. Wood formation in the stem did not begin till a month had passed and lasted till August 18th.

WIELER (1898) applied the same method to examine the periodicity of wood formation in amongst other trees, *Pinus silvestris*, *Picea abies*, *Abies alba*, *Quercus robur* and *Fagus sylvatica* in various parts of Germany. The variation in the individual trees and species of trees between the dates for the inception and termination of wood formation was very great.

O. G. PETERSEN (1898) found in 1896 beginning wood formation on May 20th in the stems of 2—5-year-old *Fraxinus excelsior*, *Betula pendula*, *Fagus sylvatica*, *Quercus robur*, *Acer pseudoplatanus*, *Picea abies* and *Pinus Mugo*. In *Alnus glutinosa* it could only be ascertained on June 11th.

BUCKHOUT (1907) watched the periodicity of the growth in thickness from 1897—1900 in two old *Larix decidua* MILL. and *Pinus strobus* L. in Pennsylvania. Like JOST he measured at intervals how much the stem had increased in circumference.

The growth in thickness began simultaneously with bud break at the end of

April. In *Larix decidua* it ceased already in July; in *Pinus strobus* not until mid-September. The reason of this great difference he seeks in the fact, that the growth of *Larix decidua* is adapted to Alpine climates, whereas that of *Pinus strobus* is adapted to a milder climate.

The rainfall and temperature of the various years exercised no influence on the time for the beginning of the growth in thickness.

AMILON (1910) found under investigations of 20—22-year-old *Larix sibirica* LEDEBOUR in Bjurfors Kronopark North of Ystad, in Sweden, that cambial activity started earlier in spring in the upper than in the lower part of the stem.

He thinks that the reason of this is that the upper part of the stem is more thin-barked and therefore more quickly gets warmed up than its lower part. In this connection he draws attention to the fact that no thin-barked trees, by nature, grow in Sweden.

BROWN (1912) by cutting sections from the stem has through two years watched the formation of wood in 22-year-old and 100-year-old *Pinus rigida* MILL. in Ithaca in North America.

Contrary to the abovenamed investigators he found that wood formation began in the stem at some distance from the top shoot; not until 19 days later did it reach up into the latter.

The time for the beginning of wood formation in the lower part of the stem was dependent upon the insolation, thickness of the bark, etc.

The extension growth of the roots preceded the growth in thickness.

By applying the same methods BROWN (1915) examined the periodicity of wood formation in *Pinus strobus* L. The trees were of all ages and grew in different parts of North America.

He found that the growth in thickness might be divided into a) growth in thickness without division into cells and b) growth in thickness by division into cells.

- a) It started in March and was due to an extension radially of the cambium cells and the youngest sieve tissue cells.
- b) It started a few days before bud break at the end of April.

As in *Pinus rigida* MILL. wood formation began in the stem at some distance from the top shoot.

Wood formation continued in branches, stem and roots as long as temperature conditions permitted it.

The formation of summer wood started in the middle of August, and first in the branches.

The formation of sieve tissue continued longer into the autumn than wood formation.

KNUDSON (1913) in 1909 watched the formation of wood in the stem of four 13-year-old *Larix laricina* KOCH in a nursery in Ithaca in North America. At intervals he cut out 1 cm deep sections from the stem under each circle of branches from top to root and measured the width of the fresh-formed wood ring.

He found, like BROWN, that the cambium cells extended radially before the beginning of the division into cells.

In contrast to BUCKHOUT he found, that wood formation did not begin till a month after bud break.

During the period from May 25th till June 3rd over one third of the new annual ring was formed. By July 6th wood formation was almost completely finished in the whole stem.

New investigations (1911) showed that wood formation in the stem by far preceded wood formation in the branches.

KNUDSON supports his opinion on not named works and arrives at the conclusion, that wood formation can only begin after the young needles are so far developed that they yield a sufficiently large assimilation surplus.

MACDOUGAL (1921 and 1924) constructed a dendrograph which in similarity with FRIEDRICH'S "Zuwachs-Autograph" may be placed round the stem and which carefully records the changes in its circumference. With a series of such instruments he through several years followed the course of the growth in thickness in many various species of trees in North America.

In *Fraxinus excelsior* and *Pseudotsuga taxifolia* the growth in thickness preceded bud break. In most of the other species of trees—amongst others *Quercus robur*—it began from a few days and up to 10—12 weeks after bud break.

The growth in thickness in the roots often lasted few weeks only, and it started later than in the stem.

The width of the annual ring increased with the duration of the growth period. "Ringed" stems did not grow in thickness under the ringing place.

KORSTIAN (1921) followed with the same dendrograph the growth in thickness from April till June in an *Acer negundo* L. and a *Picea pungens* ENGEL in Big Cottonwood Canyon, 25 miles southeast of Salt Lake City, Utah.

From this examination, which covered a short period, he arrived at the conclusion that the growth in thickness in evergreen conifers begins simultaneously with the opening of the buds. In deciduous trees it can on the other hand only begin when the foliage is so far developed, that it produces a sufficiently large assimilation surplus.

PEARSON (1924) also followed the course of the growth in thickness with a dendrograph in two young *Pinus scopulorum* ENGELM. in Arizona.

In one tree the growth in thickness of the stem started in May and ceased on September 10th. In the other tree it began on June 1st and terminated already on August 27th.

ROMELL (1925) in connection with investigations of the periodicity of shoot extension also—through three years—followed the course of the growth in thickness in the stem of *Pinus silvestris*. During the first two years he followed it by making measurements on cores extracted at certain intervals in time. The last year he measured at intervals how much the stem had increased in circumference.

The investigations were carried out in Central Sweden and comprised 20 trees evenly spread over the following four plantations:

- | | | |
|----------------|---|------------------------------|
| a) thinned | } | plantation on a south slope. |
| b) non-thinned | | |
| c) thinned | } | plantation at a flat area. |
| d) non-thinned | | |

The two first years the growth in thickness started a few days later than the shoot extension; the last year not until 18 days later.

There was no conspicuous difference between the time of the beginning of the growth in thickness in the unevenly treated and exposed plantations. On the other hand wood formation proceeded relatively more quickly in early spring in the thinned than in the non-thinned plantations.

In comparison with the shoot extension the period of growth in thickness varied much from year to year. In 1923 it was 27 days shorter than in 1922. ROMELL concludes from this, that the shoot extension and the growth in thickness are caused by widely differing factors.

In contradistinction to SCHWARZ (1899), LAITAKARI (1922) and MACDOUGAL (1921 and 1924) ROMELL found that the width of the annual ring did not increase with the length of the growth period.

MORIKAWA (1927) found by investigations in Japan that in *Pinus densiflora* SIEBOLD and ZUCCARINI and *P. Thunbergii* PARLATORE wood formation began in the two-year-old branches coincident with bud break.

CHALK (1927 and 1930) has in the neighbourhood of Oxford investigated the periodicity of wood formation in *Fraxinus excelsior* L., *F. oxycarpa* WILLD. as well as *Pseudotsuga taxifolia* BRITT. He followed the growth in thickness by means of MacDougal's dendrograph and by measurements on sections.

In *Fraxinus excelsior* wood formation started three weeks before foliation, and first in the stem. By May 26th the leaves were completely expanded, and about one third of the new annual ring was formed by then.

In *Pseudotsuga taxifolia* the growth in thickness in the stem began about 12 days before bud break.

The winter buds were fully developed by July 21st. By this time 90% of the new annual ring had been formed in *Fraxinus excelsior*, and in *Pseudotsuga taxifolia* 73%.

In *Fraxinus excelsior* wood formation ceased at the middle of August; in the *Pseudotsuga taxifolia* about the middle of September.

COSTER (1927) has through four years carried out comprehensive investigations concerning the periodicity of wood formation in a large number of species of trees within the dry monsoon area in East Java (Toeban) and the more rainy West Java (Tjibodas and Buitenzorg).

In the periodically deciduous species of trees wood formation began simultaneously with foliation. That also applied to ring porous trees (among others *Quercus robur*) introduced from Europe.

Wood formation was most active as long as the foliage was young. It ceased at leaf fall.

The lignification of the newly formed wood elements continued into the leafless period.

In tree species where the growth of the branches was not synchronous, wood formation in the branches closely followed the growth rhythm of the branches themselves. In these trees there were therefore at the same time branches with a beginning cambial activity, branches that were in the midst of the period of wood formation, and branches in which the cambium was at rest. The ring porous *Castanea sativa* MILL. introduced from South Europe belonged to these trees.

In the evergreen trees (naturally occurring *Quercus* species, *Castanea argenta* BL. and others) wood formation took place all the year round, if there was sufficient precipitation. If longer periods of drought occurred (East Java) wood formation generally ceased during the latter.

LODEWICK (1925 and 1928) in North America followed the periodicity of wood- and sieve-tissue formation in, among others *Fraxinus americana* L., *Quercus borealis* MICH., *Betula lutea* MICH., *Acer saccharum* MARCH., *Liriodendron tulipifera* L. and *Thuja occidentalis* L. The investigations were carried out partly by application of MacDougal's dendrograph and partly by measurements on sections.

In the ring porous trees wood formation started in the stem just before or simultaneously with bud break. In the diffuse porous it only began two to three weeks after bud break, when the leaves were from a quarter to completely expanded.

In *Fraxinus excelsior* in open stands wood formation began first in the stem just under the crown. In other cases it began at the surface of the ground and spread from there up through the stem. In the thin roots of *Fraxinus excelsior* it began a week later than in the stem.

Sieve tissue formation started simultaneously with wood formation.

In the ring porous trees summer wood formation began as soon as the foliage was fully developed.

A few years later LODEWICK (1930) found by investigations of *Pinus palustris* MILL. in West Florida that the width of the annual ring here increases with the rate of rainfall during the summer months.

SWARBRICK (1927a) has examined cambial activity in fruit trees. He found, like KNUDSON and BROWN, that about a fortnight before the beginning of division into cells the cambial cells extended radially. At the same time the cambium was "... translucent, and it was much more turgid than during the winter" (p. 151).

Wood formation began in the branches and spread from here in basipetal direction.

In the course of summer the cambium cells increased somewhat in size.

In the same year SWARBRICK (1927b) published the result of investigations on the effect of ringing in the stems of fruit trees.

Wood formation began first in the stem above the ring.

Between the rings of double-ringed stems no wood formation took place, even though there still were branches in this place. The cambium in stead entered into a vacuolate condition. SWARBRICK concludes from this that the connection between

wood- and sieve-tissue is of great importance for the coordinated and continuous physiological activity in the stem.

REES (1929) in 1926 and 1927 examined the periodicity of wood formation in nine 150—300-year-old *Picea rubra* LINK in different growth localities in the neighbourhood of Wanakena in the State of New York. He was content to determine the growth condition on sections taken at certain intervals from branches, stem, and roots.

Wood formation started c. a fortnight before bud break. In well drained grounds it began at the end of May; in wet and cold soil on the other hand not until the middle of June.

COCKERHAM (1930) at Leeds in England at intervals of four to five weeks in the course of a year felled in all thirty sycamores and each time carefully investigated the cambial activity from top to root.

The cambium began to swell at the end of March. Immediately afterwards the formation of sieve tubes started.

Wood formation began simultaneously with bud break at the end of April.

The differentiation of the sieve tubes was most active just before bud break and after the termination of wood formation in autumn.

PRIESTLEY (1930) in a way reviews the hitherto obtained results concerning the periodicity of wood formation.

PRIESTLEY, SCOTT and MALINS (1933) at Leeds in England investigated the time for the beginning of cambial activity in thirty six hardwood- and conifer-species.

For the investigations a special method was used, the so-called "strip" method. The bark is loosened from the stem, and the new-formed wood is scraped off with a knife. In this way we get long strips of it which float out in water and are excellent objects for microscopic study. The process has been described by DETLEV MÜLLER (1943).

Of conifers only young trees were examined at a newly planted area. In these young vigorous trees cambial activity started in the stem a few days after it had begun at bud base. In the *Pinus*-, *Picea*- and *Abies*-species it began before bud break. In *Larix decidua* it only began after the needles on the dwarf shoots were fully developed.

The hardwoods are divided into the following three groups:

1) *Fraxinus excelsior*, *Quercus robur* group. To this also *Aesculus hippocastanum* and *Ulmus glabra* belong, so that all "English-grown timber" trees with ring porous wood belong to this group.

In these trees wood formation started on the young branches before bud break and rapidly spread in basipetal direction, so that it reached stem base before the buds were well open.

2) *Alnus glutinosa*, *Fagus sylvatica* group. Here wood formation started on the one-year-old branches after bud break only. When shoot extension began wood formation quickly increased, and it soon reached down to stem base.

3) A large and varied group comprising i. a. *Rosaceae*, *Acer*, *Salix*, and *Populus*. Cambial activity began in the latter "at various stages relative to the opening of the buds" (p. 372), and comparatively long time passed before it reached stem base.

Investigators seek the reason why wood formation in the ring porous trees begins before, and in the diffuse porous not till after bud break, in the difference between the annual ring formation of the two groups.

WIGHT (1933) five miles from Leeds in England each month through a period of a year—except in the summer months—felled a 20-year-old *Pinus silvestris*. From each tree he took sections from top to root and examined wood formation and starch content. Like many of the abovementioned workers he found that wood formation began at bud base and from there spread in basipetal direction. In the stem it began about bud break time.

IWANOV (1934) in Russia through a period of three years followed the growth in thickness in *Picea abies* and *Pinus silvestris*.

He found that as a consequence of lower temperature wood formation was not so lively in the lower, shaded parts of the stem as in the upper, sunny ones.

The summer wood percentage was greatest in the lower part of the stems.

He draws the conclusion from the investigations that as a consequence of the effect of the shade on the stems of the dominant trees the undergrowth in the forests reduce the production of stem wood.

KIENHOLZ (1934) in connection with measurements of the growth of the top shoot and the needles in a series of North American species of trees also followed the course of growth in thickness in two *Pinus resinosa* AITON by means of MacDougal's dendrograph.

The growth in thickness began between May fifth and May twelfth and terminated in October.

There was a certain correlation between the growth in the various organs. The extension growth of the roots and the top shoot and the most active growth in thickness thus took place simultaneously at the beginning of July.

ELLIOTT (1935) has examined the time of the sieve-tube formation in *Acer pseudoplatanus*.

He found that as long as wood is formed, no sieve tubes are formed. When wood formation ceases in the autumn, sieve tube formation begins and continues until the fall of the leaves.

The last formed sieve tissue cells winter in incomplete condition. Before the cambium begins to divide in the spring, these sieve tissue cells grow and form a special type of sieve tissue, which he calls the spring type of sieve tubes.

SIGMOND (1935) has through a period of three years investigated when cambial activity at breast height ceases in *Picea abies*, *Abies alba*, and *Pinus silvestris* in the heights around the Lunzer Lake in Niederösterreich. In all the trees the division of the cambium ceased at the beginning of September. The walls of the summer wood cells on the other hand continued to grow in thickness into late October.

BROWN (1935) examined on sections the cambial activity in *Populus tremuloides* MICHX. and *P. balsamifera* L. at Alberta in Canada.

Wood formation began at bud base in the second week of May; ten to twenty days later it started in the roots. It took shortest time in the youngest trees.

In root shoots wood formation began simultaneously with that in the branches of the mother tree. From the root shoots wood formation spread to the older roots.

GÄUMANN (1935, pp. 227—229) has on sections followed the course of wood formation in *Fagus sylvatica*. Wood formation began in the middle of May and ceased in the middle of September.

ABELL (see DETLEV MÜLLER (1943, p. 163)) found that cambial activity in *Fagus sylvatica* in Geel Forest in Denmark began c. eight days after foliation.

III. Technique, Locality and Climate.

Technique.

The investigations are carried out on sections taken in the course of 1944 and 1945 from branches, stem, and roots. The sections were as a rule cut with a sharp knife. Some times also cores were taken with an increment borer.

Of the sections or the cores there was by means of a razor blade made a micron section which after being stained with haematoxylin (after DELAFIELD) was examined under the microscope while still wet¹.

All measurements on the sections were made with a Zeiss Zeichnenapparat. The sections were projected down on the table in 50 to 200 times magnifications. Then the measurements were taken with compasses and read on a transversal plotting scale.

A more detailed description of the technique used will be found in the introductions to the separate parts of the investigations.

Locality.

The investigations concerning the time of the beginning of wood formation have chiefly been carried out in Geel Forest, Rude Forest and Store Dyrehave at Hillerød as well as in Bogø Forest.

The investigations concerning the course of wood formation within the growth period have all been carried out in Bogø.

Climate.

Climatic conditions in the various months of 1944 and 1945 for Bogø and Geel Forest (Lyngby) appear from Table I.

With exception of May and June 1944 the vegetation period in both years was considerably warmer than normal. Particularly August 1944 was extremely hot.

In Bogø July and August 1944 were very poor in rain.

¹ As the young unligified wood elements shrink on drying it is of the greatest importance that all observations and measurements are carried out before the sections become dry.

TABLE I.

The Monthly Mean Temperature and Rainfall in 1944 and 1945 and Averagely for the Years from 1886—1925 Measured at Bogø and Lyngby Meteorologic Station.

Month	Mean Temperature C°						Rainfall mm.					
	Bogø			Lyngby			Bogø			Lyngby		
	1886-1925	1944	1945	1886-1925	1944	1945	1886-1925	1944	1945	1886-1925	1944	1945
January	0.1	3.2	-0.9	-0.5	3.0	-1.5	40	45	57	39	66	58
February	0.0	1.4	2.3	-0.7	0.9	1.7	33	14	60	30	20	59
March	2.0	1.5	5.2	1.3	1.3	4.9	38	30	18	37	35	13
April	5.8	6.2	7.7	5.5	5.9	7.5	36	37	45	42	21	40
May	10.8	9.9	11.6	10.9	9.9	11.2	41	73	18	39	53	36
June	14.5	13.6	15.3	14.5	13.9	14.8	47	67	80	52	50	111
July	16.4	17.4	18.0	16.3	17.9	17.4	71	34	45	63	55	74
August	15.9	19.1	17.3	15.4	19.0	17.1	67	19	58	82	33	112
September	13.0	13.3	13.9	12.3	12.9	13.4	47	59	16	53	116	59
October	8.7	9.7	10.4	7.9	9.4	9.9	57	54	46	56	41	63
November	4.4	4.9	..	3.6	4.4	..	45	92	..	47	91	..
December	1.7	1.5	..	1.0	1.8	..	50	41	..	53	39	..
The year	7.8	8.5	..	7.3	8.4	..	573	565	..	592	620	..

IV. The Cambium during the Rest Period.

The appearance of the cambium during the rest period has been examined on sections taken in the course of winter from new-felled trees.

During the rest period the secondary cambium is usually four to eight cells wide. The number is greatest in those parts of the branches, that grow most in thickness, smallest in older branches and roots with slight growth in thickness. It is on the whole wider in conifers than in hardwoods.

After BROWN (1915) the cambium in *Pinus strobus* L. is two to four cells wide in the two-year-old branches, and seven to ten cells wide in the stem. After HANSON and BRENKE (1926) it is in *Fraxinus campestris* BRITT. four to six, and in *Acer Saccharinum* L. three to four cells wide. SWARBRICK (1927 a) states that in the branches of fruit trees it is seven cells wide.

The cambium cells consist of an initial cell and young not yet differentiated protoplasm-filled wood- and sieve-tissue cells formed at the end of the preceding growth period, cf. COCKERHAM (1930, Fig. 1) and ELLIOT (1935).

The young wood- and sieve-tissue cells are distributed round the initial cell in the following way:

Secondary bark:

The cambium { two to five undifferentiated sieve tissue cells.
the initial cell.
one to three undifferentiated wood cells.

Secondary wood:

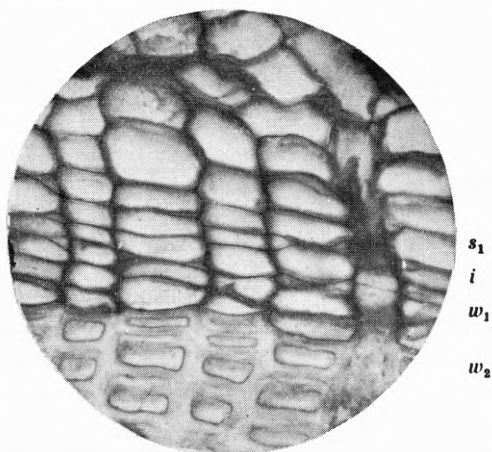
During the resting stage the cell walls of the cambium generally stand out sharply and distinctly under the microscope. The form of the cell is most often rectangular, see Fig. 1.

V. The Preliminary Change of the Cambium.

When the temperature begins to rise in spring and the buds begin to swell the appearance of the cambium alters as described by SWARBRICK (1927 a).

The cell walls become semi-transparent and appear more slurred under the microscope than in the resting period (comp. Figs. 1 and 2). The protoplasm simultaneously passes from a gel-like into a sol-like condition.

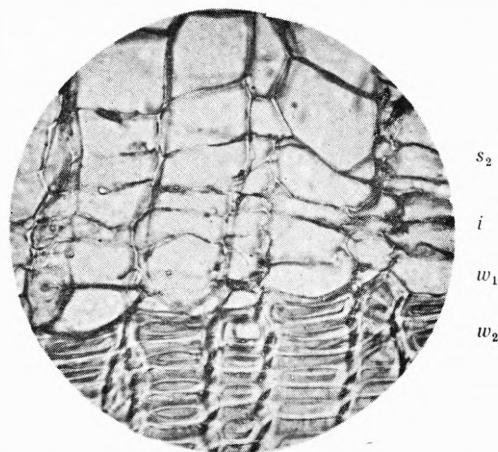
At the same time the radial cell walls of the cambium begin to extend, and the cambium as a whole increases in width: comp. KNUDSON (1913), BROWN (1915),



(480 ×).

Fig. 1. The cambium of a *Larix decidua* during the resting period. Transverse section taken at breast height in 15-year-old *Larix decidua* at the beginning of February, 1945.

- s_1 Young, undifferentiated sieve tissue cells formed at the end of preceding growth period.
- i The initial cell.
- w_1 Undifferentiated wood cells formed at the end of preceding growth period.
- w_2 Summer wood from preceding year.



(480 ×).

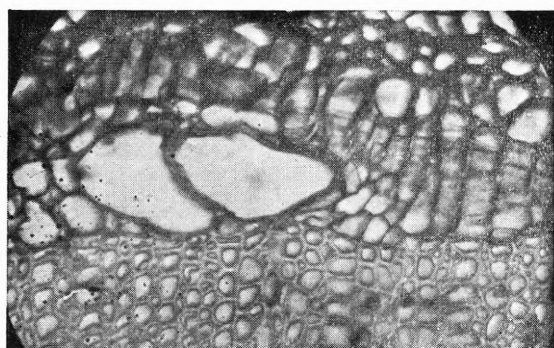
Fig. 2. The cambium of the *Larix decidua* at the preliminary change. Transverse section taken at the middle of April 1945 at breast height of the same *Larix decidua* as the section in Fig. 1.

- s_2 Spring sieve tissue.
- i The initial cell.
- w_1 Young wood cells under differentiation (see w_1 , Fig. 1).
- w_2 Summer wood from preceding year.

SWARBRICK (1927 a), REES (1929), COCKERHAM (1930), PRIESTLEY, SCOTT and MALINS (1933) and WIGHT (1933). Often the width of the cambium is almost doubled before the beginning of the division into cells¹.

The sieve tissue cells (s_1 , Fig. 1) are differentiated in the course of short time into spring sieve tissue (s_2 , Fig. 2) as described by ELLIOTT (1935).

In broad leaved trees a few of the young wood cells (w_1 , Figs. 1 and 2) increase much more in size than the others and press the neighbouring cells strongly together



(340 ×).

Fig. 3. Transverse section through the cambium in an older *Ulmus glabra* a few days after the beginning of cell division. Two large vessels are almost completely differentiated. The cambium appears as a slurred belt winding round the vessels. In the wedges to the right and left of the vessels fully differentiated parenchyma cells are seen.

s_3 Collapsed sieve tissue.
 s_2 Spring sieve tissue.
 c Cambium at division stage.
 w_2 Last year's summer wood.



(340 ×).

Fig. 4. Transverse section in same *Ulmus glabra* as in Fig. 3. The section was taken c. one week after the beginning of cell division. To the left is seen a fully formed and lignified² vessel. To the right a vessel under differentiation.

s_2 Spring sieve tissue.
 c Cambium at division stage.
 w_2 Last year's summer wood.

and the cambium outwards (see Figs. 3 and 4). These particularly quick growing cells develop into the first spring vessels, which do not, however, succeed in becoming completely differentiated before the beginning of cell division.

This change in the cambium in the spring, which may be called the preliminary change, begins first in the one-year-old branches, whereafter it spreads in basipetal direction. Same observation is made by WIGHT (1933) in *Pinus silvestris* L.

After my own observations the lignification of the cell walls of the vessels proceeds considerably quicker in the ring porous than in the diffuse porous trees.

In Figs. 5 and 6 is stated the approximate time of the beginning of the preliminary change in the springs of 1944 and 1945.

¹ BROWN (1915) found that the cambium in *Pinus strobus* L. was 70 % wider, and REES (1929) that in *Picea rubra* LINK it was over 100 % wider.

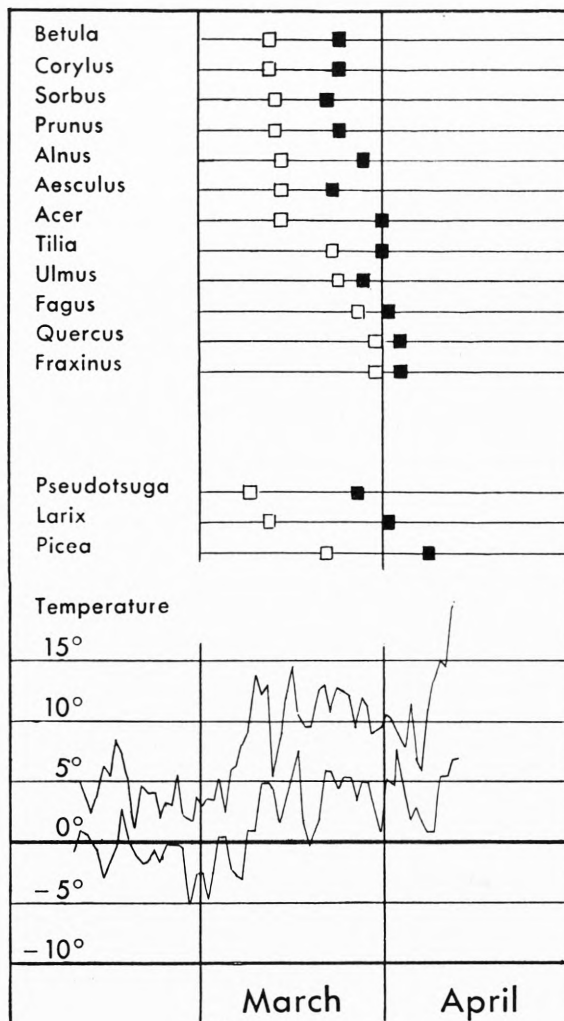
² SWARBRICK (1927 a, p. 151) writes about the lignification of the cell walls of the vessels in fruit trees: "After becoming empty the lignification of the vessel walls did not take place for at least ten days".

Fig. 5. The approximate time of the transition of the cambium from the resting stage to the preliminary change in the spring of 1944:

- in 1-year-old top branches.
 ■ at 1.3 m height in the stem.

The dates apply to the older trees in close stands.

Entered the maximum and minimum temperatures measured at the Meteorological Station at Lyngby.



Pseudotsuga taxifolia and *Picea sitchensis*: In 1945 the preliminary change in the branch cambium might already be observed in the middle of March. The mean temperature was at this time about 4°–5° C. The maximum temperature had not exceeded 12° C.

Pinus silvestris, *Larix decidua*, *Picea abies*, *Betula pendula*, *Alnus glutinosa*, *Corylus avellana*, *Carpinus betulus*, *Ulmus glabra*, *Tilia cordata*, *Aesculus hippocastanum*, *Acer pseudoplatanus*, *Prunus avium*, and *Sorbus aucuparia*: In these species the preliminary change could not be observed in the branch cambium till the end of March (1945) or the beginning of April (1944) after some warm spring days with a maximum temperature above 12° C.

Fagus sylvatica, *Quercus robur*, and *Fraxinus excelsior*: In these species the pre-

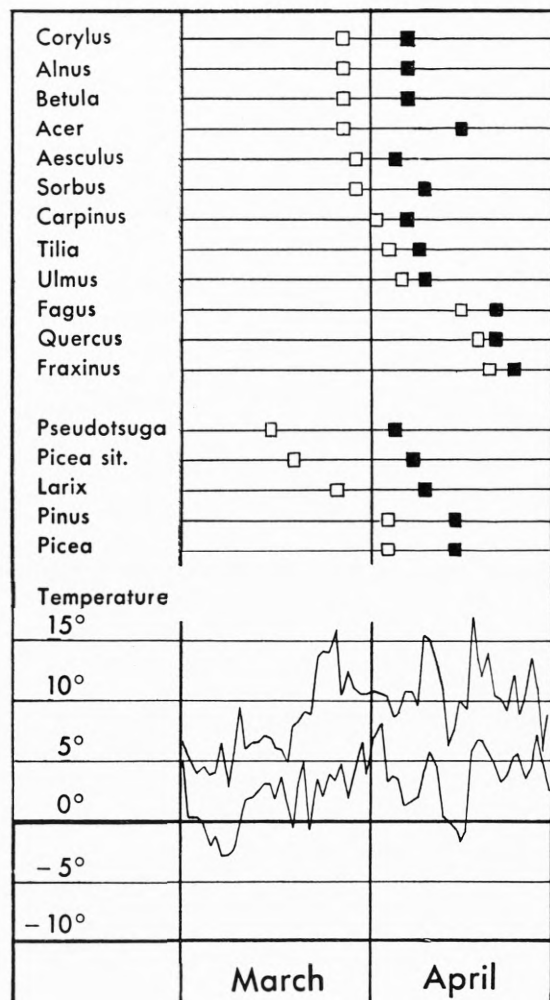


Fig. 6. The approximate time of the transition of the cambium from the resting stage to the preliminary change in the spring 1945:

□ in 1-year-old top branches.
■ at 1.3 m height in the stem.

The dates apply to the older trees in close stands.

Entered the maximum and minimum temperatures measured at the Meteorological Station at Lyngby.

liminary change in the branch cambium only occurred towards the end of April. The time seems to be more autonomously determined than in other species of trees.

In young trees in sheltered and warm localities the change in the cambium began some days earlier than shown in Figs. 5 and 6.

The condition of the soil was apparently of subordinate importance.

The change in the cambium spread more quickly from the young branches and down to stem base in the hardwoods than in the conifers. And it took shorter time in hardwoods in the ring porous than in the diffuse porous trees (see Figs. 5 and 6).

When the cambium is at the stage of change it is sensitive towards frost. On March 20th 1945 I laid a packing with a cold mixture round vigorous 3-year-old branches of a young *Pseudotsuga taxifolia* and a *Picea sitchensis*. In both branches the change in the cambium was already quite distinct. The packing was placed by

means of the same process as I had previously used in a similar experiment, see BORNEBUSCH and LADEFOGED (1940). The temperature reached down to -8° and -10° C.

In July both branches were cut off. In the cold-affected places frost ring formations appeared similar to those found by me in the same species of wood after the spring frost in 1938, see LADEFOGED (1938).

VI. The Time of the Inception of Cell Division.

The transition between the preliminary change of the cambium and the stage of division occurs gradually. It has therefore only been possible to determine the time of the inception of cell division (the wood formation) with an exactitude of about 3 to 5 days.

Methods, Material, and Elaboration.

For each species of tree is determined:

a) The date of the inception of cell division in the branches and the other part of the stem in relation to bud break.

The determinations have been made by a comparison of bud development and cambial activity in young and older new-felled trees. The summer felling in 1945 was of great value for the said investigations.

b) The date of the inception of cell division at breast height and in the roots in relation to bud break.

These determinations are made by following the development of buds and cambial activity at breast height and in the roots of the following trees:

	Number		Age Years		Number		Age Years
	1944	1945			1944	1945	
a) Trees over 10 Years:							
Conifers:							
<i>Pinus silvestris</i>	—	5	25—30	<i>Aesculus hippocastanum</i>	3	2	c. 100
<i>Larix decidua</i>	6	7	25—100	<i>Acer pseudoplatanus</i>	6	6	30—100
<i>Picea abies</i>	8	8	25—35	<i>Prunus avium</i>	6	—	10—35
<i>Picea sitchensis</i>	—	6	18—25	<i>Sorbus aucuparia</i>	7	6	10—25
<i>Abies alba</i>	—	5	35—40	<i>Fraxinus excelsior</i>	7	7	35—45
<i>Pseudotsuga taxifolia</i>	5	8	14—20	b) Trees under 10 Years:			
Hardwoods:				Conifers:			
<i>Betula pendula</i>	6	6	35—60	<i>Picea abies</i>	5	—	7
<i>Alnus glutinosa</i>	8	8	15—35	Hardwoods:			
<i>Corylus avellana</i>	6	8	c. 10	<i>Betula pendula</i>	6	6	2—8
<i>Carpinus betulus</i>	—	5	c. 30	<i>Alnus glutinosa</i>	8	8	3—8
<i>Fagus sylvatica</i>	6	8	35—100	<i>Fagus sylvatica</i>	6	5	7—9
<i>Quercus robur</i>	8	8	25—40	<i>Quercus robur</i>	6	6	7—8
<i>Ulmus glabra</i>	9	6	15—60	<i>Ulmus glabra</i>	4	6	2—7
<i>Tilia cordata</i>	6	4	20—60	<i>Acer pseudoplatanus</i>	6	6	2—9
				<i>Fraxinus excelsior</i>	6	5	2—7

TABLE II. Number of Days between the Inception of Cell Division at Breast Height and Bud

Species of Tree	Number of Trees		Age	Bud Break	
	1944	1945		1944	1945
Hardwoods					
Ring porous:					
<i>Fraxinus excelsior</i>	7	7	35—45	$23\frac{3}{5} \pm 1.3$	$19\frac{1}{5} \pm 2.3$
<i>Quercus robur</i>	8	8	25—40	$19\frac{1}{5} \pm 2.5$	$15\frac{1}{5} \pm 2.4$
<i>Ulmus glabra</i> with flowers	4	3	20—60	$7\frac{1}{5} \pm 3.1$	$13\frac{3}{4} \pm 0.3$
— without flowers	5	3	15—25	$29\frac{1}{4} \pm 2.0$	$9\frac{1}{4} \pm 1.1$
Diffuse porous:					
<i>Carpinus betulus</i>	—	5	c. 30	—	$15\frac{1}{4} \pm 1.9$
<i>Tilia cordata</i>	6	4	20—60	$15\frac{1}{5} \pm 1.3$	$20\frac{1}{4} \pm 1.9$
<i>Sorbus aucuparia</i>	7	6	10—25	$3\frac{1}{5} \pm 2.7$	$16\frac{1}{4} \pm 1.7$
<i>Prunus avium</i>	6	—	10—35	$4\frac{1}{5} \pm 1.9$	—
<i>Fagus sylvatica</i>	6	8	35—100	$9\frac{1}{5} \pm 1.5$	$5\frac{1}{5} \pm 1.7$
<i>Aesculus hippocastanum</i>	3	2	c. 100	$5\frac{1}{5} \pm 2.1$	$12\frac{1}{4} \pm$
<i>Acer pseudoplatanus</i>	6	6	30—100	$4\frac{1}{5} \pm 2.8$	$21\frac{1}{4} \pm 3.7$
<i>Corylus avellana</i>	6	8	c. 10	$29\frac{1}{4} \pm 0.9$	$8\frac{1}{4} \pm 1.1$
<i>Betula pendula</i>	6	6	25—60	$26\frac{1}{4} \pm 3.1$	$9\frac{1}{4} \pm 1.5$
<i>Alnus glutinosa</i>	8	8	15—35	$7\frac{1}{5} \pm 1.9$	$7\frac{1}{4} \pm 0.3$
Conifers					
<i>Picea abies</i>	8	8	25—35	$25\frac{1}{5} \pm 1.7$	$11\frac{1}{5} \pm 3.2$
<i>Pseudotsuga taxifolia</i>	5	8	14—20	$2\frac{1}{5} \pm 2.7$	$4\frac{1}{5} \pm 1.8$
<i>Picea sitchensis</i>	—	6	18—25	—	$3\frac{1}{5} \pm 2.6$
<i>Abies alba</i>	—	5	35—40	—	$27\frac{1}{4} \pm 2.7$
<i>Pinus silvestris</i>	—	5	25—30	—	$30\frac{1}{4} \pm 1.3$
<i>Larix decidua</i>	6	7	25—100	$27\frac{1}{4} \pm 2.2$	$2\frac{1}{4} \pm 1.9$

The results appear from Tables II and III.

Different trees were used each year.

The forest trees grew in close stands. The *Tilia cordata* were open-grown. The *Corylus avellana*, *Sorbus aucuparia* and most of the *Prunus avium* grew as undergrowth under older hardwoods and conifers. The young trees stood in open culture areas or as natural reproduction under older hardwoods.

The trees were all growing well.

The bud break was determined by examinations from day to day.

The sections from the stem were taken at 2 to 4, from the roots at 8 to 10 days intervals.

The examinations were supplemented with a number of sections taken from newly felled trees.

Break in 1944 and 1945 in Trees over 10 Years, and of the Inception of Growth in the Roots.

Cell Division at 1.3 m. Height in the Stem. Began the Following Number of Days				Extension Growth in the Roots Began		Cell Division in the Roots Began	
Before Bud Break		After Bud Break		1944	1945	1944	1945
1944	1945	1944	1945				
8 ± 0.9	9 ± 0.9	29/5	20/5	12/6	22/5
5 ± 0.7	8 ± 1.0	16/5	27/4	24/6	8/6
4 ± 1.2	3 ± 0.7	15/5	28/4	27/6	10/6
..	..	1 ± 0.4	1 ± 0.8
..	..	—	7 ± 2.1	—	3/5	—	7/6
..	..	8 ± 1.6	4 ± 0.1	25/5	27/4	25/6	11/6
..	..	10 ± 1.0	13 ± 4.0	25/5	10/5	25/6	15/6
..	..	15 ± 3.7	..	25/5	—	25/6	—
..	..	13 ± 3.1	15 ± 1.8	14/5	14/4	26/6	13/6
..	..	15 ± 2.1	30	25/5	5/5	18/6	29/5
..	..	18 ± 3.4	29 ± 3.2	17/5	28/4	25/6	12/6
..	..	20 ± 1.6	33 ± 2.4	28/5	25/5	25/6	11/6
..	..	24 ± 2.2	39 ± 2.3	14/5	14/5	25/6	27/5
..	..	27 ± 2.6	43 ± 1.8	14/5	3/5	25/6	16/6
4 ± 0.7	6 ± 1.7	5/5	20/4	3/6	21/5
2 ± 0.2	6 ± 0.7	11/5	30/4	25/5	22/5
—	5 ± 3.1	—	24/4	—	24/5
..	..	—	2 ± 3.3	—	27/4	—	26/5
..	..	—	3 ± 1.1	—	28/4	—	14/6
..	..	26 ± 2.6	46 ± 3.3	18/4	8/4	3/6	25/5

The successive Order of the Inception of Cell Division.

Division of cells begins at bud base. From here it spreads in basipetal direction through the branches, the stem, and finally stretches down into the roots; cf. TH. HARTIG (1857), GULBE (1888a and b), STRASBURGER (1891), JOST (1892), SWARBRICK (1927a), COCKERHAM (1930), PRIESTLEY, SCOTT, and MALINS (1933), WIGHT (1933) and BROWN (1935).

RUSSOW (1884), KNUDSON (1913), BROWN (1912 and 1915) and CHALK (1927) found in contradistinction to this that division of cells begins first in the stem. TH. HARTIG (1857), LODEWICK (1925, 1928 and 1930) found that in some cases it may begin at stem base.

PRIESTLEY (1930) has gone through the lastmentioned results critically. His view is that they rest on insufficient investigations.

TABLE III.

Number of Days between the Inception of Cell Division at Bases of Stem and Bud Break in 1944 and 1945 in Trees under 10 Years.

Species	Number of Trees		Age	Bud Break		The Division at Stem Base Began on the Following Number of Days			
	1944	1945		1944	1945	Before Bud Break		After Bud Break	
						1944	1945	1944	1945
Hardwoods									
Ring porous:									
<i>Quercus robur</i>	6	6	7—8	$20/5 \pm 1.7$	$15/5 \pm 2.4$	5 ± 0.9	8 ± 1.0
<i>Fraxinus excelsior</i> . . .	6	5	2—7	$18/5 \pm 0.9$	$15/5 \pm 2.1$	4 ± 0.2	1 ± 0.7
<i>Ulmus glabra</i>	4	6	2—7	$26/4 \pm 1.3$	$10/4 \pm 1.9$	at bud break	3 ± 0.9
Diffuse porous:									
<i>Fagus sylvatica</i>	6	5	7—9	$8/5 \pm 0.1$	$8/5 \pm 2.0$	18 ± 2.2	9 ± 1.8
<i>Acer pseudoplatanus</i>	6	6	2—9	$24/4 \pm 1.9$	$13/4 \pm 4.9$	12 ± 5.5	$22 \pm 3,3$
<i>Betula pendula</i>	6	6	2—8	$22/4 \pm 1.9$	$8/4 \pm 1.1$	12 ± 1.0	32 ± 4.4
<i>Alnus glutinosa</i>	8	8	3—8	$7/5 \pm 1.9$	$7/4 \pm 0.3$	13 ± 1.9	17 ± 2.1
Conifers									
<i>Picea abies</i>	5	—	7	$1/6 \pm 1.7$	—	4 ± 0.7

The Time of the Inception of Cell Division in Relation to Bud Break.

1. At Bud Base.

The division of cells at bud base begins some days before or simultaneously with bud break except in *Larix decidua* (see Figs. 7, 8, 9 and 10).

Among the tree species there are the following general differences:

a) Hardwoods.

α) The diffuse porous

In the diffuse porous the time of the inception of cell division in relation to bud break depends on how much the buds extend before bursting.

In *Betula pendula*, *Alnus glutinosa*, *Corylus avellana*, *Fagus sylvatica* and *Tilia cordata* where bud extension as a rule is comparatively slight the division of cells begins simultaneously with or at the earliest two days before bud break.

In *Sorbus aucuparia*, *Acer pseudoplatanus*, *Aesculus hippocastanum* and *Prunus avium*, where the shoot extension is often fairly considerable, cell division begins up to one week before bud break.

β) The ring porous

In *Quercus robur*, *Fraxinus excelsior* and flower-bearing *Ulmus glabra* cell division begins 1 to 9 days before bud break. The same applies to cases where the bud extension is very slight only (*Fraxinus excelsior*).

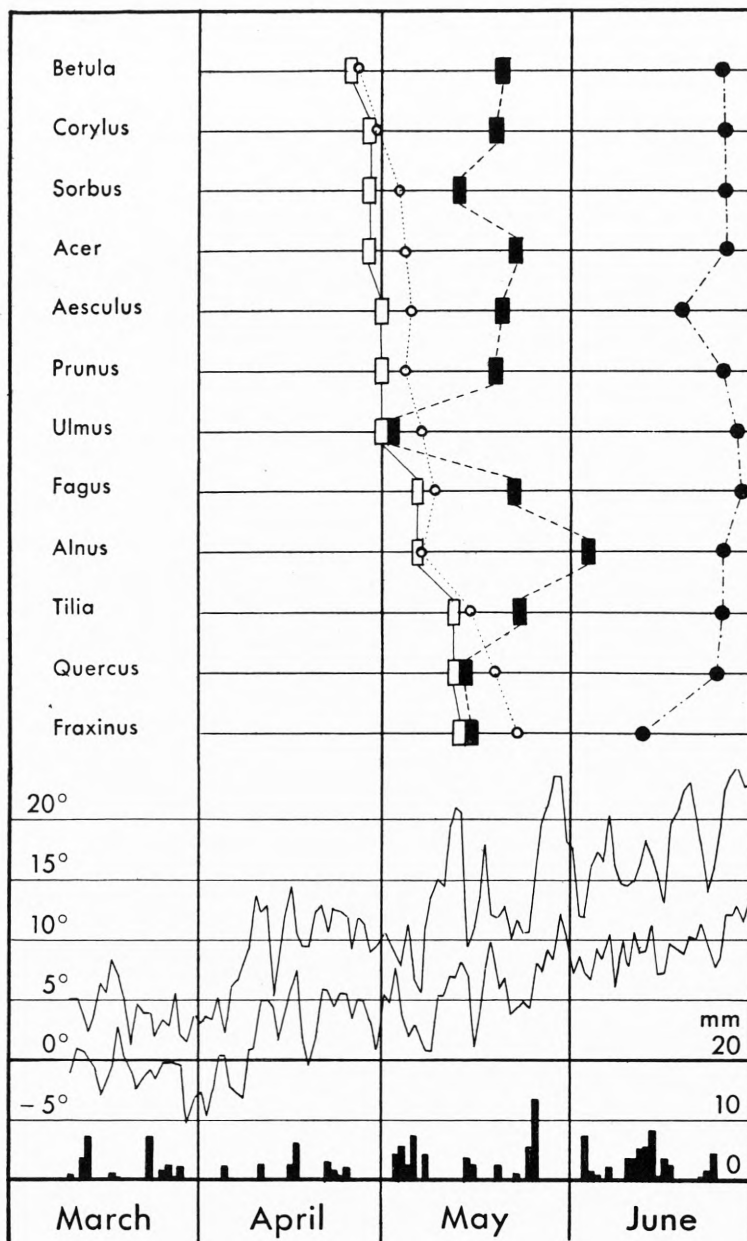


Fig. 7. Mean time for the inception of cell division (wood formation) in 1944 in hardwoods over ten years:

- At bud base.
- At 1.3 m height in the stem.
- In the roots at ten cms depth and c. 1.5 m from stem base.
- Time of bud break.

Rainfall and maximum and minimum temperatures recorded as measured at the Meteorological Station at Lyngby.

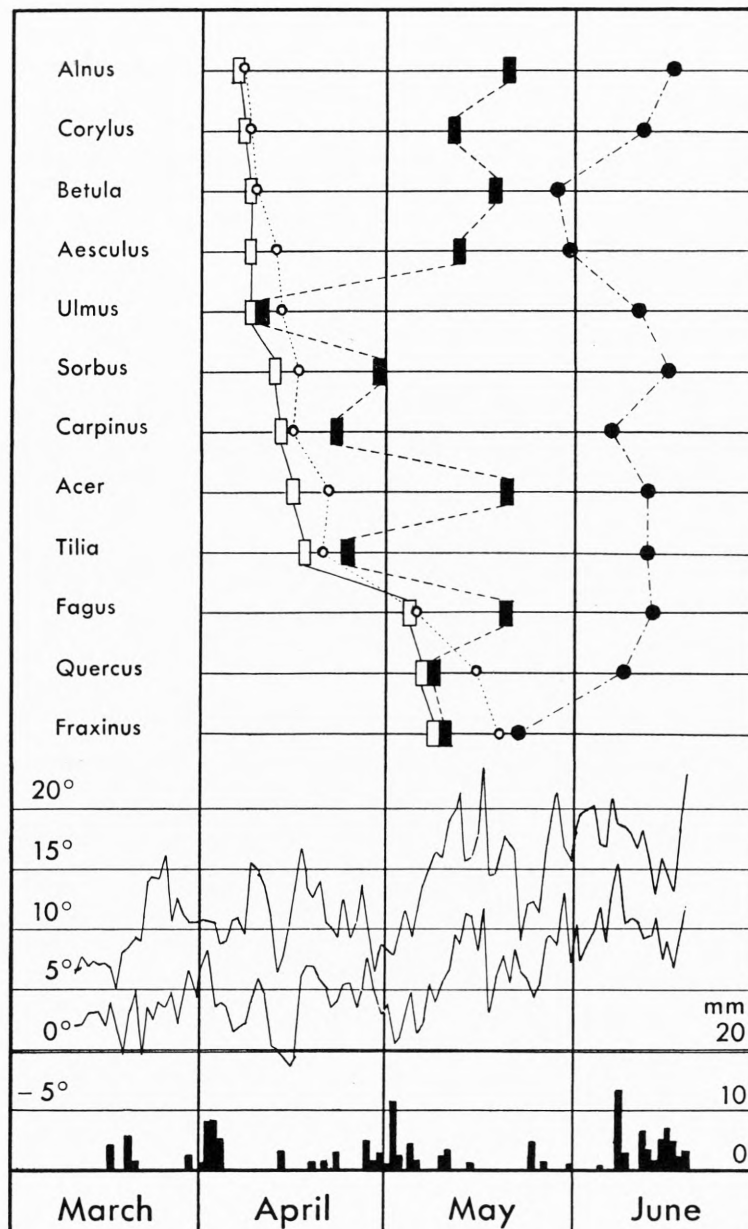


Fig. 8. Mean time of inception of cell division (wood formation) in 1945 in hardwoods over ten years:

- At bud base.
- At 1.3 m height in stem.
- In roots at 10 cms depth and 1.5 m from stem base.
- Time of bud break.

Rainfall and maximum and minimum temperatures recorded as measured at the Meteorological Station at Lyngby.

In *Ulmus glabra* without flowers cell division on the other hand in many cases only begins simultaneously with bud break¹, cp. Russow (1884).

b) *Conifers*.

In *Pinus silvestris*, *Picea abies*, *Picea sitchensis*, *Abies alba* and *Pseudotsuga taxifolia* cell division generally begins 5 to 15 days before bud break.

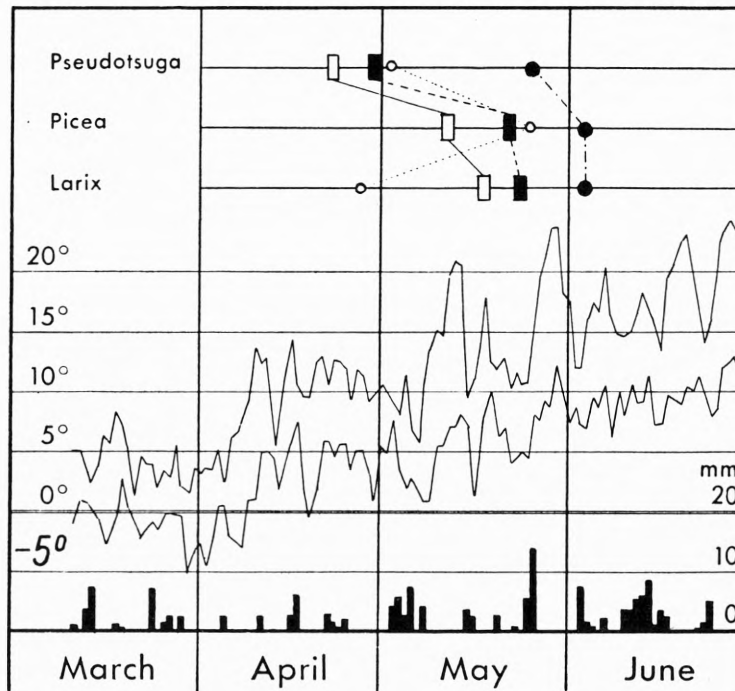


Fig. 9. Mean time of the inception of cell division (wood formation) in 1944 in conifers over ten years:

- At bud base.
- At 1.3 m height in the stem.
- In the roots at 10 cms depth and 1.5 m from stem base.
- Time of bud break.

Rainfall and maximum and minimum temperatures recorded as measured at the Meteorological Station at Lyngby.

In *Larix decidua* where little shoot extension takes place only in connection with bud break of the dwarf shoots, cell division does not begin till shortly before, or simultaneously with, the bursting of the long shoots.

¹ CHALK (1927) found that in *Fraxinus excelsior* cambial activity begins one week before the flower buds burst. COSTER noticed the same thing in *Prunus puddum* ROXB. and *Magnolia obovata* THUNB. which also flower before foliation.

After GILL (1933) there is, however, no beginning cambial activity in connection with the growth and development of catkins.

Literature only gives one piece of information of the time of the inception of cell division at bud base in relation to bud break. After BROWN (1935) it here begins after bud break only in *Populus tremuloides* Michx. and *P. balsamifera* L.

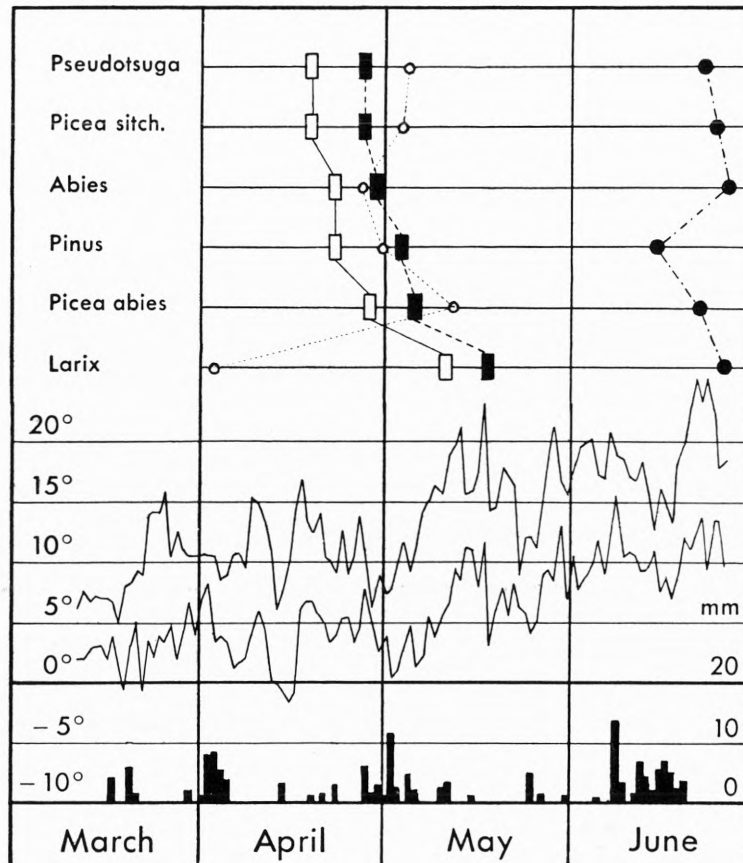


Fig. 10. Mean time for the inception of cell division (wood formation) in 1945 in conifers over ten years:

- At bud base.
- At 1.3 m height in the stem.
- In the roots at 10 cms depth and 1.5 m from stem base.
- Time of bud break.

Rainfall and maximum and minimum temperatures recorded as measured at the Meteorological Station at Lyngby.

There is on the other hand more information about the time of its inception in the young branches.

After R. HARTIG (1891) it here begins before or simultaneously with bud break in *Pinus silvestris*, *Picea abies*, and *Fagus silvatica*. ANTEVS (1917) after own investigations states that cambial activity in the young branches only begins after the foliage more or less has developed. NYDAM (see COSTER, 1927, pp. 77—78) found new-formed vessels in young *Fraxinus excelsior*- and *Quercus robur*-branches before the buds had begun to swell. COCKERHAM (1930) thinks that cambial activity begins in the young branches in *Acer pseudoplatanus* about the time

of bud break. PRIESTLEY, SCOTT and MALINS (1933) found, as mentioned above (pp. 371—372), that wood formation in ring porous species began before bud break; in the diffuse porous on the other hand “at various stages relative to the opening of the buds”. In *Pinus*, *Picea*, and *Abies* wood formation begins “within a short time of any signs of movement in the uppermost buds”. In the branches of *Larix decidua* it only begins after the needles of the dwarf shoots are fully developed.

In the diffuse porous species cell division most often begins in the branches in the lower parts of the crown. The reason of this is probably that the shaded buds burst before the sunny ones¹.

In 45-year-old *Acer pseudoplatanus* in 1945 up to 11 days and in 120-year-old *Fagus sylvatica* up to 9 days elapsed between bud break in the lower and upper parts of the crown.

In the ring porous trees and in conifers the buds almost burst simultaneously all over the crown, and in conformity with this cell division begins practically simultaneously in all branches.

2. At Breast Height (1.3 m.) in the Stem.

Cell division takes place at a quicker rate in basipetal direction in the ring porous than in the diffuse porous trees and conifers (comp. Figs. 7, 8, 9 and 10).

In the ring porous and in evergreen conifers cell division begins in the lower part of the stem a few days before or at the latest simultaneously with bud break. In the diffuse porous and in *Larix decidua* it does not on the other hand begin till after the foliage (the needles of the shoots in *Larix decidua*) are partly or completely expanded (see Tables II and III).

This is conformity with most statements found in literature. At variance with this MACDOUGAL (1921 and 1924) found that in *Quercus robur* the growth in thickness in the stem began after bud break only.

HUBER (1935) connects the generally late foliation in the ring porous species with the fact that they must have formed some fresh spring wood before foliation, because the rising of the sap (in contradistinction to the diffuse porous species) mainly takes place in the new spring vessels (mentioned by DETLEV MÜLLER 1943, p. 163 and CARL MAR: MØLLER (1945), pp. 281 and 282).

The relation between bud break and the inception of cell division in the stem varies on the whole somewhat with α) age, β) exposure to light and γ) the size of the crown.

¹ ENGLER (1913) thinks that the reason of this is that the sunny buds have greater difficulty in bursting than the shaded ones on account of more and thicker raments.

HUBER (1931) gives quite a different explanation. According to him the sunny buds always possess a larger “Treibwilligkeit” than the shaded ones. When the latter nevertheless are the first to burst it is due to the fact that—as a consequence of their being placed within the crown—they may sooner benefit by the rising water flow than the sunny buds.

MÜNCH (1936) after experimental investigations arrives at the result, that ENGLER's explanation must be considered the most probable one.

a) *Age.*

In the diffuse porous species a shorter time elapses between bud break and the inception of cell division at stem base in the young (low) trees than in the older (high) ones (comp. Tables II and III).

The difference is undoubtedly due to the fact, that the distance between crown and stem base is shorter in the young than in the older trees.

β) *Exposure to Light.*

In sun exposed c. 30-year-old *Picea abies*, *Pseudotsuga taxifolia* and *Pinus silvestris*-stems cell division began in the lower parts of the stems in 1945 up to two weeks before bud break and, approximately estimated, one week earlier than in shaded stems within close-grown stands.

The reason must be sought in the fact that the sun-exposed stems are more quickly warmed up in spring than the shaded ones, comp. R. HARTIG (1891), AMILON (1910) and IWANOV (1934).

In conformity with MER (1892), BROWN (1912), CHALK (1927), and LODEWICK (1928) I have not observed that cell division begins earlier in the sun-exposed side of the stem than in their shaded side as stated by WALTER (1898) and SCHUITMAKER (see COSTER, 1927, pp. 79 and 80).

γ) *The Size of the Crown:*

In the diffuse porous species a shorter time elapses between the inception of cell division at bud- and stem-base when the trees have large crowns than when they have small ones (see Table IV). In trees with very small crowns, poor in leaf, (whips) wood formation may completely fail to appear in the lower part of the trunk, comp. R. HARTIG (1869), O. G. PETERSEN (1904, p. 180), RUBNER (1910, pp. 246—250) and PRIESTLEY (1930, p. 335).

The explanation must be sought in difference in stuff production, possibly also in difference in growth hormone production (see pp. 34 to 36).

TABLE IV.

The Number of Days by which Cell Division at Breast Height Started after Bud Break in 1944 and 1945 in *Fagus silvatica*, *Betula pendula* and *Acer pseudoplatanus* With Large and Medium Sized Crowns Respectively. The Figures were Arrived at by Dividing the Trees in Table II after Crown Breadth.

Species	Trees with:			
	Large Crowns		Medium Sized Crowns	
	1944	1945	1944	1945
<i>Fagus silvatica</i>	5 ± 0.7	13 ± 2.6	18 ± 2.2	19 ± 0.3
<i>Acer pseudoplatanus</i>	11 ± 1.5	35 ± 0.7	25 ± 1.8	41 ± 3.0
<i>Betula pendula</i>	21 ± 3.0	23 ± 2.0	27 ± 2.7	35 ± 3.7

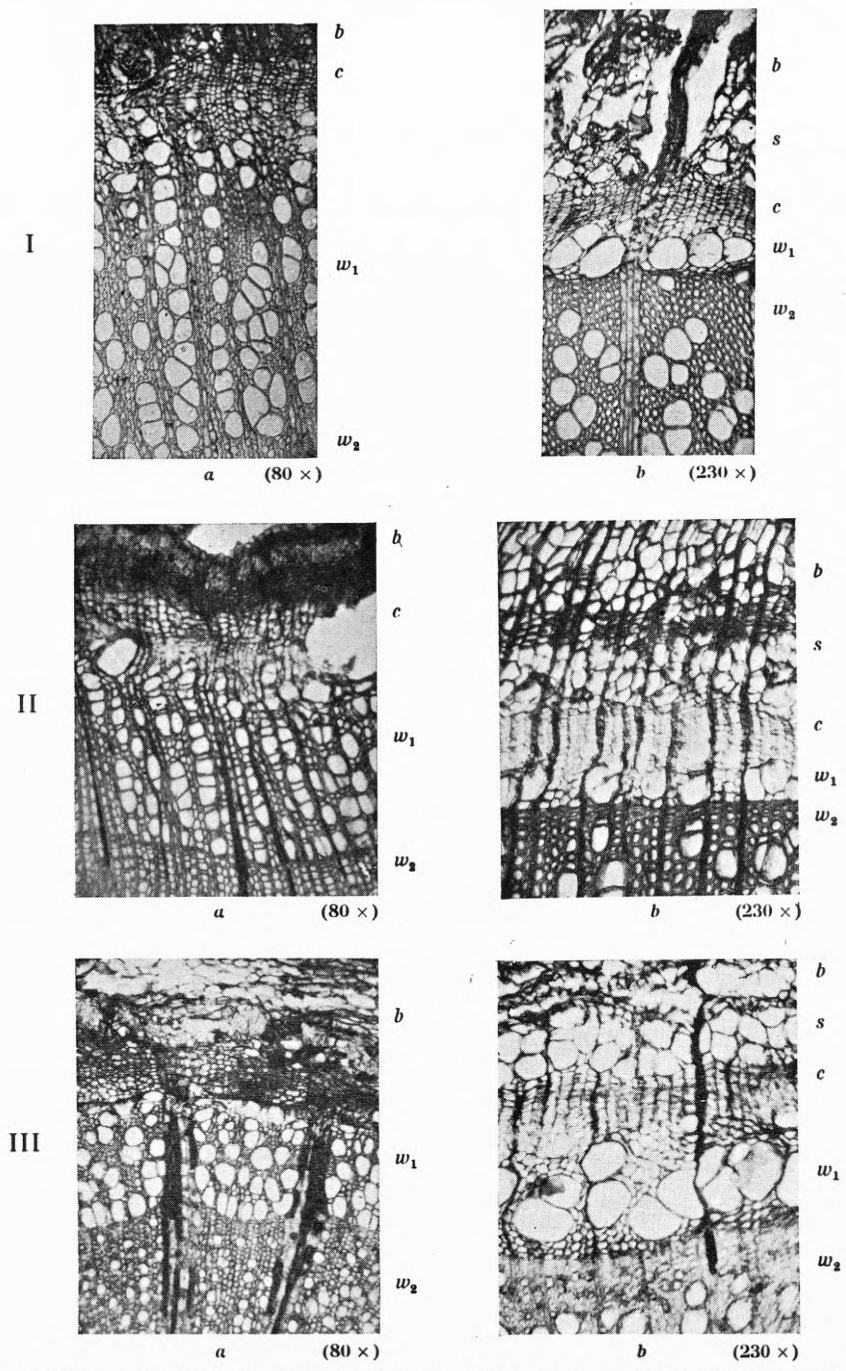


Fig. 11. The difference in wood formation per June 1, 1945 in a one-year-old, vigorous top branch (a) and at 1.3 m height in the stem (b) in

I: A 35-year-old *Prunus avium*.

II: A 35-year-old *Alnus glutinosa*.

III: A 120-year-old *Fagus sylvatica*.

b = bark, s = sieve tissue, c = cambium, w₁ = new-formed wood and w₂ = summer wood, from last year.

As a consequence of the relatively long period that elapses between the beginning of cell division at bud- and stem-base in the diffuse porous trees and the conifers a relatively great part of the annual ring has already formed in the young branches in the said species at the time, when wood formation is to begin in the lower part of the stem (see Fig. 11).

In the ring porous trees there is on the contrary little difference between the wood formation in the young branches and in the lower part of the stem as long as the differentiation of the large spring vessels is taking place.

3. In the Roots.

Cell division in the roots only begins when the ground temperature has reached 10° to 13° C.

On May 15th, 1945 cell division had started in branches and stem in young *Fraxinus excelsior* and *Acer pseudoplatanus* that stood in the shade under older *Fagus silvatica*, *Fraxinus excelsior* and *Acer pseudoplatanus* in Geel forest. In the roots the cambium was on the other hand still in the resting period.

On the same day I placed a maximum and a minimum thermometer (model "Six") at 5 cms depth in the ground among the young trees. I then read the temperature at 2 to 3 days' interval. Simultaneously I followed the cambial activity in the roots.

The cell division started within a time when the ground temperature ranged between 10° and 12° C.

Thereafter I moved the thermometer out into some swamp-like, pretty watery and cold soil under a mixed stand of uneven-aged *Betula pendula*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Alnus glutinosa*, *Fagus silvatica*, *Prunus avium*, *Ulmus glabra* and *Sorbus aucuparia*, all of different ages.

In this place cell division in the roots began within a period when the temperature of the ground ranged between 10° and 13° C.

Cell division starts first in the roots in the uppermost layer of the ground, which is most quickly warmed up. If a root grows so near the surface of the ground, that part of its surface is bare from stem basis and a piece outward, cell division begins in this part of the root either simultaneously with or a few days after cell division has begun in the lower part of the stem.

In older *Fagus silvatica* and *Quercus robur* in clayey lands from 4 to 6 weeks may pass between the beginning of cell division in the surface roots and the deepest roots¹.

In well drained shaded forest lands cell division begins in the roots at 10 cms depth two to eleven weeks after bud break, and two to eight weeks after it has begun at breast height (see Table II and Figs. 7, 8, 9 and 10). The variation in individuals as well as in species is very considerable. The times stated in the tables must therefore not be taken too rigoristically.

¹ In 1944 I observed this condition in c. 120-year-old *Fagus silvatica* and *Quercus robur* that grow just above the slope to the Baltic in Fanefjord forest. By digging into the slope I easily reached the deepest roots.

Existing literature also gives us the impression that there is much variation. The various investigators record the following intervals between the beginning of cell division in stem and roots:

TH. HARTIG (1857): 1 month in *Larix decidua* and *Pinus silvestris*, 2½ months in *Quercus robur*, and 14 days in *Acer pseudoplatanus*.

RUSSOW (1884): A few days in *Quercus robur*, *Fraxinus excelsior*, *Pinus silvestris* and *Larix decidua*. In *Tilia cordata* cell division begins in the roots earlier than in the stem.

GULBE (1888a and b): Averagely 14 days.

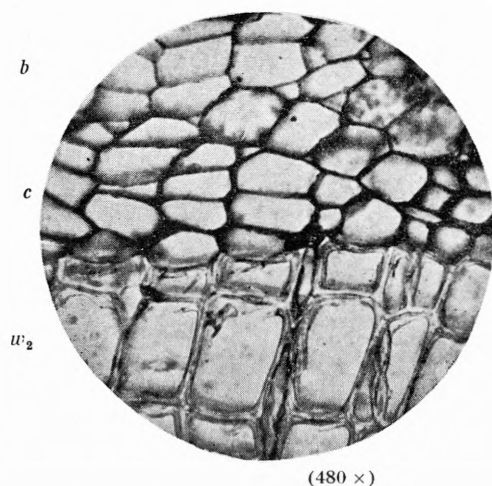


Fig. 12. Transverse section through the cambium in an 1-year-old *Picea abies* root 14 days after the beginning of extension growth. The cambium is still at the rest stage.

b Secondary bark.

c Cambium.

*w*₂ Summer wood from last year.

MER (1892a): 10 to 15 days in *Fagus silvatica*, *Quercus robur*, *Carpinus betulus*, *Tilia cordata* and *Picea abies*.

BROWN (1915): Over 1 month in *Pinus strobus* L.

LODEWICK (1928): 1 week between stem base and the thick roots in *Fraxinus americana* L.

COCKERHAM (1930) found that in thin roots in *Acer pseudoplatanus* cambial activity may continue all through winter.

In the main roots in older trees O. G. PETERSEN (1898) found beginning wood formation on 2nd to 5th June in *Fraxinus excelsior* and *Sorbus aucuparia*; from 7th to 9th July in *Acer pseudoplatanus*, *Betula pendula*, *Populus*, *Tilia cordata*, *Larix decidua*, *Picea abies* and *Pinus silvestris*; and from 24th to 26th August in *Quercus robur*.

None of the said investigators give any information about soil, insolation or root depth.

There is not the same state of interdependence between the growth in length and thickness in the roots as between that of the branches. In spring one often sees fresh new-formed root tips in young roots in which the secondary cambium is not yet in the rest stage (see Fig. 12).

VII. The Reason why Cambial Activity Begins at Bud Base.

Investigations in the years 1934—41 have shown why cambial activity begins at bud base and from here spreads in basipetal direction. When the buds of the trees begin to swell in spring, new growth hormones are formed within them. From the buds the growth hormones proceed down through the cambium of branches, stem and root and cause it to resume growth.

a) Earlier Assumptions.

Already JOST (1893, p. 192) draws attention to the fact "... dass nicht immer und nicht allein die Zufuhr von Baustoffen die Cambialtätigkeit bedingt ...".

He arrived at this result partly from his observation that cambial activity begins first at bud base, and partly through a series of experiments.

He thus found, that if the buds are removed from a branch at some time before bud break, it does not grow in thickness, comp. TH. HARTIG (1858 and 1862), LUTZ (1895) and WIELER (1897). He showed that the reason was not due to failing assimilation by letting intact branches shoot in the dark. Even if the leaves under such conditions are unable to assimilate wood formation nevertheless takes place in the branches at the cost of the stored nutrient materials, comp. WIELER (1897).

He further found, that if we at some time before bud break remove all buds on the branches of fir, they do not grow in thickness even though the old assimilative needles still are left on the branches. On the other hand they grow in thickness if all the old needles are removed, but the buds are left to develop into new shoots. Even in darkness such branches grow in thickness.

He also found that if the stems or branches of the trees are "ringed" little or no wood formation takes place under the ringing belt. But above it wood formation is lively, compare i. a. TH. HARTIG (1862), STRASBURGER (1891), MER (1892a) and SWARBRICK (1927b).

COSTER (1927) after similar observations and experiments as JOST advances the assumption that some hormone issues from buds and leaves which somehow influences the growth in thickness. He writes among other things (p. 77): "Durch die vielen Versuche ist vorerst unzweideutig bewiesen, dass der Anfang des neuen Dickenwachstums bei periodisch kahlstehenden Laubhölzern von einem Reiz abhängig ist, der von den sich entfaltenden Knospen oder anderen auswachsenden Organen ausgeht".

MÜNCH (1932) and SNOW (1933) take a similar view.

β) The Presence of Growth Substances.

The presence of growth substances has been shown by CZAJA (1934), ZIMMERMANN (1936—37), SÖDING (1936, 1937, and 1940—41), AVERY, BURKHOLDER and CREIGHTON (1937) and BENNET and SKOOG (1938). These investigators have come to the following results:

a) During the rest stage buds and cambium contain no—or very small—quantities of active growth hormones.

b) Swelling buds, leaves, and flowers that are growing contain and produce considerable quantities of active growth hormones.

c) The growth hormone proceeds from the said organs down through the cambium¹ in branches, stem and roots and is followed by beginning cell division.

d) As long as the cambium is growing it contains larger and smaller quantities of growth hormones. When growth ceases in autumn the growth hormone content declines and becomes very small.

SÖDING (1937 and 1940—41), MÜNCH (1938) and JOST (1940) think, by the way, that the cambium is itself able to produce growth hormones after a first supply is received from the young shoot organs that are developing.

γ) The Effect of Growth Hormones.

That the growth hormones are able to make the cambium in trees resume growth is shown by experiments by SÖDING (1936 and 1940—41), GOUWENTAK (1936 and 1941) and GOUWENTAK and MAAS (1940). By means of auxin preparations or extractions from swelling buds these investigators have produced wood formation in different species of trees.

The experiments have chiefly been carried out by decapitating branches or young stems and thereafter applying a paste with the growth hormone onto the cut surface. In these branches or young stems wood formation began long before it started in untreated control-branches or -stems placed under completely similar external conditions.

After GOUWENTAK and MAAS (1940) and GOUWENTAK (1941) the periodicity of cambial activity cannot, however, directly be explained by a difference in the growth hormone production, as the cambium is not always equally susceptible to the influence of growth hormones. They found that it had an "independent", presumably material-physiologically determined, resting period which may be divided into a preliminary, middle and subsequent resting period. Under the middle resting period there cannot by means of experiments be produced any wood formation by growth substance influence, except after a preceding rest-breaking treatment.

δ) Various Reflections.

There is reason to assume that the change in the cambium (its preliminary change) preceding the beginning division into cells (see p. 16) is due to the beginning spread of growth hormones downwards from the swelling buds².

The growth hormones possibly proceed downwards through the cell walls of

¹ After HUBER, SCHMIDT and JAHNEL (1937) the transport of the growth hormone also takes place in the sieve tissue, comp. KASTENS (1924).

SÖDING (1940—41) has made a close study of this and found that the sieve tissue may contain growth materials.

BOYSEN JENSEN (1943, p. 330) writes: "In leaves the growth hormone transport seems to take place in the leaf traces, presumably in their sieve part".

After HELLINGA (1937) the growth hormone transport may only take place in a direction leading away from buds and leaves.

² SÖDING (1937 and 1940—41) found fairly large quantities of growth substances in the cambium some time before the inception of wood formation.

the cambium, cf. WEIJ 1932. The change in the appearance of the latter seems to indicate that this is so (comp. Figs. 1 and 2).

The formation of growth hormones in flower buds under expansion offer an explanation of the reason why cell division in the young branches begins simultaneously with flowering when this occurs before bud break (*Ulmus glabra*, see also footnote p. 24).

The downward progression of growth hormones from the swelling buds of the

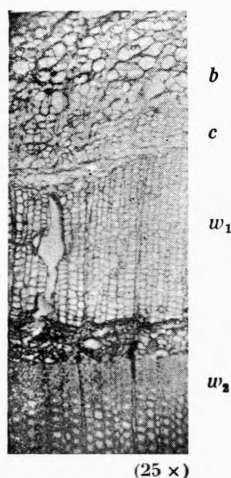


Fig. 13. Cross section through the new formed wood under a callus growth at the end surface of a *Larix decidua* billet cut at the end of February 1945. The section was taken on August 1, same year, $2\frac{1}{2}$ cms from the cut surface of the billet.

b Bark.
c Cambium.
*w*₁ New formed wood.
*w*₂ Last year's summer wood.

root shoots and young leaves explains why wood formation begins locally in roots with root shoots, compare BROWN (1935).

Beginning wood formation is not absolutely dependent of any connection with shoot organs under development.

In forests it is often seen that callus growths form between bark and wood at bruises on stumps or on clean boled stems.

If we examine such stumps or stems a new formation of wood from the callus tissue will often be found 2 to 10 cms inside the stem or the stump (see Fig. 13). The new-formed wood ring is widest just under the callus growth and narrows inwards like a wedge. In stems it proceeds in acropetal as well as in basipetal direction.

It is to be supposed that this wood formation is due either to the wound effect from the cut surface¹, growth hormones formed in the callus tissue, or wintered growth hormones (see MÜNCH, 1938, p. 621).

The wood formed is just as ineffectually differentiated as the wood which SÖDING (1937), GOUWENTAK and MAAS (1940) and GOUWENTAK (1941) succeeded in producing experimentally by external supplies of growth hormones. On cross sections the width of the tracheids is less than in normally built wood. The cell walls are thin and give the impression of incomplete lignification. The wood is very crisp when cut with a knife.

¹ After GOUWENTAK and MAAS (1940) the wound effect is able to produce a much limited wood formation.

VIII. The Course of Wood Formation and the Time of its Termination.

Methods.

1. A Survey of Applicable Methods.

The process of wood formation may be determined by two different processes:

a) By measurements on the outside of the stem of its diameter or circumference.

By this method the process of wood formation may only be determined with approximate exactness; as established diameter- or circumference-changes are due not only to growth in the wood, but also to the growth in the bark and the \pm changes in the circumference of the stem that is due to difference in the sap tension.

In the night when the transpiration is reduced the stem "swells". Reversely its volume decreases in daytime when the transpiration increases, compare KAISER (1879), FRIEDRICH (1897), and KORSTIAN (1921), MACDOUGAL (1921 and 1924), PEARSON (1924) and CHALK (1927).

During rainy periods the stem is for the same reason relatively thicker than during periods of drought, see HAASIS (1932).

In cold periods its volume decreases, see FRIEDRICH (1907).

β) By measuring the width of the new formed wood ring in sections or increment cores.

We get an approximate determination by this method only, as the width of the new formed wood ring may vary considerably even within rather narrow areas of a stem, i. a. as a consequence of eccentric growth.

2. The Method Applied.

The present examinations are carried out after the latter method (β)¹.

In order to some extent to avoid the uncertainty due to local variations in the width of the annual ring the width of the new formed wood ring at the various dates in the summer is stated in percentage of the width of the preceding year's annual ring. This method has previously been used by CHALK (1927) and gives a fairly safe determination of the process of wood formation.

Measurements which during the winter 1945 I have made on a great number of cut stems have shown that if one sticks to the same side of the stem there proves to be a fairly constant relation between the width of the two adjoining annual rings, comp. CHALK (1930, p. 10). For trees with a diameter of over 10 cms one may usually calculate with a correlation coefficient of 80 to 90. An absolute condition is, however, that the stem is well formed in the place in question. There must be no gnarls, furrows or other irregularities.

¹ Circumference measurements with sensitive, selfrecording measuring instruments had to be abandoned in advance as they were too expensive to buy.

In 1944 circumference measurements were tried till mid-June with a steel band with Vernier scale. The variations in the records were so large from one measurement to the next that this method was abandoned.

In order more easily to compare the process of wood formation in the various trees the per cents found are calculated in relation to 100 at the time of the termination of wood formation.

Material.

The examinations comprise the following species of trees:

1944		1945	
	Age		Age
Conifers:			
<i>Picea abies</i>	15—35	<i>Larix decidua</i>	13—45
Hardwoods:		<i>Picea abies</i>	10—35
<i>Betula pendula</i>	15—35	<i>Betula pendula</i>	10—26
<i>Alnus glutinosa</i>	10—45	<i>Alnus glutinosa</i>	14—55
<i>Fagus silvatica</i>	20—120	<i>Fagus silvatica</i>	14—70
<i>Quercus robur</i>	20—35	<i>Quercus robur</i>	14—70
<i>Ulmus glabra</i>	15—60	<i>Acer pseudoplatanus</i>	20—35
<i>Acer pseudoplatanus</i>	12—40	<i>Fraxinus excelsior</i>	20—59
<i>Fraxinus excelsior</i>	15—30		

The trees for which the process of wood formation is stated separately in Tables and Figures are described in Tables V—XIII.

The other trees were dominant or co-dominant trees in closed well nursed stands. The *Acer pseudoplatanus* on the whole were found as undergrowth under older *Fagus silvatica*, *Acer pseudoplatanus* and *Fraxinus excelsior*.

The growth conditions may no doubt be counted among the very best in Denmark.

The soil was in most cases deep, very mouldy and had a suitable content of clay.

The ground flora chiefly consisted of such herbs that characterize a soil rich in nutrients in good biological condition.

Taking of Sections.

In 1944 sections were taken 3 to 5 times during the summer from 20—25 trees within each species. With the exception of a few trees (see Tables V—XIII) new trees were used every time. The sections were taken at breast height (1.3 m) and from 1.5 to 2 cms thick, leafy branches in the uppermost half of the tree.

In the spring of 1945 4 to 10 trees were chosen within each species. From these trees 8 sections were taken from the stem during summer from the middle of the crown, and at breast height. The first place corresponds to $\frac{2}{3}$ to $\frac{3}{4}$ of the full height of the trees¹.

The sections were each time extracted at the same side of the stem and at the same height over the ground (see Fig. 14). The method mentioned p. 15 was applied.

¹ As the sections are to be taken in places free of adjoining branches, callus growths etc. it has been impossible to extract them at the same relative height in all trees.

In trees with very deep crowns they were taken somewhat above the midst of the crown.

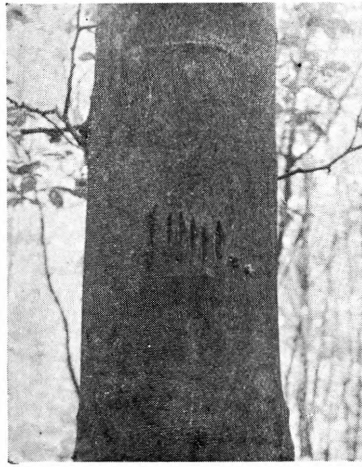


Fig. 14. Scar at breast height after 6 sections and 2 increment cores extracted in the course of the summer 1945. Photograph taken in October 1945, from the stem of *Acer pseudoplatanus* No. 2. (See Table VIII).

Tables and Figures.

The process of wood formation in the various species of trees is shown by curves in Figs. 15—30.

In the Figures are entered precipitation and mean temperature measured at the Meteorological Station at Bogø.

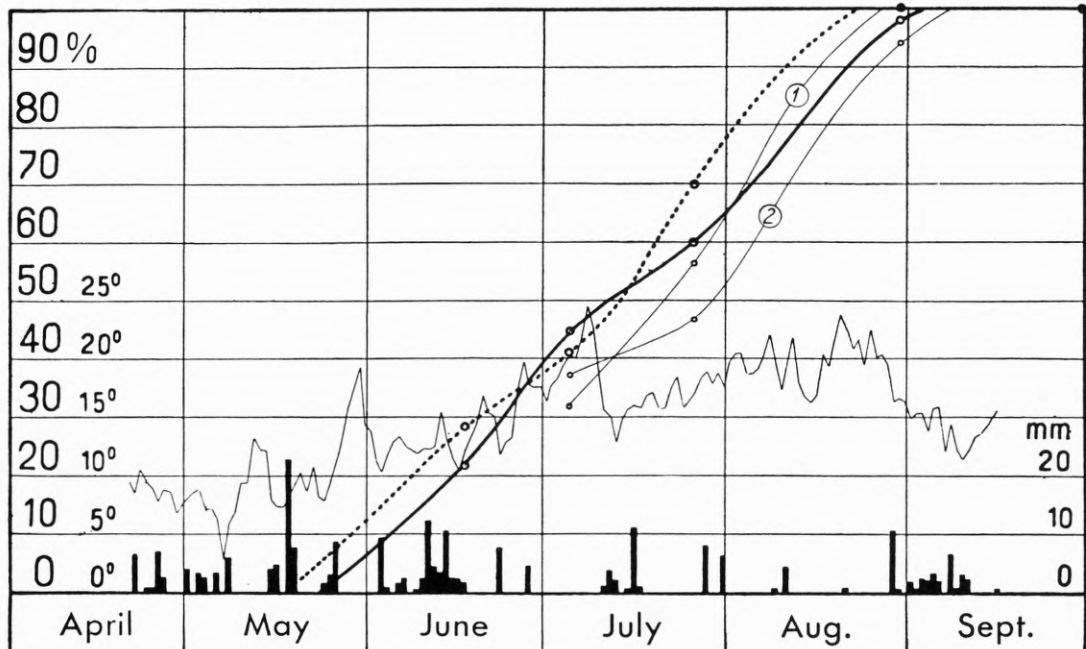


Fig. 15. *Betula pendula*. The relative process of wood formation in 1944. The thin curves show wood formation in the two trees described in Table V. The thick curves show the mean for medium sized to large crowns and in close stands in sandy and clayey ground and well drained swamp soil:
 In 1.5 to 2 cms thick, leafy branches in the upper half of the crown. — At 1.3 m height in the stem.

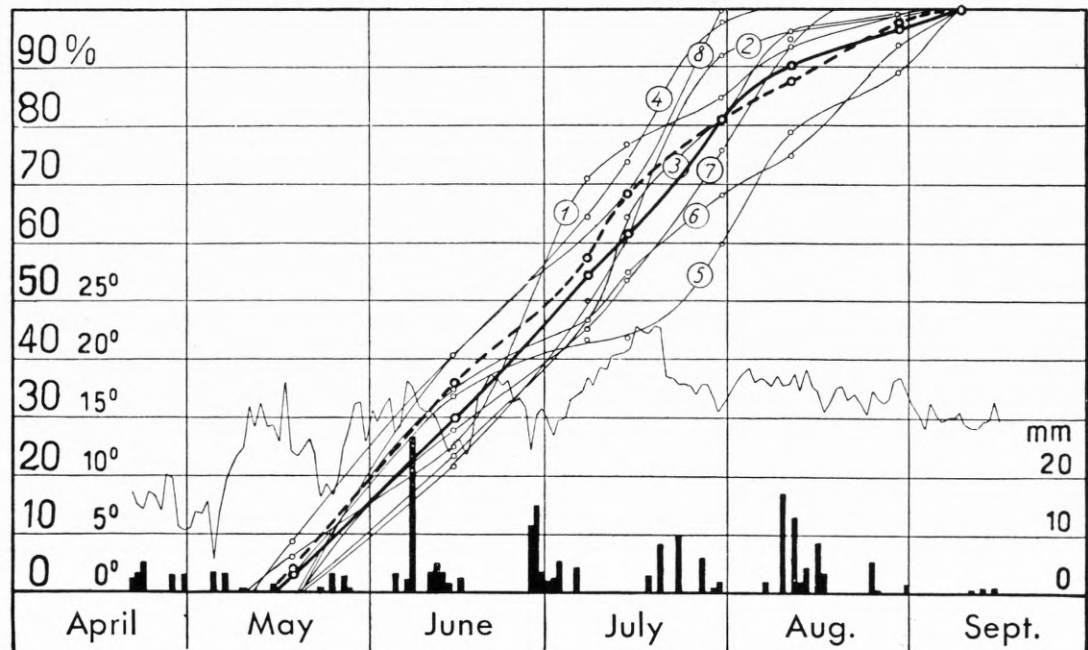


Fig. 16. *Betula pendula*. The relative process of wood formation in 1945. The thin curves show wood formation in the 8 trees described in Table V. The thick curves show the mean for trees Nos. 1—6:
 In the stem in the middle of the crown. — In the stem at 3 m height.

TABLE V.
Betula pendula Roth. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter		ratio	Crown		Soil		Ground flora
			cm	incre- ment mm		N-S m	E-W m	Surface soil	Subsoil	
1944: The two trees whose wood formation was followed from July 4th Both were medium-sized trees in closed <i>Betula</i> stands										
1	25	12.3	12	4	0.35	3.0	3.3	30 cms slightly clayey sand. Coarse grained, deep and loose mould.	Clayey sand. 1 m to ground water	<i>Urtica, Rubus fruticosus</i>
2	25	12.5	14	8	0.40	3.9	3.5			
1945: An open-grown tree over young <i>Picea abies</i>										
1	10	6.0	6	6	0.80	2.0	1.5	25 cms clayey sand. Coarse grained, fairly thin layer of mould	Sand to slightly clayey sand. Presumably 2 m to ground water	No herbaceous vegetation
II. Trees in closed <i>Betula</i> stand with a mixture of even-aged <i>Fagus sylvatica</i>										
A. Dominant trees										
2	26	11.8	17	5	0.66	4.4	4.1	22 cms sand. Coarse grained deep, loose mould	Sand to 50 cms depth. Then slightly clayey sand. Ground water at 75 cms depth	Undergrowth of <i>Alnus glutinosa</i> (<i>Urtica</i>), (<i>Rubus idaeus</i> and <i>R. fruticosus</i>), (<i>Anemone</i>)
3	26	12.3	16	6	0.40	3.1	3.3			
4	26	13.0	16	5	0.54	4.0	3.7			
5	26	13.7	20	11	0.50	4.0	4.8			
6	26	14.0	19	10	0.58	4.2	5.0			
B. Intermediate trees with very small crowns (whips)										
7	26	10.2	7	3	0.14	1.5	1.2			
8	26	11.0	7	3	0.28	1.2	0.9			

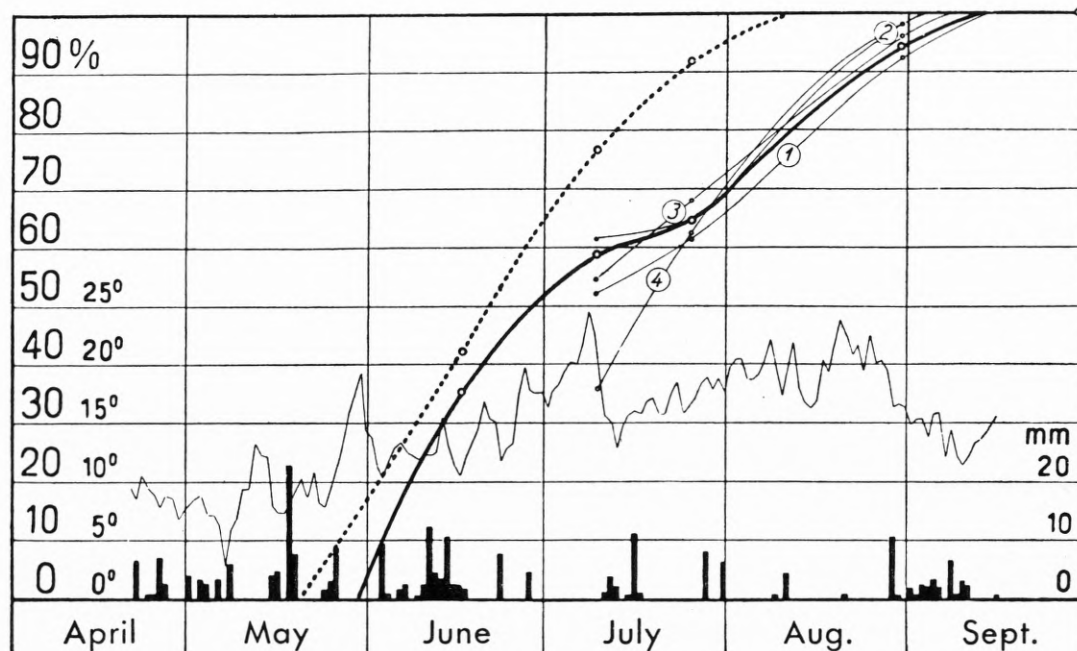


Fig. 17. *Alnus glutinosa*. The relative process of wood formation in 1944. The thin curves show wood formation in the 4 trees, that are described in Table VI. The thick curves show it in the mean for trees with medium sized to large crowns and in close-grown plantations in very watery swamp soil:
 In 1.5 to 2 cms thick leafy branches in the upper half of the crown. — At 1.3 m height in the stem.

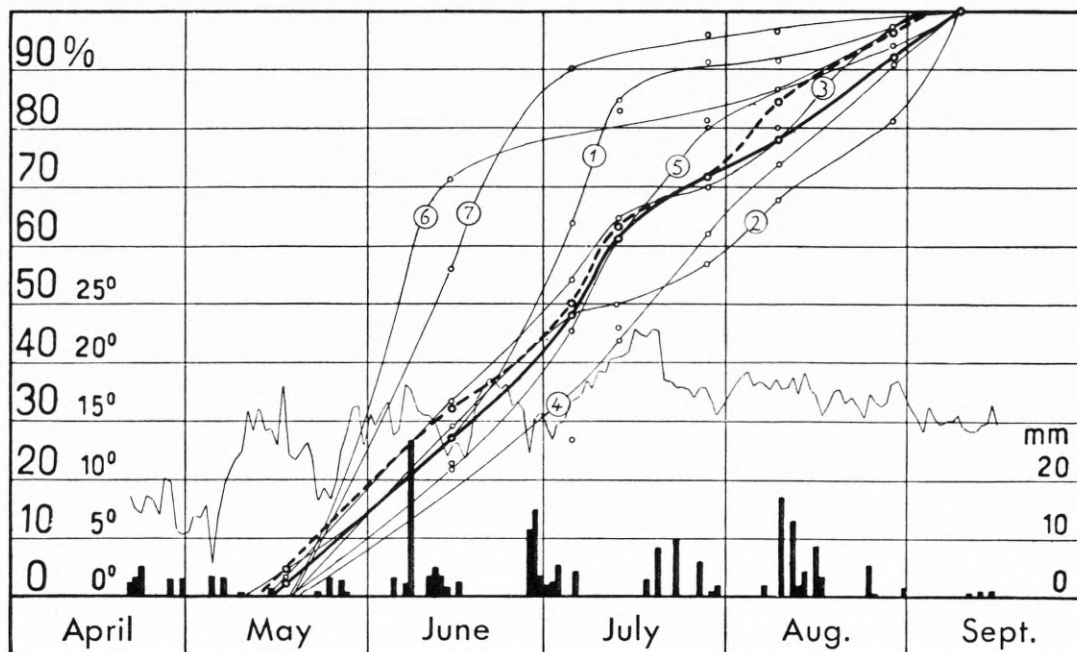


Fig. 18. *Alnus glutinosa*. The relative process of wood formation in 1945. The thin curves show wood formation in the 7 trees, that are described in Table VI. The thick curves show it in the mean for tree Nos. 1—5:
 In the stem in the middle of the crown. — In the stem at 1.3 m height.

TABLE VI.
Alnus glutinosa (L.) GAERT. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter		ratio	Crown diameter		Soil		Ground flora
			cm	increment mm		N-S m	E-W m	Surface soil	Subsoil	
<p>1944: The four trees whose wood formation was followed from July 9th All trees in an uneven-aged <i>Alnus glutinosa</i> plantation</p>										
1	10	6.1	5	8	0.50	2.5	2.2	Very moist marsh soil	Marsh still at 1 m depth. Ground water at 20—30 cms depth	Undergrowth of a few bushes, <i>Urtica</i>
2	14	8.0	8	8	0.45	2.9	2.5			
3	19	12.5	10	10	0.33	3.1	2.6			
4	25	12.7	18	10	0.33	3.2	4.0			
<p>1945: Trees in pure <i>Alnus glutinosa</i> stands or mixed in even-aged ash stands</p>										
A. Dominant trees										
1	14	7.6	8	6	0.40	3.1	2.0	18 cms clayey sand. Coarse grained, very humusrich and moist mould	Sand to stiff clay. Ground water at c. 50 cms depth	<i>Urtica</i>
2	18	9.0	13	13	0.60	5.1	3.3	60 cms rich and very wet swamp soil	Stiff clay. Ground water at 20—30 cms depth	Undergrowth of a few <i>Sambucus nigra</i> , <i>Urtica</i> , <i>Geranium</i> , <i>Galium</i>
3	—	9.1	10	9	0.45	2.8	2.2			
4	40	14.0	26	9	0.33	5.3	4.0			
5	55	18.1	33	8	0.53	4.3	6.1	24 cms clayey sand. Coarse grained, rich moist mould	Sand to stiff clay. Ground water at c. 50 cms depth	<i>Urtica</i> , <i>Rubus fruticosus</i> , (<i>Anemone</i>), (<i>Geranium</i>)
B. Intermediate and overshadowed trees with small crowns										
6	14	5.8	5	1	0.20	1.5	1.0	18 cms clayey sand. Coarse grained, very humus rich and moist mould	Sand to stiff clay. Ground water at c. 50 cms depth	<i>Urtica</i>
7	—	7.3	6	2	0.25	1.9	2.0			

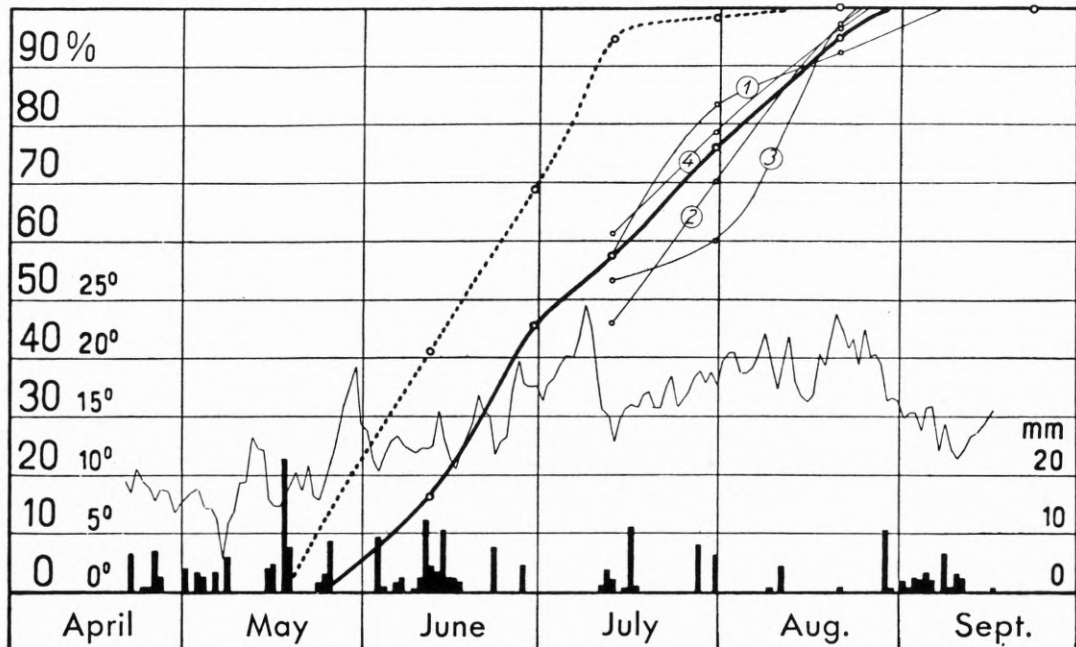


Fig. 19. *Fagus silvatica*. The relative process of wood formation in 1944. The thin curves show wood formation in the four trees, that are described in Table VII. The thick curves show the mean for trees with medium sized to large crowns and in close-grown plantations:
 In 1.5 to 2 cms thick leafy branches in the upper half of the crown. — At 1.3 m height in the stem.

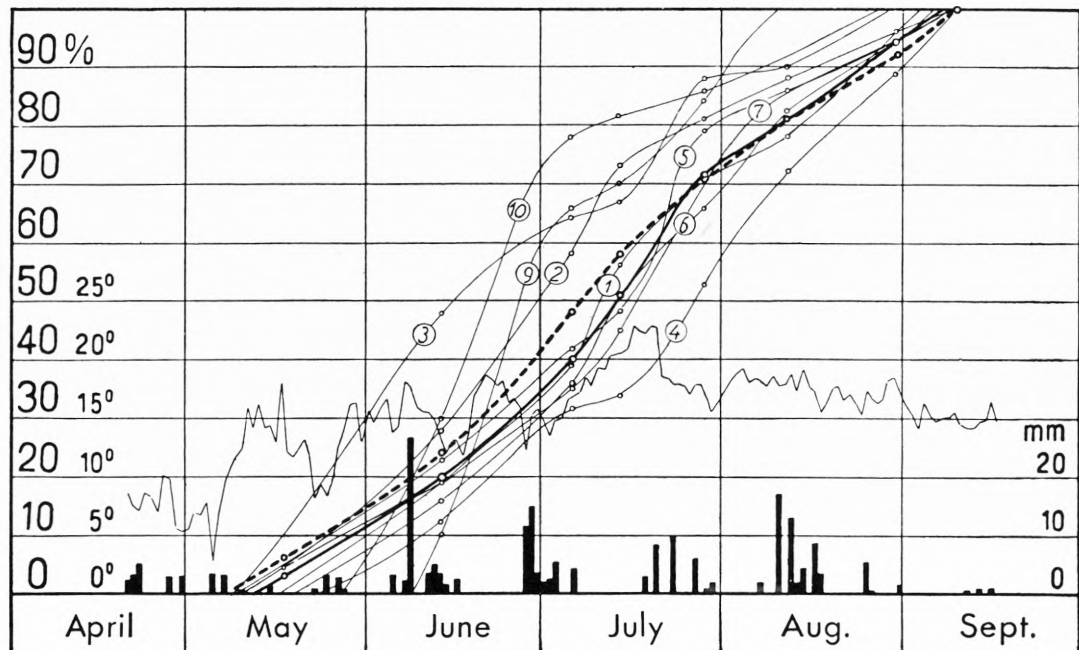


Fig. 20. *Fagus silvatica*. The process of wood formation in 1945. The thin curves show wood formation in 9 of the 10 trees, that are described in Table VII. The thick curves show it in the mean for trees Nos. 1—8:
 In the stem in the middle of the crown. — In the stem at 1.3 m height.

TABLE VII.
Fagus sylvatica L. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter		ratio	Crown		Soil		Ground flora
			cm	increment mm		N-S m	E-W m	Surface soil	Subsoil	
1944: The four trees whose wood formation was followed from July 12th										
All dominant trees in closed stands										
1	30	11.4	14	6	0.60	4.0	4.4	20—35 cms clayey sand.	Sandy clay to clayey sand.	<i>Anemone,</i> <i>Asperula,</i> <i>Rubus idaeus</i>
2	45	15.9	23	12	0.50	4.8	5.2	Coarse grained, rather deep mould	1.5 to 2 m to ground water	
3	45	16.2	20	10	0.50	4.6	4.3			
4	60	21.0	24	6	0.60	5.5	5.0			
1945: I. Partly isolated trees										
1	40	14.0	31	11	1.00	6.7	9.2	45 cms sand. Coarse grained to fine-grained mould	Sand and gravel. Fairly high ground water level	<i>Urtica, Rubus</i> <i>idaeus</i>
2	70	18.6	43	8	0.90	9.8	9.2	40 cms clayey sand. Coarse- grained mould	Clayey sand to sandy clay c. 1.5 m to ground water	<i>Anemone,</i> <i>Asperula,</i> <i>Trientalis,</i> <i>Stachys</i>
II. Trees in closed stands										
A. Dominant trees										
3	14	5.1	5	6	0.50	2.1	1.9	20 cms clayey sand. Coarse- grained, rich mould	Lime-rich friable clay. Fairly high ground water level, swamp border	<i>Anemone</i>
4	28	12.8	17	10	0.64	5.0	4.1	20 cms slightly clayey sand.	Sandy clay 1 to 2 m to ground water	<i>Anemone</i>
5	28	12.9	18	8	0.72	6.0	4.4	Coarse-grained, loose, deep mould		
6	28	14.1	20	12	0.58	4.8	5.0	24 cms clayey sand. Rich humusrich mould	Friable clay. Fairly high ground water level	<i>Anemone,</i> <i>Asperula,</i> <i>Urtica</i>
7	60	22.0	32	10	0.64	6.3	5.3			
B. Strongly suppressed trees										
8	26	10.1	4	0	0.10	0.9	1.1	15 cms clayey sand. Coarse- to fine-grained mould	Sandy clay. 1—2 m to ground water	<i>Anemone</i>
9	28	9.0	6	0.6	0.18	0.9	1.6	20 cms slightly clayey sand.	Sandy clay.	<i>Anemone</i>
10	28	4.5	5	1	0.10	0.9	0.9	Coarse-grained, loose, deep mould	1.5 to 2 m to ground water	

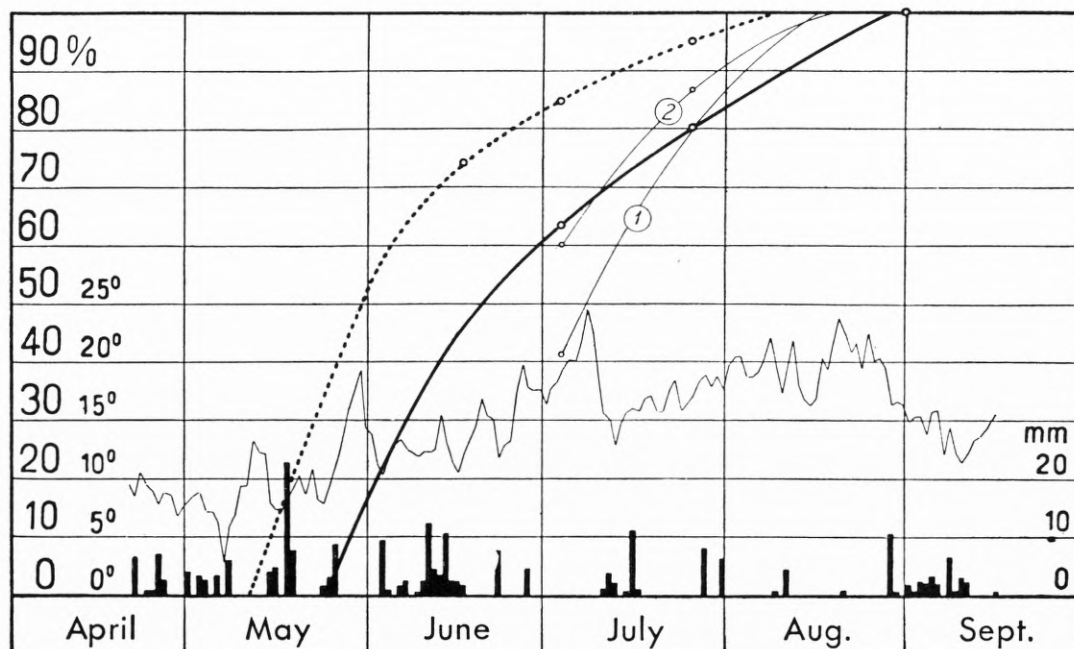


Fig. 21. *Acer pseudoplatanus*. The relative process of wood formation in 1944. The thin curves show wood formation in the two trees, that are described in Table VIII. The thick curves show the mean for trees with medium sized to large crowns and in closed stands in clayey soil:
 In 1.5 to 2 cms thick, leafy branches in the upper half of the crown. — At 1.3 m height in the stem.

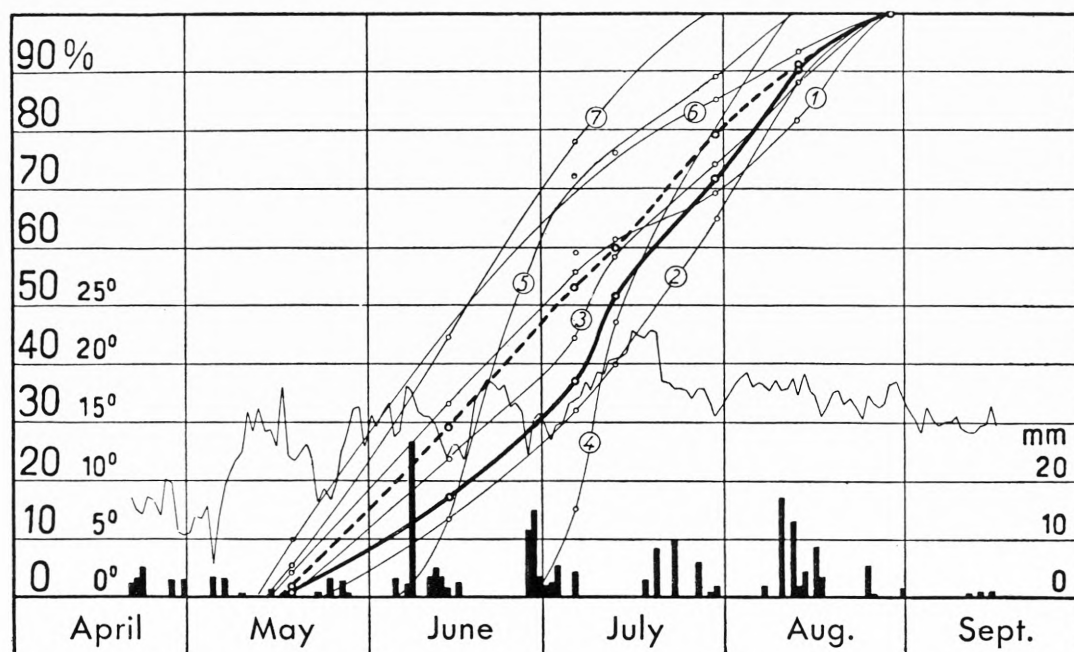


Fig. 22. *Acer pseudoplatanus*. The relative process of wood formation in 1945. The thin curves show wood formation in the 7 trees, that are described in Table VIII. The thick curves show the mean for trees Nos. 1—4:
 In the stem in the midst of the crown. — In the stem at 1.3 m height.

TABLE VIII.
Acer pseudoplatanus L. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter		ratio	Crown		Soil		Ground flora
			cm	increment mm		diameter		Surface soil	Subsoil	
						N-S m	E-W m			

1944: The two trees whose wood formation was followed from July 3rd
Trees in a stand of *Acer pseudoplatanus* and *Fagus sylvatica*

1	25	10.7	9	5	0.66	3.2	3.2	20—30 cms sandy clay to clayey sand. Coarse-grained, loose mould	Sandy clay to clayey sand. Presumably c. 2 m to ground water	Self-sown growth of <i>Acer pseudoplatanus</i> , <i>Anemone</i> , <i>Asperula</i>
2	25	15.5	14	5	0.38	5.2	4.1			

1945: Trees in stand of *Acer pseudoplatanus*, *Fraxinus excelsior* and *Fagus sylvatica*.

A. Dominant trees

1	26	11.9	16	8	0.50	4.0	3.6	15 to 20 cms sandy clay to clayey sand. Coarse-grained, loose mould	Sandy clay. c. 1 m to ground water	<i>Anemone</i> , <i>Asperula</i> , <i>Melica</i>
2	—	14.6	19	7	0.65	4.1	3.0			
3	—	14.9	24	11	0.65	8.0	5.8			
4	35	15.8	32	5	0.50	6.6	5.8			

B. Undergrowth

5	18	7.2	5	3	0.40	2.4	3.6	30 cms moist swamp soil	Stiff clay. Ground water at 50 cms depth	<i>Anemone</i> , <i>Hepa- tica</i> , <i>Geranium</i> , <i>Ficaria</i> , <i>Urtica</i>
6	20	8.1	4	2	0.35	2.6	2.0	60 cms clayey sand. Coarse- grained, humus- rich deep, loose mould	Stiff clay. Ground water at 65 cms depth	<i>Urtica</i> , <i>Milium</i> <i>Mercurialis</i> , (<i>Rubus fruti- cosus</i> and <i>R idaeus</i>)
7	—	9.0	3	3	0.40	2.4	1.8			

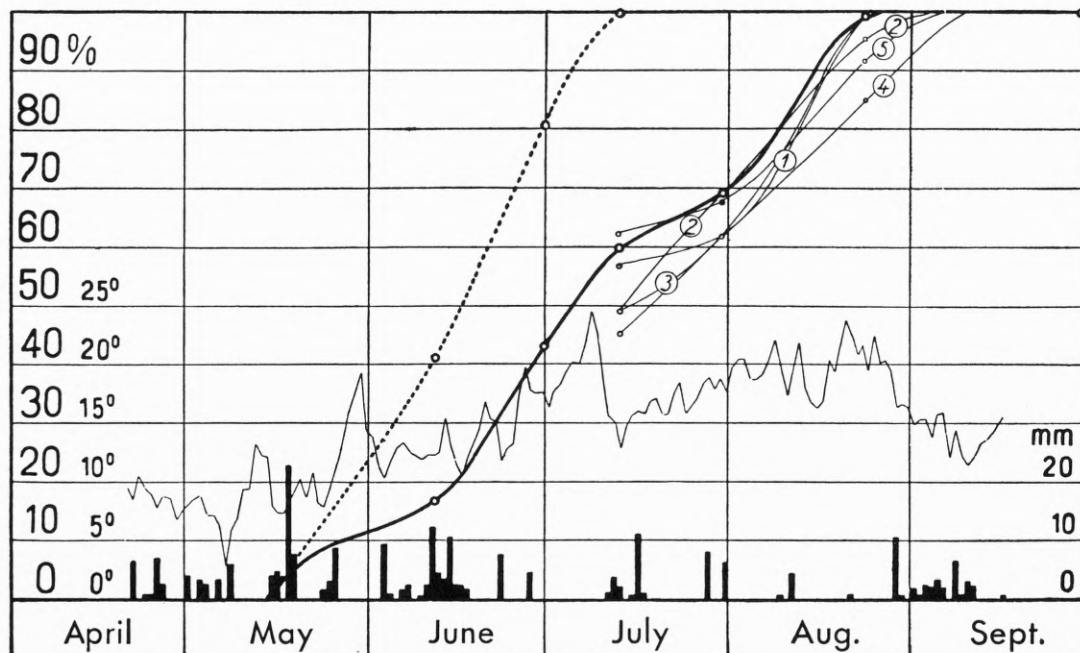


Fig. 23. *Quercus robur*. The relative process of wood formation in 1944. The thin curves show wood formation in the five trees, that are described in Table IX. The thick curves show the mean for trees with medium sized to large crowns in close-grown plantations in deep and clayey soil:
 In 1.5 to 2 cms thick, leafy branches in the upper half of the crown. — At 1.3 m height in the stem.

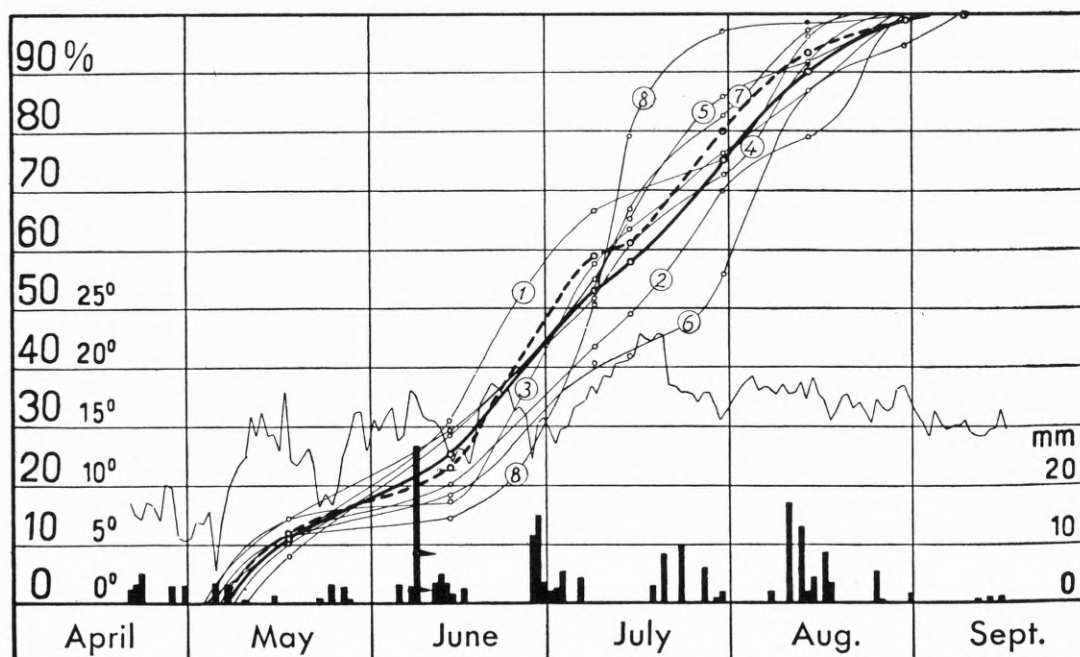


Fig. 24. *Quercus robur*. The relative process of wood formation in 1945. The thin curves show wood formation in the first eight of the ten trees, that are described in Table IX. The thick curves show the mean for trees Nos. 1—7:
 In the stem in the middle of the crown. — In the stem at 1.3 m height.

TABLE IX.
Quercus robur L. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter			Crown			Soil		Ground flora		
			cm	incre- ment mm	ratio	diameter		Surface soil	Subsoil				
						N-S m	E-W m						
1944: The five trees whose wood formation was followed from July 12th													
All trees in a closed stand													
A. Dominant trees													
1	23	9.2	8	14	0.70	2.7	4.0	Clayey sand. Coarse-grained, rich mould. In patches remains of old morformation	Sandy clay. Presumably between 1 and 2 m to ground water	<i>Anemone</i> in patches <i>Pteridium</i> <i>aquilinum</i>			
2	23	10.0	10	18	0.66	3.1	2.4						
B. Smaller trees (to be felled)													
3	23	8.1	6	8	0.50	1.9	2.1						
4	23	8.5	6	6	0.45	1.6	1.6						
5	23	8.7	8	8	0.50	1.7	2.0						
1945: I. Partly isolated trees													
1	14	6.5	7	10	0.79	3.3	2.9	30 cms sand. Coarse-grained, loose mould	Clayey sand. Between 1 and 1.5 m to ground water	<i>Urtica</i>			
2	26	12.6	30	14	0.90	8.3	6.5	32 cms rich swamp-soil	Stiff clay. 75 cms to ground water	<i>Picea sitchensis</i> undergrowth			
3	70	18.0	42	8	0.90	9.8	13.4	35 cms fine- grained strongly humus coloured mould	Gray sand and gravel. At beach. High ground water level	<i>Asperula</i> , <i>Pteridium aqui-</i> <i>linum</i> , <i>Rubus</i> <i>fruticosus</i>			
II. Trees in closed stand													
A. Dominant trees													
4	33	14.0	18	9	0.50	5.0	4.4	25 cms slightly clayey sand. Coarse-grained, loose, deep mould	Stiff clay, in patches sandy clay and marl. Between 1 and 2 m to ground water	<i>Anemone</i> , <i>Asperula</i> , <i>Rubus fruticosus</i> (<i>Deschampsia</i> <i>flexuosa</i>)			
5	33	14.2	18	6	0.60	5.0	5.0						
6	33	14.6	22	6	0.45	3.3	4.3						
7	33	14.0	24	8	0.60	6.0	4.1						
B. Strongly suppressed trees													
8	33	7.6	5	1	0.14	0.9	0.7						
9	33	7.0	4	(0)	0.09	0.7	0.5						
10	33	8.1	4	(0)	0.11	0.7	0.8						

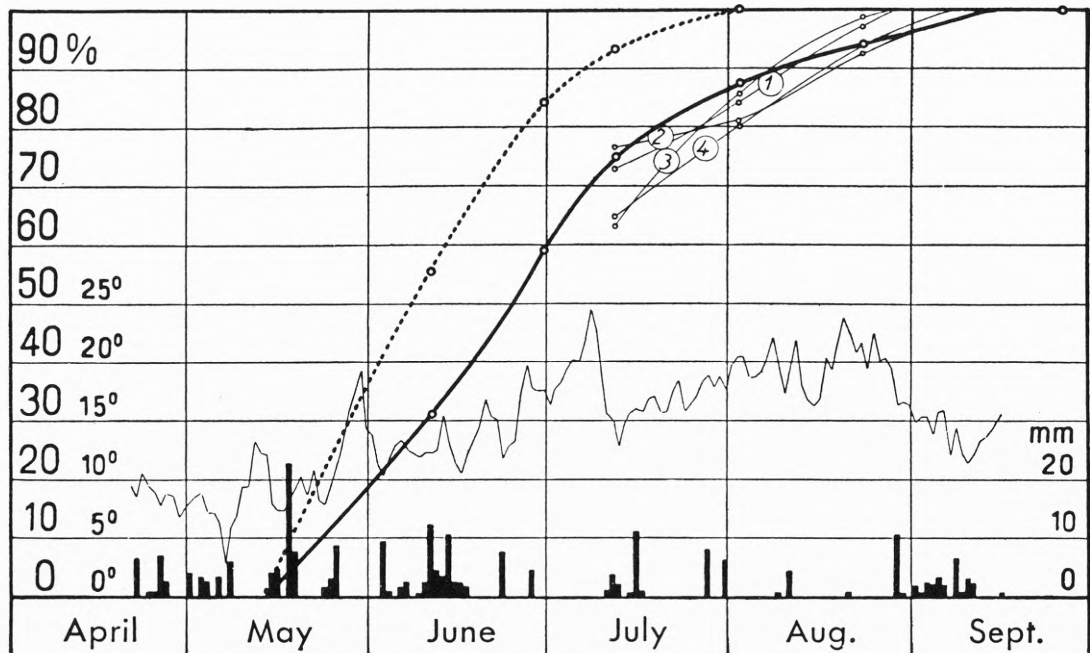


Fig. 25. *Fraxinus excelsior*. The relative process of wood formation in 1944. The thin curves show wood formation in the four trees, that are described in Table X. The thick curves the mean for trees with medium sized to large crowns and in closed stands on sandy and clayey soil as well as along the swamp borders and on well drained swamp soil:
 In 1.5 to 2 cms thick leafy branches in the upper half of the crown. — At 1.3 m height in the stem.

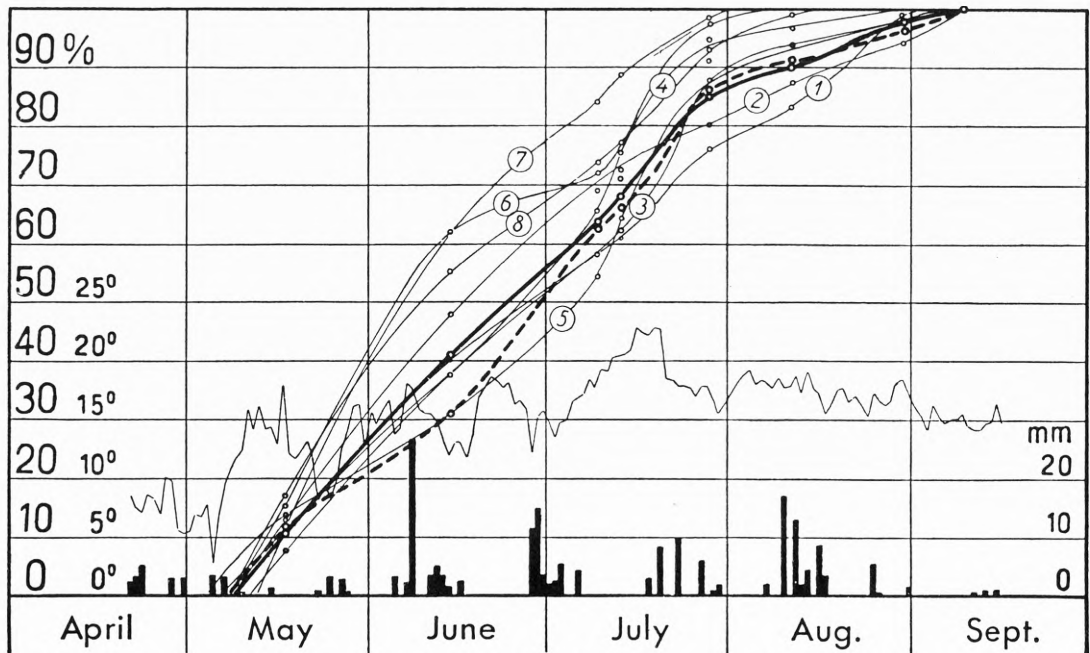


Fig. 26. *Fraxinus excelsior*. The relative process of wood formation in 1945. The thin curves show wood formation in the 8 trees, that are described in Table X. The thick curves show the mean for trees Nos. 1—4:
 In the stem in the middle of the crown. — In the stem at 1.3 m height.

TABLE X.
Fraxinus excelsior L. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter		ratio	Crown		Soil		Ground flora
			cm	increment mm		N-S m	E-W m	Surface soil	Subsoil	
1944: The four trees whose wood formation was followed from July 12th										
All dominant trees in a closed stand										
1	17	7.4	8	15	0.50	3.1	2.2	30—40 cms swamp soil. Edge of a swamp	Stiff clay to sandy clay. High ground water level	<i>Urtica, Rubus idaeus. Scat- tered Alnus glutinosa bushes</i>
2	17	7.9	7	14	0.40	2.7	2.7			
3	17	8.1	7	8	0.50	3.3	3.6			
4	17	10.1	12	12	0.50	4.0	3.7			
1945: I. Trees in closed stands in relatively well drained soil										
A. Dominant trees										
1	28	12.1	18	11	0.50	5.0	5.0	Edge of a swamp. Coarse- grained, deep, rich and humus- rich soil	Marl and sandy clay. C. 50 cms to the ground water	Scattered <i>Alnus glutinosa</i> bu- shes. <i>Urtica. Geranium Impatiens</i>
2	28	13.2	19	10	0.40	4.0	3.8			
3	28	14.4	22	16	0.43	5.2	4.3	20 cms slightly clayey sand. Coarse-grained, loose and deep mould	Sandy clay. 1.5 to 2 m to ground water	<i>Anemone</i>
4	59	16.0	30	5	0.63	7.0	6.6	25 cms clayey sand. Coarse- grained, rich mould	Stiff clay, marl in patches. C. 50 cms to ground water	<i>Deschampsia caespitosa</i>
B. Suppressed tree										
5	28	8.0	5	4	0.12	1.1	1.6	20 cms slightly clayey sand. Coarse-grained, deep and loose mould	Sandy clay. 1.5 to 2 m to ground water	<i>Anemone</i>
II. Dominant trees in closed stands in very watery swamp soil										
6	20	9.0	10	8	0.85	2.6	2.7	Very watery swamp soil	Ground water at 25 cms depth. C. 30 cms deep ditches	<i>Urtica, Geranium Valeriana</i>
7	20	7.1	9	7	0.50	3.3	2.5			
8	20	10.5	18	6	0.50	6.0	4.1			

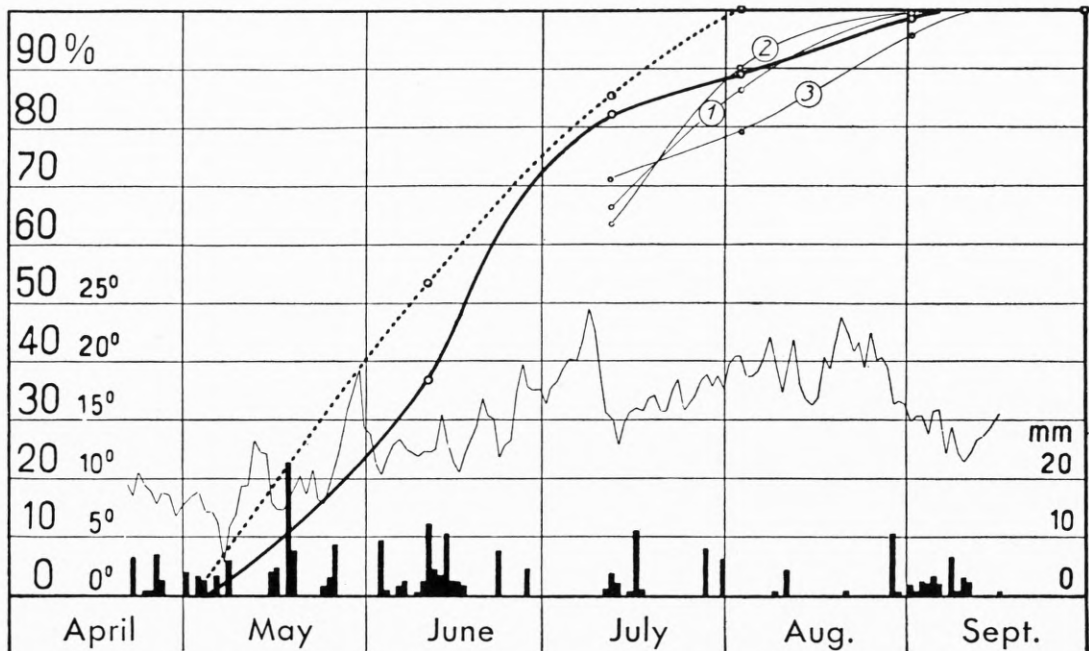


Fig. 27. *Ulmus glabra*. The relative process of wood formation in 1944. The thin curves show wood formation in the three trees, that are described in Table XI. The thick curves show the mean for wind-exposed trees with medium sized crowns in clayey soil:

..... In 1.5 to 2 cms thick leafy branches in the upper half of the crown. — At 1.3 m height in the stem.

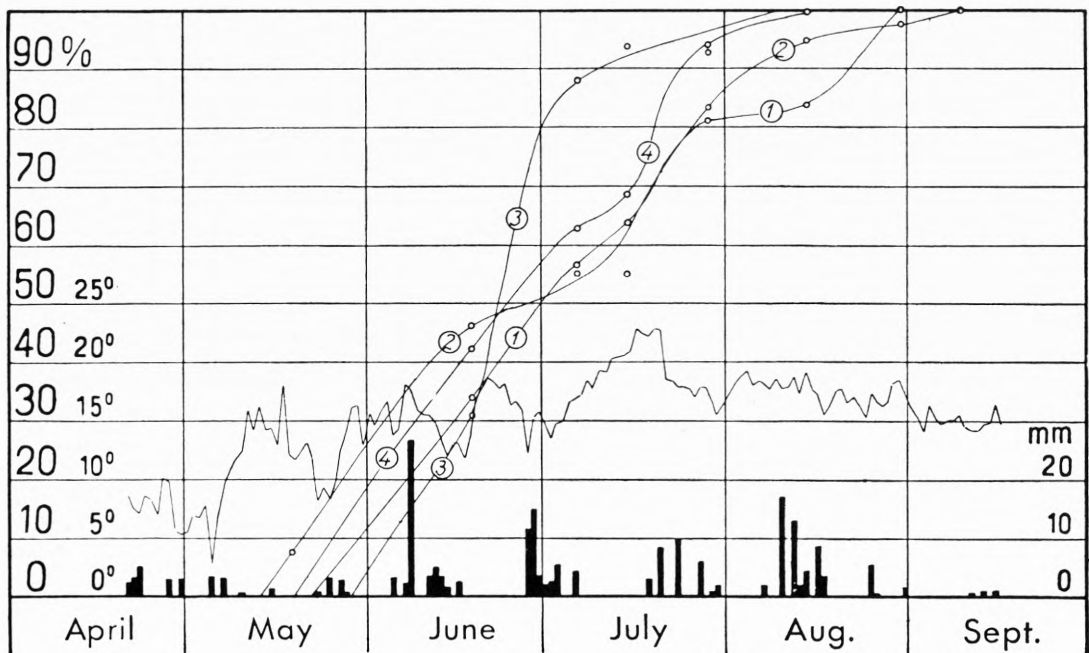


Fig. 28. *Larix decidua*. The process of wood formation at 1.3 m height in 1945. The individual trees are described in Table XII.

TABLE XI.
Ulmus glabra HUDS. 1944. Description of the Trees Whose Wood Formation was
Followed from July 11th.

Tree No.	Age	Height m	Diameter		ratio	Crown		Soil		Ground flora
			cm	incre- ment mm		diameter		Surface soil	Subsoil	
						N-S m	E-W m			
1	16	9.4	10	7	0.25	3.1	3.0	25 cms clayey sand. Coarse-grained mould	Sandy clay. Ground water at 0.5 m depth	<i>Anemone</i> , <i>Asperula</i> , (<i>Mercurialis</i>)
2	16	10.6	10	8	0.25	2.9	3.0			
3	45	16.9	29	14	0.40	5.5	4.1	20 cms clayey sand. Coarse-grained, loose mould	Sandy clay. Ground water at 65 cms depth	Undergrowth of <i>Alnus glutinosa</i> bushes. <i>Mercurialis</i> , <i>Urtica</i>

All three trees intermixed in *Fagus sylvatica* stands

TABLE XII.
Larix decidua MILL. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter		ratio	Crown		Soil		Ground flora
			cm	incre- ment mm		diameter		Surface soil	Subsoil	
						N-S m	E-W m			
1	13	8.0	7	10	0.75	2.2	1.8	30 cms clayey sand. Coarse-grained, deep and loose mould	Clayey sand. C. 1 m to ground water	(<i>Anemone</i>)
2	13	8.4	9	14	0.75	1.9	2.1	20 cms slightly clayey sand. Coarse-grained mould	Sandy clay. C. 1 m to ground water	<i>Anemone</i>
3	45	16.9	30	4	0.30	4.5	4.3	24 cms clayey sand	Friable clay. Fairly high ground water level	<i>Anemone</i> , <i>Asperula</i> , (<i>Rubus fruticosus</i>)
4	45	20.0	44	7	0.33	7.0	6.4			

B. *Larix decidua*

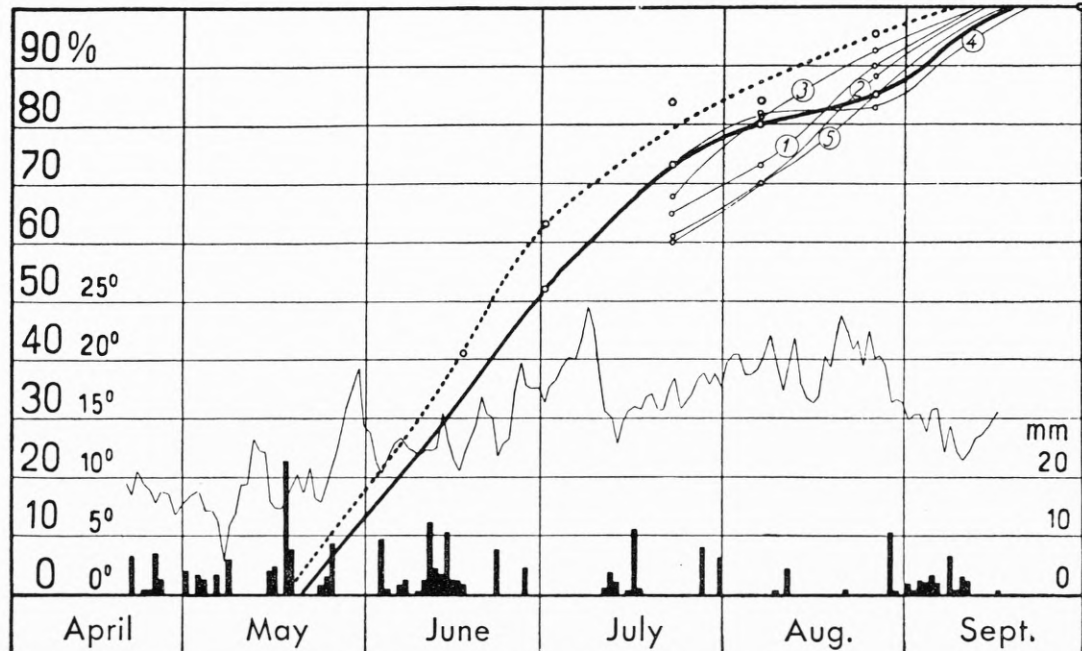


Fig. 29. *Picea abies*. The relative process of wood formation in 1944. The thin curves show wood formation in the five trees, that are described in Table XIII. The thick curves show the mean for trees with medium sized to large crowns in closed stands, in sandy and clayey soil:
 In 1.5 to 2 cms thick, leafy branches in the upper half of the crown. — At 1.3 m height in the stem.

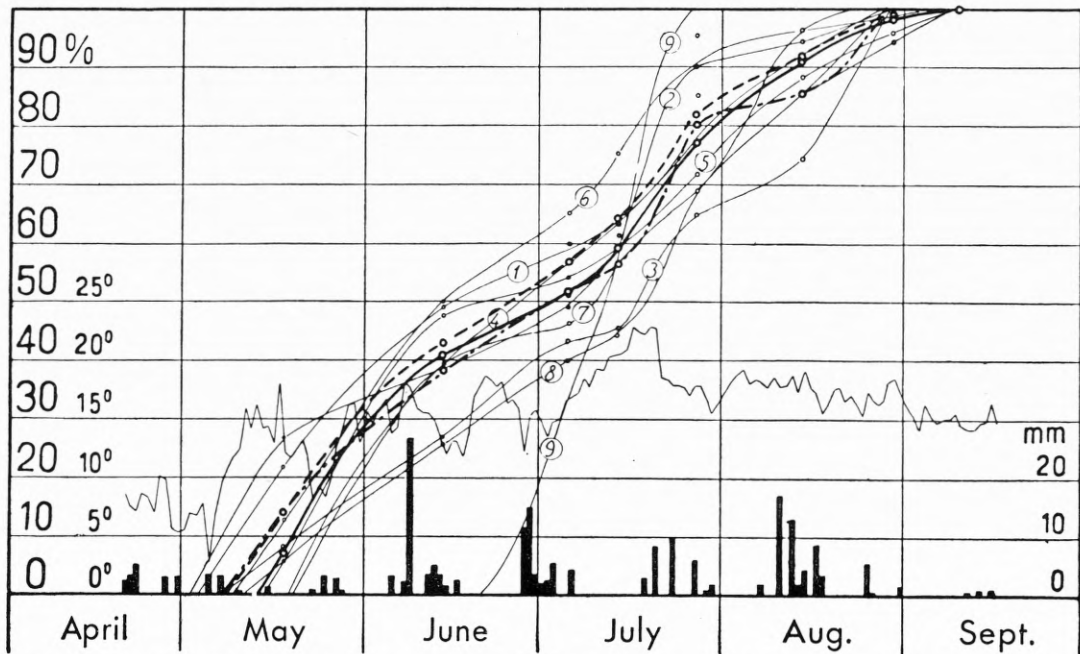


Fig. 30. *Picea abies*. The relative process of wood formation in 1945. The thin curves show wood formation in the first 9 of the trees described in Table XIII. The thick curves show the mean for
 -.-.- 1.3 m height in the stem of trees Nos. 1—4. — 1.3 m height in the stem of trees Nos. 5—8.
 The stem in mid-crown of trees Nos. 5—8.

TABLE XIII.
Picea abies L. KARST. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter			Crown			Soil		Ground flora
			cm	incre- ment mm	ratio	diameter		Surface soil	Subsoil		
						N-S m	E-W m				

1944: The five trees whose wood formation was followed from July 22nd

Border trees

1	15	5.6	8	7	1.00	2.2	2.6	20—30 cms clayey sand. Coarse-grained to fine-grained mould	Clayey sand. C. 1.5 m to ground water	None
2	15	6.5	10	6	0.90	3.0	2.4			
3	15	6.9	10	7	0.90	2.1	2.1			
4	15	7.0	12	7	0.90	3.2	3.4			
5	15	7.2	9	4	0.90	3.4	3.5			

1945: I. Partly isolated trees

1	10	4.0	5	8	1.00	2.2	2.4	20—30 cms slightly clayey sand. Coarse- grained to fine- grained mould	Sandy clay. Between 0.5 to 2 m to ground water	(Oxalis)
2	12	4.9	5	8	1.00	2.2	2.0			
3	16	6.8	8	6	0.80	3.0	3.2			
4	27	10.4	12	4	0.82	2.8	2.2			

II. Trees in closed stands

A. Dominant trees

5	27	13.6	16	6	0.64	3.6	3.8	30 cms slightly clayey sand. 1 cm raw humus	Clayey sand. C. 1.5 m to ground water	(Oxalis)
6	27	14.1	19	4	0.70	4.6	3.2			
7	35	19.8	22	5	0.40	4.8	2.9	20 cms slightly clayey sand. Coarse-grained to fine-grained mould	Sandy clay. C. 2 m to ground water	(Anemone)
8	35	22.0	38	8	0.50	6.8	5.1			

B. Strongly suppressed trees

9	27	7.0	6	0.6	0.12	1.2	0.9	30 cms slightly clayey sand. Raw humus	Clayey sand. C. 1.5 m to ground water	(Oxalis)
10	27	7.1	6	0	0.20	1.5	2.0			
11	27	8.5	5	0	0.09	1.3	1.0			

Wood Formation in the Branches.

In the young branches the main part of the new annual ring is formed during the period in which the most active shoot extension takes place.

a) *The Short Shoots.*

The short shoots have a minimal growth in length and thickness. The extension growth is practically terminated when the foliage is completely expanded.

Wood formation often ceases at the end of May or during the first half of June.

As a rule only few new vessels are formed. Often there is no summer wood formation, so that it may be very difficult to distinguish the individual annual rings from each other (comp. HERRMANN (1916)).

β) *The Long Shoots.*

In *Quercus robur*, *Fraxinus excelsior*, *Ulmus glabra* and *Fagus silvatica* that have short shoot extension periods (see Table XVII) wood formation in the young branches is most active in May and at the beginning of June. In one-year-old branches $\frac{3}{4}$ of the new annual ring are often formed at the close of May.

In most branches wood formation is completed at the end of June or the beginning of July. The cambium, however, does not enter into the resting period (see Fig. 1) till September.

If repeated shoots are formed wood formation continues until these shoots are fully grown. Wood formation in the young branches has in such cases two annual maximum periods, one in May and the beginning of June, and one at the end of June and the beginning of July.

In *Acer pseudoplatanus*, *Betula pendula*, *Picea abies*, and *Larix decidua*, that have long shoot extension periods, wood formation proceeds more slowly in the young branches.

Maximum occurs in May and June. An almost equally great quantity of wood is formed during both months. At the end of June approximately $\frac{3}{4}$ of the new annual ring are formed in the one-year-old branches.

Wood formation generally terminates at the end of July or the beginning of August.

Literature offers little information only about wood formation in the branches.

R. HARTIG (1882b, pp. 118 and 119) found that in *Acer pseudoplatanus* and *Fagus silvatica*-branches wood formation terminates at the beginning of August, in *Larix decidua* in mid-August, and in *Pinus silvestris*-branches at the beginning of September. The age of the branches is not given.

JOST (1892) found that by July 1st 75 % of the new annual ring were formed in 2—4-year-old *Fagus silvatica*-branches and 90 % in 1—2-year-old *Quercus robur*-branches. In the *Fagus silvatica*-branches wood formation ceased in August, in the *Quercus robur*-branches in July.

ANTEVS (1917, p. 341) found that wood formation proceeds quickly in the branches and reaches maximum about the middle of June. It then continues "recht gleichmässig".

Wood formation is relatively more advanced in the terminal than in the basal parts of the branches. The difference may be very considerable, particularly in the younger parts of the branches (see Fig. 31) and it does not increase evenly downwards.

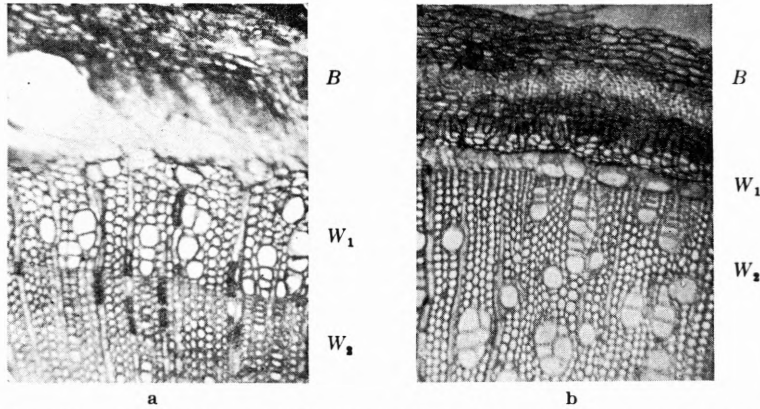


Fig. 31. Cross section through a one-year-old vigorous branch of a young *Acer pseudoplatanus* the section shows wood formation on April 27, 1945.

$a = 5$ cms and $b = 30$ cms from bud base ($80\times$).

$B =$ bark, $W_1 =$ new formed wood, and $W_2 =$ last year's summer wood.

There is a relatively greater difference among the one- and two-year-old branch parts etc. than in the two- and three-year-old branch parts, comp. SWARBRICK (1927 a, p. 152). It is greatest in trees with short shoot extension period.

Wood Formation in the Stem.

The length of the wood formation period increases from the young branches and down into the stem, and a relatively greater part of the new annual ring is formed late in summer.

1. A Comparison between the Tree Species.

In Table XIV a general survey is given of the relative wood formation at breast height during the various months in 1944 and 1945.

It appears from the latter that there is some difference between the development of wood formation in the various species of trees. They may be divided into the following groups:

Fraxinus excelsior: It is among the trees examined the one in which the formation of the annual ring takes place at the relatively earliest time in summer. Wood formation is lively from the very start. About three fifths of the new annual ring are formed in May and June. After July there is little wood formation only (see Figs. 25 and 26).

Picea abies and *Larix decidua*: Wood formation is lively from the start as in *Fraxinus excelsior*. About half of the annual ring is formed in May and June. After July wood formation is not very active (see Figs. 28, 29 and 30).

Betula pendula, *Fagus silvatica*, *Alnus glutinosa*, *Acer pseudoplatanus* and *Quercus robur*: In most cases some time passes before wood formation becomes really active. Only between one third and one half of the annual ring is formed in May and June. In contrast to *Fraxinus excelsior*, *Picea abies* and *Larix decidua* wood formation is on the other hand very active still in August. Between one third and one fourth of the annual ring is formed in this month and during the first days of September (see Figs. 15, 16, 17, 18, 19, 20, 21, 22, 23 and 24).

TABLE XIV. The Relative Wood Formation (Formation of the Annual Ring) at Breast Height during the Various Months of 1944 and 1945. The Percentages are Read on the Thick Curves in Figs. 15—30¹ and Give the Average for Opengrown Trees and Dominant and Co-dominant Trees in Close Stands. The Mean Temperature and Precipitation is Measured at Bogo Meteorological Station (see Table I).

Species of Tree	Average Diameter-increment mm.	May	June	May-June	July	August	Sept.	Σ
1944:								
<i>Betula pendula</i>	—	6	33	39	26	33	2	100
<i>Quercus robur</i>	—	11	32	43	26	31	—	100
<i>Fagus silvatica</i>	—	5	41	46	30	24	—	100
<i>Alnus glutinosa</i>	—	4	48	52	17	26	5	100
<i>Fraxinus excelsior</i>	—	19	41	60	26	10	4	100
Average	—	9	39	48	25	25	2	100
<i>Picea abies</i>	—	14	37	51	27	10	12	100
Mean temperature	9.9	13.6	..	17.4	19.1	13.3	..
Precipitation	73	67	..	34	19	59	193 ²
1945:								
<i>Fagus silvatica</i>	9.3	12	22	34	40	22	4	100
<i>Acer pseudoplatanus</i>	8.7	12	26	38	38	24	—	100
<i>Betula pendula</i>	9.0	16	25	41	29	25	5	100
<i>Alnus glutinosa</i>	9.0	14	28	42	31	20	7	100
<i>Quercus robur</i>	8.4	18	26	44	32	23	1	100
<i>Fraxinus excelsior</i>	10.5	26	30	56	31	11	2	100
Average	16	26	42	34	21	3	100
<i>Larix leptolepis</i>	12.0	19	31	50	33	16	1	100
<i>Picea abies</i>	6.1	29	20	49	32	18	1	100
Mean temperature	11.6	15.3	..	18.0	17.3	13.9	..
Precipitation	18	80	..	45	58	16	201 ²

¹ *Acer pseudoplatanus* and *Ulmus glabra* are not included in 1944. It is because these tree-species grow under other conditions than the other species (see p. 38 and 53). In 1945 *Acer pseudoplatanus* No. 4 is left out (see Table VIII and Fig. 22). In the same year the average for *Betula pendula* is calculated for trees Nos. 3, 5 and 6 only (see Table V and Fig. 16). The other *Betulas* are left out as they showed small diameter increment only.

² Summary for May, June, July and August.

This difference among the tree species is on the whole confirmed by earlier investigations (see Table XV).

TABLE XV. The Relative Wood Formation (Growth in Thickness) during the Individual Months after Various Investigations Carried out Abroad. The Mean Temperature and Precipitation are Added in such Cases where Information has been Received on these Points.

Species of Tree	April	May	June	April May June	July	Aug.	Sept.	Oct.	Σ
<i>Fagus silvatica</i>									
R. HARTIG (1891)..... (Germany)	—	(17)	(28)	45	39	16	—	—	100
CHRISTISON (1889)..... (Edinburgh, Engl.)	38
JOST (1892)..... (Strassburg, Germany)	1	14	32	47	27	20	5	1	100
Mean temperature.....	9.0	14.5	17.1	..	18.1	18.6	15.6	10.0	..
Precipitation mm.....	28	73	74	..	76	45	46	84	..
FRIEDRICH (1897)..... (Mariabrunn, Austria)	2	23	33	58	28	10	3	1	100
Mean temperature.....	10.6	13.2	16.3	..	19.1	16.8	13.0	7.8	..
Precipitation mm.....	75	78	121	..	79	69	31
GÄUMANN (1935)..... (Germany)	—	3	27	30	18	34	18	—	100
<i>Acer pseudoplatanus</i>									
CHRISTISON (1889)..... (Edinburgh, Engl.)	38
JOST (1892)..... (Strassburg, Germany)	1	15	33	49	31	15	4	1	100
Mean temperature.....	9.0	14.5	17.1	..	18.1	18.6	15.6	10.0	..
Precipitation mm.....	28	73	74	..	76	45	46	84	..
<i>Quercus</i>									
CHRISTISON (1889)..... (Edinburgh, Engl.)	38
JOST (1892)..... (<i>Quercus cerris</i>) (Strassburg, Germany)	2	23	27	52	31	14	2	1	100
Mean temperature.....	9.0	14.5	17.1	..	18.1	18.6	15.6	10.0	..
Precipitation mm.....	28	73	74	..	76	45	46	84	..
<i>Fraxinus</i>									
LODEWICK (1925)..... (North America)	10	15	40	65	30	5	—	—	100
Mean temperature.....	—	11.1	18.3	..	20.0	18.1
Precipitation mm.....	..	70	82	..	56	36
CHALK (1930)..... (Oxford, Engl.)	6	11	32	49	39	12	—	—	100
Mean temperature.....	8.3	10.8	14.6	..	16.5	17.1

TABLE XV (continued).

Species of Tree	April	May	June	April May June	July	Aug.	Sept.	Okt.	Σ
<i>Picea abies</i>									
MISCHKE (1890) (Germany)	4	26	27	57	26	17	—	—	100
Mean temperature	6.5	13.5	17.4	..	16.7	17.0
Precipitation mm.	25	17	27	..	94	43
FRIEDRICH (1897) (Mariabrunn, Austria)	4	15	23	42	29	20	7	2	100
Mean temperature	—	12.7	15.8	..	18.7	17.0	13.2	8.3	..
Precipitation mm.	73	83	125	..	61	50	54
WIELER (1898)	(47)

Wood formation proceeds practically speaking in the same way in the upper and lower parts of the stem (see Figs. 16, 18, 20, 22, 24, 26 and 30).

In well-grown trees wood formation is terminated in the stem at the close of August or during the first half of September. The time varies somewhat according to the tree species¹ and the climate of the individual year (comp. Figs. 15—30).

2. The Individual Variation.

The individual variation is fairly considerable and to some extent relative to the diameter increment (comp. Figs. 16, 18, 20, 22, 24, 26 and 30 with Tables V, VI, VII, VIII, IX, X and XIII).

In trees with small radial growth wood formation is most lively up to the beginning or the middle of July. It varies somewhat according to the species of the tree. Thereafter it decreases quickly. It often terminates at the close of July or the beginning of August.

In trees with large diameter increment wood formation proceeds quite evenly all through summer. As a rule it only terminates at the close of August or the beginning of September.

The difference is most distinct in the diffuse porous and the conifers (*Picea abies*). In these trees one third of the annual ring is generally speaking formed after June, while $\frac{2}{3}$ are formed in trees with large diameter increment (see Fig 32).

The reason of this correlation between diameter increment and the formation of wood is no doubt that the more unfavourable the growth conditions are (decreasing growth in thickness) the more will the growth possibilities relatively decrease during the last half of the summer.

This may be due to the α) external conditions and β) the internal, nutrition physiological conditions.

¹ Wood formation does not continue later in autumn in *Fraxinus excelsior*, *Alnus glutinosa* and *Quercus robur* whose foliage keeps fresh and green till defoliation in October (comp. BURGER 1942) than in the broad leaved trees whose foliage begins to discolour relatively early in autumn.

a) *External conditions.*

The food material in the soil is greatest in May and during the first half of June. It thereafter decreases, cf. LUNDEGÅRDH (1925) and HONCAMP (1931). Particularly the nitrogen¹ content decreases. The reason is decreasing biological activity.

HONCAMP (1931, II, p. 84) writes: "Im Frühjahr erwacht mit steigender Wärme ein immer regeres Bakterienleben, das aber schon in der wärmsten Jahreszeit, Juli bis August, merklich nachlässt und erst zum Herbste hin wieder ansteigt, um dann gegen den Winter hin wieder einzuschlafen".

The growth retarding effect of this must according to the minimum law presumably be relatively stronger the poorer the soil is in food stuffs and particularly in nitrogen (sluggish assimilation, humus accumulation etc.).

β) *Internal conditions of the physiology of nutrition.*

During the first part of the growth period the volume increment is determined by the equation:

A) Consumption of reserve food + assimilation surplus² = volume increment + seed (if any).

The reserve nutrients are consumed during the leafing period and the first part of the shoot extension period, when great quantities are consumed during a comparatively short time for formation of leaves, shoots, and spring wood, cf. RAMANN and BAUER (1911)³.

There exist no exact investigations showing how late in summer the reserve nutrients are consumed. After the many investigations made concerning the starch content of the trees etc. there is, however, every reason to assume that it is used up to 2 to 4 weeks after foliation, cf. R. HARTIG (1888c), FISCHER (1891), WOTCZAL (1890), LUTZ (1895), FABRICIUS (1905), RAMANN and BAUER (1911), KÜBLER (1912), PRICE (1915), BUTLER, SMITH, and CURRY (1917), CAMERON (1923), SWARBRICK (1927a), COCKERHAM (1930), WIGHT (1933), and GÄUMANN (1927 and 1935)⁴.

In Denmark the growth of the trees presumably proceeds by means of reserve foods until the close of May to the middle of June. Probably it varies somewhat according to how long time the leaves take to expand, how long the shoot extension lasts, and whether the trees are seed-bearing or not.

¹ It is worth noticing that the trees at the same time require increased nitrogen supply, cf. RAMANN and BAUER (1911, p. 74).

² The assimilation surplus = the net assimilation of the leaves — loss of leaves — loss of branches — (root loss) respiration in the stem, branches, and roots, cf. BOYSEN JENSEN (1910).

³ In older trees with well developed crowns only the young branches are completely depleted of reserve nutrients in spring, cf. SWARBRICK (1927), COCKERHAM (1930), and GÄUMANN (1927 and 1935). A complete depletion of reserve nutrients in the older branches and in the stem only takes place in seed years, cf. BOYSEN JENSEN (1943, p. 228).

A relatively greater quantity of the reserve food is consumed in quite young than in older trees, comp. RAMANN and BAUER (1911), KÜBLER (1912), and GÄUMANN (1935).

⁴ According to MÜNCH (1938, p. 641) the branches only supply assimilates to the stem after the young shoots are fully developed.

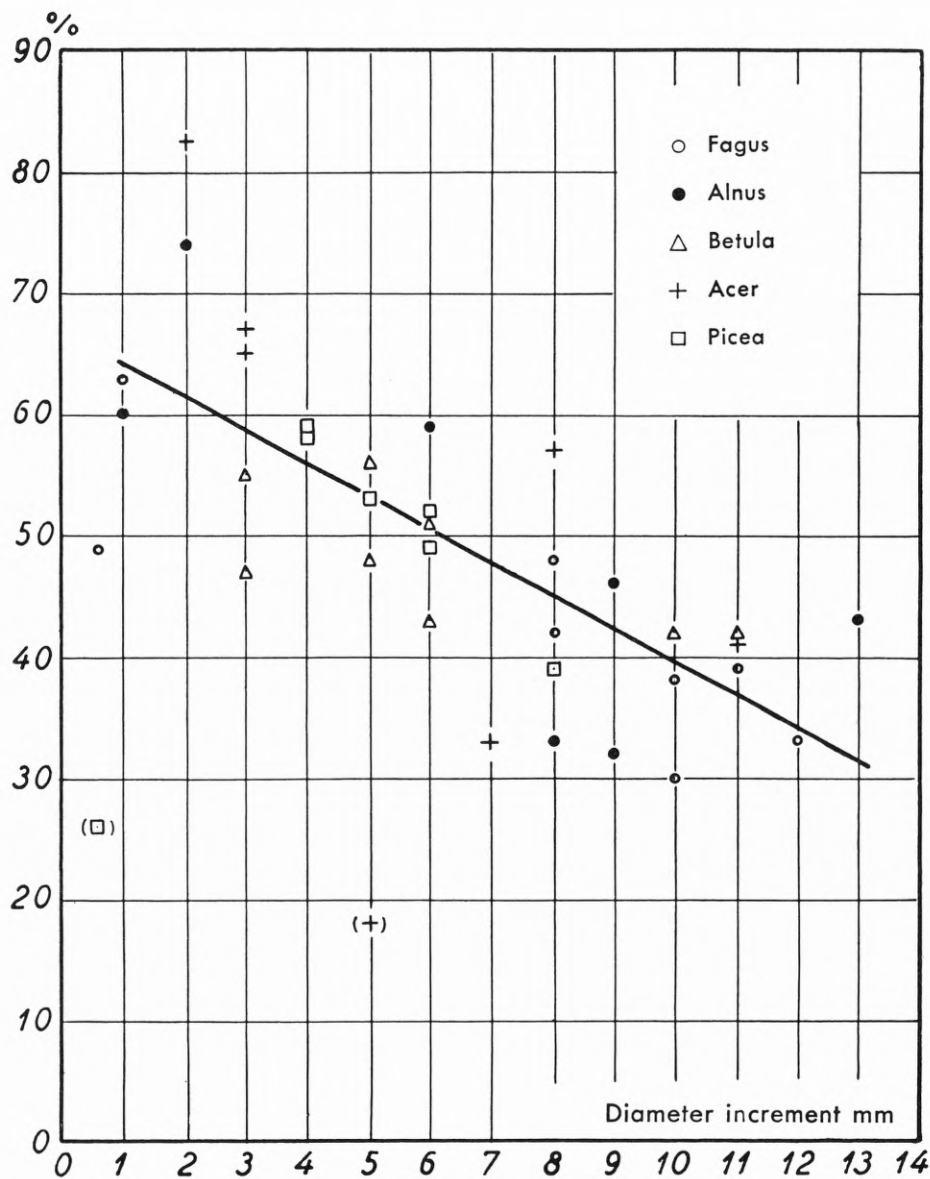


Fig. 32. The relation between the diameter increment of the trees and the relative annual ring formation per July 1, 1945.

The per cents give the mean for the stem in the middle of the crown and at breast height.

The curve is drawn assuming a rectilinear regression¹.

The correlation coefficient is 0.75².

¹ The regression equation is: $y = 67.10 - 2.74 x$

² Judged by the t -criterion: $\frac{r}{m_r} = 6.5$; $t = c. 2$.

The volume increment during the last part of the growth period appears from the equation:

B) Assimilation surplus — reserve nutrients = volume increment + seed (if any).

In conformity with the minimum law it is to be assumed that the closer the assimilation surplus is to minimum wood formation will decrease relatively more by the transition from equation A) to B).

This may also explain why there is relatively less wood formation after June in the strongly suppressed trees with small crowns of scanty foliage (small diameter increment) than in trees with large crowns (large diameter increment).

The Course of Wood Formation in the Roots.

Judging by the sections taken from the roots wood formation in the latter proceeds very irregularly.

It terminates somewhat later than in the stem, often not until the beginning of October, comp. TH. HARTIG (1857, 1863a), GULBE (1888a und b), LODEWICK (1928) and REES (1929).

The Effect of Temperature and Precipitation on the Course of Wood Formation.

The correlation between the course of wood formation and temperature and precipitation is made the object of investigations in the following way:

- a) By a comparison of the growth curves in 1944 and 1945 with mean temperature and precipitation.
- b) By a comparison of the results of these investigations with the result of investigations carried on abroad in countries with a different climate. This comparison is made on the basis of the figures in Tables XIV and XV.

1. Temperature.

If we compare the thick growth curves in Figs. 15—30 with the temperature curve it will appear that wood formation was most active during the warmest periods.

TABLE XVI. The Correlation Coefficients for the Wood Formation and a) the Mean Temperature and b) the Precipitation in the Period from April—July. The Coefficients are Calculated after the Figures in Tables XIV and XV.

Species of Tree	Mean Temperature					Precipitation	
	<i>r</i>	%	F.V.	$\frac{r}{m_r}$	<i>t</i>	<i>r</i>	%
<i>Acer pseudoplatanus</i>	0.96	92	5	7.2	2.6	0.56	31
<i>Fagus sylvatica</i>	0.80	64	12	4.6	2.2	0.25	6
<i>Quercus</i>	0.76	58	8	3.3	2.3	0.39	15
<i>Fraxinus</i>	0.73	53	11	3.5	2.2	0.16	2
<i>Picea abies</i>	0.72	52	12	3.6	2.2	± 0.06	(0)

A correlation calculation on the basis of the figures in Tables XIV and XV shows that in April, May, June and July there is a distinct positive correlation between wood formation and temperature (see Table XIV).

After July the course of wood formation seems chiefly to be autonomously determined.

2. Precipitation.

We get information of the effect of precipitation by examining how wood formation reacts in periods of drought.

July and August 1944 were by the Danish standard both warm and dry. In July the mean temperature was 1.0° , and in Aug. 3.2° over normal (see Table I). August was the warmest month of the year. Normally July is the warmest time.

Precipitation in July was only 34 mm against normally 71 mm, and in August 19 mm only against normally 67 mm (see Table I).

The water content in the ground under close-grown *Fagus silvatica*, *Acer pseudo-platanus*, *Quercus robur*- and *Picea abies*-stands in higherlying areas decreased in the uppermost 20 cms to only 11–14 % of the dry weight. A lower water content is scarcely reached in good forest soils in this country, except in quite exceptional periods of drought.

The *Fagus silvatica* and the *Quercus robur* did not react to this strong drying out of the soil (see Figs. 19 and 23). In the *Quercus robur* wood formation on the contrary reached maximum during the first half of August.

In a number of the *Picea abies* wood formation on the other hand decreased strongly in August (see Fig. 29). The wood that was formed during this month was typical summer wood with thick-walled tracheids of small widths.

When the drought ceased at the end of the month wood formation increased. During a short period wood was formed with proportionally thin-walled tracheids of fairly great widths.

In many of the trees a "false annual ring" appeared as a consequence of this.

The reason why the drought retarded wood formation in *Picea abies*, but not in *Fagus silvatica* and *Quercus robur*, may possibly be sought in the difference in the building of the root system. *Picea abies* has a shallow root and is therefore more sensitive to the drying up of the uppermost layer of the soil than *Fagus silvatica* that has a main root, and *Quercus robur* that has a tap-root. During periods of drought it is easier for these trees to get their supplies of water from the deeper lying layers of the soil than for *Picea abies*.

Fraxinus excelsior grew chiefly along swamp-borders where the soil was more watery. It is difficult on the basis of the curves to determine whether wood formation in this species of tree was retarded owing to lack of water under the drought (comp. Figs. 25 and 26).

In 1945 wood formation was at first relatively livelier in *Fraxinus excelsior* Nos. 6, 7, and 8, that were growing in watery marsh soil than in the other *Fraxinus excelsiors* on the

higher lands (see Fig. 26 and Table X). The reason of this may possibly be sought in a presumably livelier nitrification in the marsh soil during May and June when a vigorous and dense nettle-vegetation grew up here.

The *Betula pendula* and the *Alnus glutinosa* in most cases grew in moist marsh soil and have scarcely suffered from lack of water during the drought. On the contrary it must be supposed that the drought has improved the physical condition of the marsh soil. In both species of trees wood formation was accordingly also particularly lively during most of the drought-period (see Figs. 15 and 17).

According to the figures in Tables XIV and XV there is little positive correlation between wood formation and precipitation during the various summer months (see Table XVI).

Literature gives spare information only about the connection between the course of wood formation and external factors. Most investigators have paid little attention to this question.

MISCHKE (1890) followed wood formation in *Pinus silvestris* and *Picea abies* in a year of pronounced drought (see Table XIV) and found that drought retarded wood formation more in *Pinus silvestris* than in *Picea abies*.

FRIEDRICH (1897, p. 145) found: "... dass die Perioden der grössten oder grösseren Baumzuwachses mit den Perioden der höheren Lufttemperatur, und zwar sowohl hinsichtlich der mittleren als auch der maximalen zusammenfallen".

The investigations were carried out in a rainy area (see Table XIV) and therefore did not give any certain information about the effect of precipitation.

JOST (1892), CHRISTISON (1889), BROWN (1915), LODEWICK (1928) and CHALK (1930) found that wood formation has two annual maximum periods which stand in no relation to external factors.

KORSTIAN (1921) found no correlation between temperature and the course of wood formation in *Acer Negundo* L. and in *Picea pungens* ENGEL.

According to MACDOUGAL (1924) cold storms or short periods of drought may cause wood formation to decrease or terminate.

LODEWICK (1925) found that a decline in temperature may cause decreasing wood formation in *Fraxinus americana* L.

The influence of climatic factors on the width of the annual ring has on the other hand been the subject of many investigations. It would take us too far here to deal in detail with all of them. A survey of the older literature is to be found in ANTEVS (1914—17) and of later literature in KNUCHEL (1933) and ORDING (1940).

The investigations in Central- and Northern Europe chiefly comprise *Pinus silvestris* and *Picea abies*.

The main results may be summed up as follows:

In the colder climate of Sweden and Norway the width of the annual ring is chiefly determined by the summer temperature. The precipitation is on the other hand of inferior importance, cf. HESSELMAN (1904), WALLÉN (1917), KOLMODIN (1923 and 1935), EIDE (1926), AANDSTAD (1934), ERLANDSON (1936) and ORDING (1940—41).

In the warmer climates in Central Europe the width of the annual ring is on the other hand determined chiefly by the quantity of precipitation, cf. HENRY (1894), MER (1895), SCHWARZ (1899), CIESLAR (1907), WIEDEMANN (1925), KNUCHEL and BRÜCKMANN (1930) and KNUCHEL (1933).

Here in Denmark LÜTKEN (1891) found that in Bornholm the basal area increment of *Abies alba* is chiefly determined by the annual amount of precipitation: the mean temperature in April—October.

HOLMSGAARD (1945) has investigated the connection between precipitation and temperature and the variation in the width of the annual ring in *Picea abies* in Gludsted Plantation, where the soil on the whole is meagre. The measurements were carried out on 510 increment cores from 19 stands in the ages from 38—69 years.

He found that precipitation in April—July has a decisive influence upon the width of the annual ring. Of particular importance is the precipitation in May and June.

On the other hand he could not show any certain relation between the temperature and the width of the annual ring.

IX. The Thickening of the Cell Walls.

The thickening of the cell walls, which presumably takes place by apposition, continues later in autumn than wood formation (growth in thickness) by cell division and growth in size.

In well-grown broad leaved trees it ceases about the middle of September, in well-grown coniferous trees at the end of September or the beginning of October (see Fig. 33).

SIGMOND (1935) has made the same observation. He writes i. a. (p. 562): "Die Verstärkung der Spätholzeinheiten dauert bei der Fichte und sehr wahrscheinlich auch bei den übrigen Nadelbäumen unserer Breiten bis in den Herbst hinein an. Auf Grund gewisser Beobachtungen kann man sogar vermuten, dass die Vollendung des Spätholzanteiles erst während

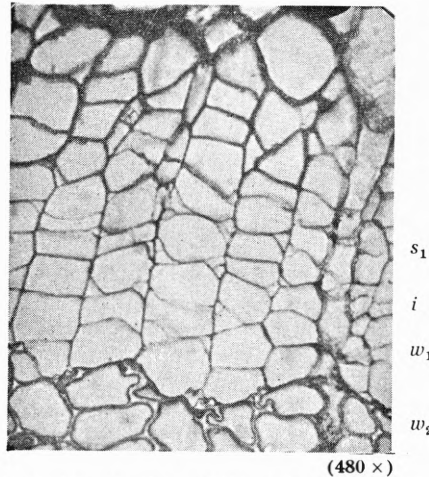


Fig. 33. The cambium of the *Larix decidua* in the middle of September, 1945. Transverse section taken at breast height from *Larix decidua* No. 2 (see Table XII). Cell division had ceased, it was at any rate impossible to prove further wood increment. On the other hand the cell walls of the summer wood cells had not yet ceased growing in thickness.

- s_1 Young, undifferentiated sieve tube cells which presumably next spring will differentiate into spring tissue.
- i The approximate position of the initial cell.
- w_1 Young, undifferentiated wood cells, which presumably next spring will differentiate into spring wood.
- w_2 Summer wood cells whose cell walls have not yet terminated their growth in thickness. Under the preparation the cell walls have shrunk to a certain extent.

des Winters, ja sogar noch im Laufe der darauffolgenden Wuchszeit erfolgt. Demnach bleibt das Kambium noch lange nach Abschluss der Teilungsvorgänge tätig, indem es die zur abschliessenden Verstärkung der letzten Spätholzeinheiten notwendigen Bildungstoffe abgibt. Vereinzelt Fälle deuten sogar darauf hin, dass man Kambium während der Wuchszeit die verfügbaren Baustoffe nicht ausschliesslich für die Bildung des neuen Jahreszuwachses und gelegentliche Speicherung verbraucht, sondern auch zur Vollendung des vorletzten Jahres ringes verwendet".

X. The Change in the Width of the Vessels and Tracheids during the Growth Period.

An attempt has been made at elucidating the above mentioned change numerically and graphically by measurements on a number of sections taken from the stem during the summers of 1944 and 1945 from 1.3 m height.

Methods.

The measurements were carried out in the following way:

All vessels or tracheids within a limited area of the last lignified part of the new annual ring were by means of a Zeiss Zeichenapparat traced on squared paper magnified 80, 120 or 240 times.

The conductive cross section area of the vessels or the tracheids was then calculated by counting how many squares were comprised.

The diameter of the vessels was calculated on the basis of the individual vessels' cross section areas by referring to MAX FRIEDRICH KUNZE: Hilftafeln für Holzmassen-Aufnahmen, 1928.

The period within which the measured sections of the annual ring was formed was approximately determined. The determination was based on curves of the previous course of wood formation. Errors in the determination have scarcely in any case exceeded one week to either side.

Tables and Figures.

The results are collected in Tables XVII and XVIII and appear graphically in Figs. 34, 35, 36, and 37.

The numbers in column 3 in the Tables refer to the trees, from which the sections examined are taken.

The mean annual ring width varied between c. 4 and 5 mm.

The total cross section area of the vessels in columns 8, 9 and 10 has been recorded in per cent of the whole cross section area of the examined core of the annual ring.

TABLE XVII. The Diameter of the Vessels and the Total Conductive Cr. Sec.

1 Tree species	2 Year	3 Tree No.	4 Date	5 6 Vesse	
				Max. mm.	Min. mm.
Ring porous:					
<i>Fraxinus excelsior</i>	1945	1, 2, 3, 4, 5, 6, 7 and 8 (cf. Table X)	May 11—May 20	0.259	0.064
			May 20—June 1	224	24
			June 1—June 8	200	21
			June 16—June 25	106	12
			June 25—July 5	69	12
<i>Quercus robur</i>	—	1, 2, 3, 4, 5, 6 and 7 (cf. Table IX)	May 17—May 25	0.216	0.033
			May 25—June 8	262	33
			June 8—June 20	185	15
			June 20—July 1	62	12
			July 25—Aug. 8	46	12
<i>Ulmus glabra</i>	1944	..	May 2—May 25	0.161	0.032
			May 25—June 7	179	29
			June 25—July 6	121	15
			Aug. 1—Sept. 1	69	9
Diffuse porous:					
<i>Carpinus betulus</i>	1944	..	till June 15	0.081	0.016
<i>Tilia cordata</i>	—	..	after July 15	48	6
			till June 15	0.078	0.009
<i>Prunus avium</i>	—	..	till June 15	46	7
			after July 15	0.073	0.017
<i>Fagus sylvatica</i>	1945	1, 3, 4, 6 and 7 (cf. Table VII)	after July 15	47	6
			May 21—June 1	0.084	0.015
			June 1—June 9	100	15
			June 9—June 24	67	8
			July 13—July 21	50	8
<i>Sorbus aucuparia</i>	1944	..	July 25—Aug. 10	58	8
			till June 15	0.058	0.009
<i>Corylus avellana</i>	—	..	after July 15	36	8
			till June 15	0.097	0.007
<i>Alnus glutinosa</i>	1945	1, 2, 3, 4 and 5 (see Table VI)	after July 15	73	7
			May 21—June 1	0.069	0.009
			June 1—June 8	69	9
			July 10—July 25	82	9
<i>Acer pseudoplatanus</i>	—	1, 2, 3 and 4 (cf. Table VIII)	July 25—Aug. 5	51	7
			May 18—June 14	0.122	0.017
			June 14—July 1	96	17
			July 1—July 8	78	17
			July 20—July 30	78	17
<i>Aesculus hippocastanum</i>	1944	..	July 30—Aug. 8	74	9
			May 21—June 15	0.042	0.017
			June 15—July 5	50	14
<i>Betula pendula</i>	1945	2, 3, 4, 5, 6, 7 and 8 (cf. Table V)	July 15—Aug. 5	32	8
			May 17—June 14	0.105	0.024
			June 25—July 5	97	24
			July 25—Aug. 6	88	16
			Aug. 11—Aug. 29	82	13

Area in Wood Formed within Different Times of the Growth Period.

Diameter	The Total Cr. Sect. Area of the Vessels			11 Percentage relation between the Total Cr. Sect. Area of the Vessels in Summer and Spring Wood %
	7 Mean mm.	8 Max. %	9 Min. %	
0.165 ± 14.2	38	20	30 ± 1.8	
127 ± 18.4	35	10	17 ± 2.7	
72 ± 18.1	23	1	10 ± 2.6	
43 ± 8.6	3	0.5	2 ± 0.4	
38 ± 2.7	2	0.1	0.7 ± 0.2	6
0.161 ± 9.2	38	22	32 ± 2.2	
127 ± 20.0	42	10	23 ± 4.5	
46 ± 8.5	8.5	1.3	3.5 ± 0.9	
26 ± 1.5	3.5	0.3	2 ± 0.4	
26 ± 2.2	3.3	0.7	2 ± 0.4	7
0.127 ± 16.1	24	22	23 ± 0.4	
97 ± 14.6	16	11	15 ± 1.2	
53 ± 12.4	11	6	7 ± 1.9	
23 ± 5.7	8	2	5 ± 1.7	26
0.045 ± 6.0	5.7	2.3	3.8 ± 1.5	
23 ± 2.8	2.0	0.9	1.3 ± 0.5	34
0.036 ± 6.1	22	7	13 ± 1.6	
24 ± 3.3	9	2	5 ± 1.4	38
0.057 ± 7.5	37	24	28 ± 2.4	
26 ± 3.6	17	8	12 ± 3.6	43
0.039 ± 7.9	31	21	26 ± 1.6	
52 ± 7.4	28	15	19 ± 2.7	
46 ± 4.7	21	10	15 ± 1.8	
28 ± 3.8	18	4	11 ± 2.4	
29 ± 2.4	11	8	9 ± 1.1	44
0.034 ± 4.7	25	15	20 ± 1.8	
20 ± 3.2	13	5	9 ± 1.2	45
0.026 ± 3.5	24	9	16 ± 1.9	
21 ± 3.2	12	6	8 ± 0.7	50
0.041 ± 7.1	29	13	20 ± 3.0	
33 ± 6.5	30	14	21 ± 2.5	
37 ± 7.5	18	12	15 ± 1.2	
29 ± 5.1	9	4	7 ± 0.8	54
0.062 ± 9.2	10	5	8 ± 1.1	
54 ± 8.4	7	4	6 ± 0.7	
45 ± 7.1	8	4	6 ± 0.8	
48 ± 7.1	6	3	5 ± 0.2	
43 ± 10.3	5	2	4 ± 0.8	64
0.026 ± 8.3	10	6	8 ± 0.5	
31 ± 3.5	7	5	6 ± 0.6	
18 ± 2.5	8	3	6 ± 0.8	75
0.060 ± 1.6	16	3	8 ± 1.6	
48 ± 1.1	11	6	8 ± 0.7	
47 ± 2.4	11	5	7 ± 1.2	
47 ± 1.8	9	4	6 ± 0.9	81

TABLE XVIII. The Cr. Sect. Area of the Tracheids in Wood

1 Tree species	2 Year	3 Tree No.	4 Date	5 The Cr. Sect. Area: Individual	
				Max. m ²	Min. m ²
<i>Larix decidua</i>	1945	1, 2, 3, and 4	May 18—June 5	0.00212	0.00044
			June 25—July 1	—	—
			July 10—July 20	—	—
			Aug. 1—Aug. 10	—	—
<i>Picea abies</i>	—	1, 2, 3, and 4 and 10	May 17—June 13	0.00176	0.00036
			June 25—July 3	—	—
			July 15—July 23	—	—
			Aug. 1—Aug. 10	—	—
			Aug. 15—Aug. 25	—	—

The Difference between Spring and Summer Wood and the Time of the Inception of Summer Wood.

1. Definition.

According to an arrangement of The International Association of Wood Anatomists (1933) spring wood = Frühholz or Weitholz—is in the future to be called early wood, and summer wood = Spätholz or Engholz is to be called late wood.

The following definition was at the same time given:

Early wood is the loosely built wood with large cells in the first part of the growth ring.

Late wood is the densely built wood with small cells in the later formed part of the growth ring.

WIKSTEN (1944) uses the terms spring and summer wood. He gives the following definition for *Picea abies* and *Pinus silvestris* (see also MORK 1928)¹:

As summer wood must thus be considered that part of the growth ring where twice the common cell wall constantly is equal to or larger than the lumen, while the remainder is considered as spring wood.

In such cases where the relation between the common cell wall and the lumen does not decline to 2.0 the relation between the tangential and the radial cell cross section ($\frac{t}{r}$) must be used which for

$$\left. \begin{array}{l} Picea \text{ (gran)} = 1.12 \\ Pinus \text{ (tall)} = 1.11 \\ \text{species} = 1.10. \end{array} \right\} \text{ or rounded off for both}$$

The part of the annual ring is thus to be considered as summer wood where the relation between the cells' tangential and radial cross section ($\frac{t}{r}$) constantly is equal to or larger than 1.10.

CHALK (1937) considers the small-porous part of the annual ring in the ring porous species as the equivalent of the whole annual ring in the diffuse porous. He writes (p. 326):

“It is suggested that the late or summer wood of ring-porous species is the equivalent of the whole ring in diffuse-porous species, and that the pore-zone represents an additional, highly specialised tissue.

The term early wood should imply early development in relation to the foliage and be limited to softwoods and ring-porous hardwoods”.

¹ The Swedish text is translated into English.

Formed within Various Times during the Growth Period.

7 of the Tracheids	8 The Total Cr. Sect. Area of the Tracheids			11 Percentage Relation between the Total Cr. Sect. Area of Area of the Tracheids in Spring and Summer Wood
	Mean m ²	Max. %	Min. %	
0.00114	71	48	61 ± 5.8	46
37	50	26	37 ± 4.9	
29	40	23	34 ± 3.7	
11	26	14	22 ± 2.7	
0.00088	62	49	57 ± 2.5	34
22	55	22	38 ± 5.2	
16	35	22	30 ± 2.5	
15	38	12	21 ± 4.6	
8	23	10	18 ± 2.3	

For purely practical reasons the old-established term for spring and summer wood in Denmark is retained in this paper even if we agree with O. G. PETERSEN (1920, p. 70) that the term is somewhat misleading.

In cases where it is difficult to distinguish between spring and summer wood such wood as is formed before June 15th is considered as spring wood, while wood formed after July 15th is to be termed summer wood.

The first formed large-porous wood in the ring porous species is considered as spring wood.

2. The Successive Order of the Formation of Summer Wood.

The formation of summer wood begins first in the young branches and later in the stem. It may often be far advanced in the branches at a time, when spring wood is still being formed in the stem, see PRIESTLEY and SCOTT (1936).

3. A Comparison between the Tree Species.

a) HARDWOODS.

According to the difference between the size and total conductive cross section area of the vessels in spring and summer wood in the stem the hardwoods may be ranged in the following succession from typical ring porous to typically diffuse porous trees:

α) *Ring porous.*

Characteristics of the structure of the annual ring: Great difference between spring and summer wood. The vessels in the spring wood are very wide. In cross sections they are conspicuous to the naked eye as small cavities. The vessels in the summer wood are very small and scantily distributed in a tissue of wood fibres and wood parenchyma. The transition between spring and summer wood is abrupt.

Quercus robur and *Fraxinus excelsior* are typically ring porous trees.

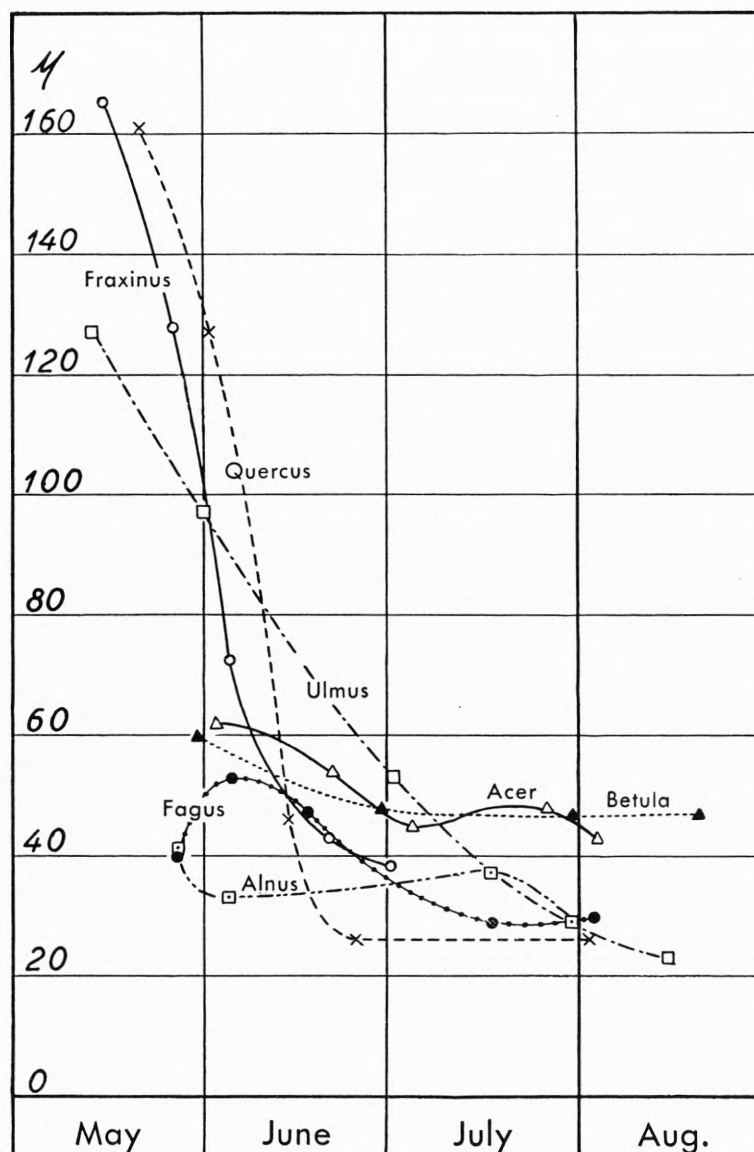


Fig. 34. The mean-diameter of the vessels formed in wood at different times in summer.

The first formed vessels in spring wood are very wide (mean diameter 0.16 mm) and cover scarcely one third of the total cross section area of the spring wood (see Table XVII and Figs. 34 and 35).

The diameter of the vessels and their total conductive cross section area is strongly decreasing till mid-June. About this time the formation of summer wood begins.

The summer wood contains only few and small vessels with a total conductive cross section area of only 2 % of the total cross section area of the summer wood.

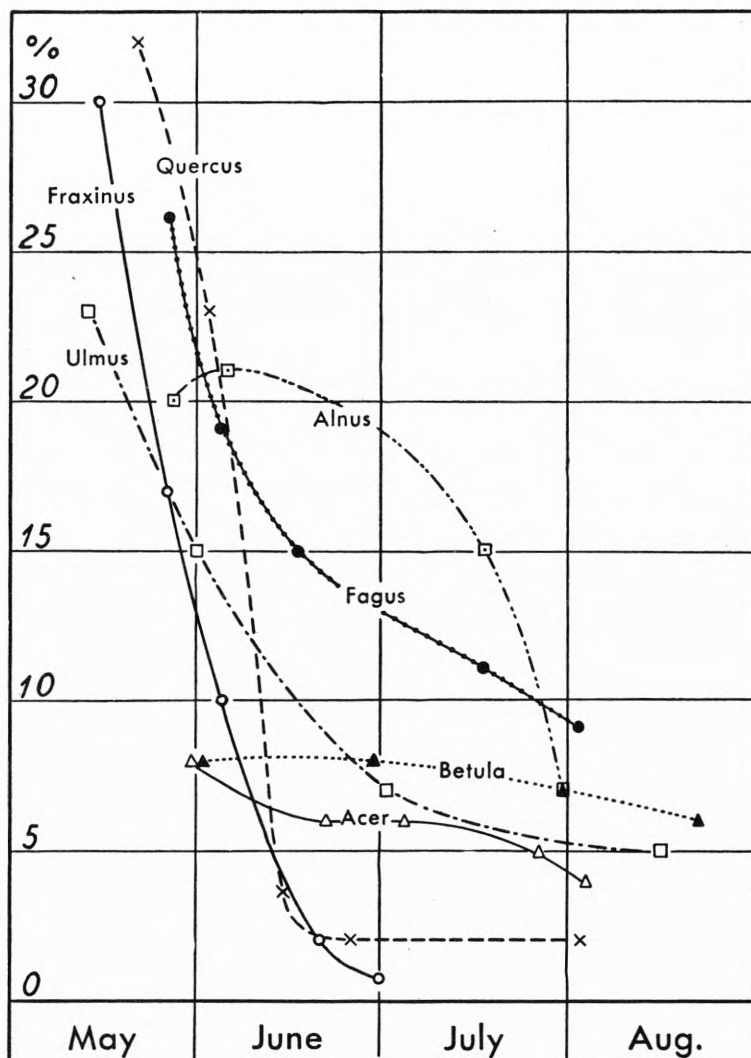


Fig. 35. The total conductive cross section area of the vessels in percentage of the cross section area of the wood formed.

Ulmus glabra is somewhat closer to the diffuse porous types.

It differs from *Quercus robur* and *Fraxinus excelsior* by having smaller spring vessels, by a more even transition from spring to summer wood, and by having more vessels in its summer wood (see Table XVII and Figs. 34 and 35).

β) Diffuse porous.

Characteristics of the structure of the annual ring: Small vessels both in spring and summer wood. Under good growth conditions the transition from spring to summer wood is even.

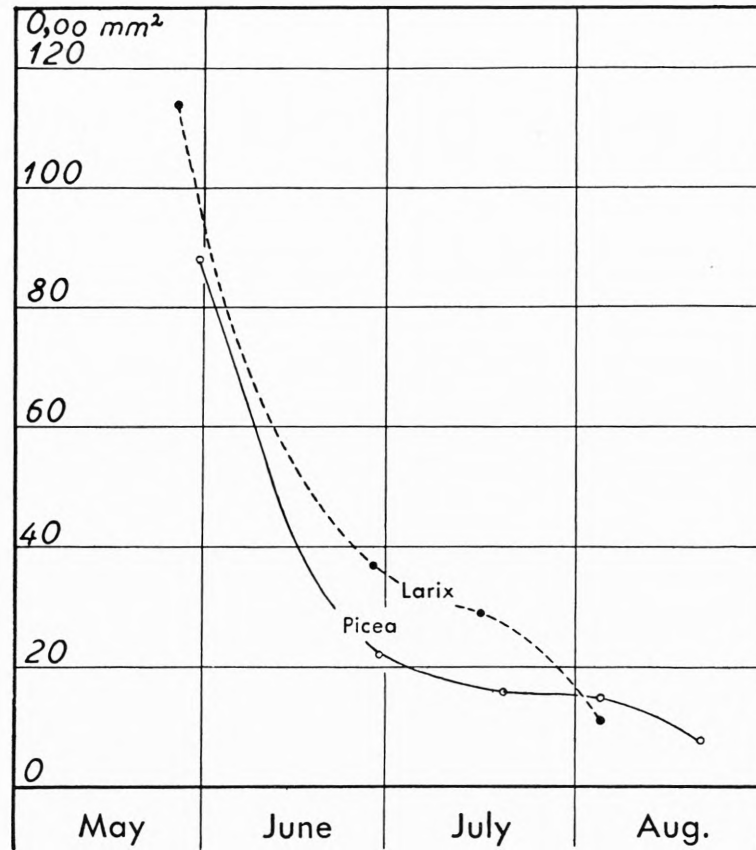


Fig. 36. The mean and cross section area of the individual tracheids in wood formed at different times in the course of summer.

Fagus sylvatica, *Alnus glutinosa*, *Prunus avium*, *Sorbus aucuparia*, *Tilia cordata*, *Corylus avellana* and (*Carpinus betulus*) are those of the diffuse porous types that are closest to the ring porous.

In summer wood there are considerably fewer and smaller vessels than in spring wood. The difference is so conspicuous that in most cases it may easily be seen on cross sections under a good magnifying glass.

In *Prunus avium* and *Fagus sylvatica* the total cross section area of the vessels in spring wood is almost as large as in *Quercus robur* and *Fraxinus excelsior* (see Table XVII and Figs. 34 and 35).

Carpinus betulus has very few vessels in its spring as well as in its summer wood.

In *Fagus sylvatica* the commencement of summer wood formation may averagely be considered to take place from the end of June, in *Alnus glutinosa* from mid-July.

Betula pendula, *Alnus glutinosa* and *Aesculus hippocastanum* are typically diffuse porous trees.

The number and size of the vessels are on the whole alike both in spring and

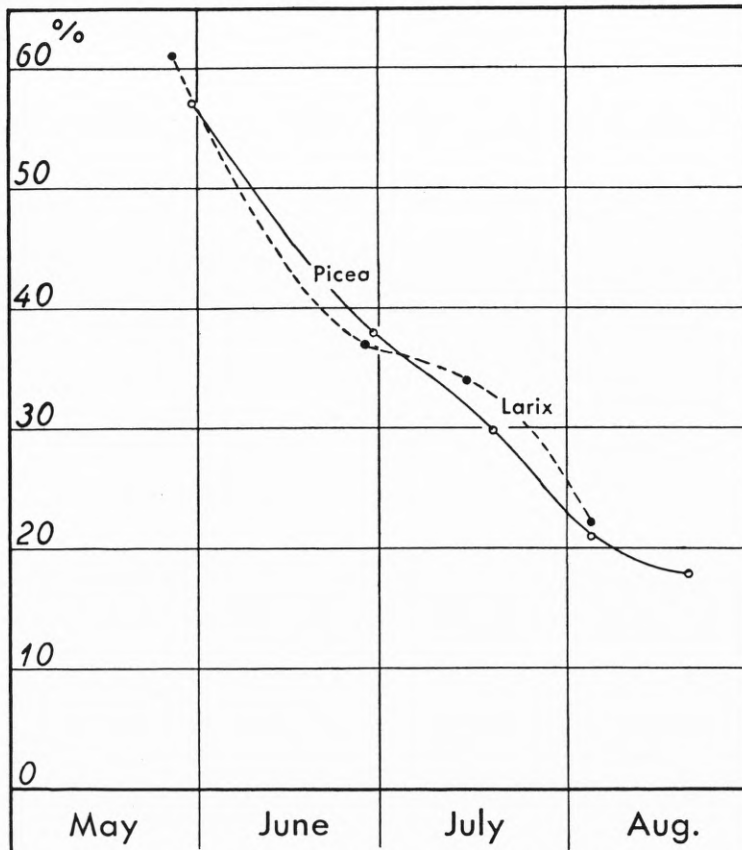


Fig. 37. The total conductive cross section area of the tracheids in percentage of the cross section area of the wood formed.

summer wood (see Table XVII and Figs. 34 and 35). Even under the microscope it may often be difficult to notice any distinct difference between spring and summer wood.

The border of the annual ring is therefore often not sharply outlined.

The number of vessels is relatively small both in spring and summer wood. In spring wood their total conductive cross section area thus makes only 8 % of the total cross section area of the spring wood.

b) CONIFERS.

Characteristics of the structure of the annual ring: Considerable difference between spring and summer wood. The spring-tracheids are thin-walled and have a fairly large volume. The summer-tracheids are thick-walled, somewhat compressed radially, and have a small volume only.

The transition between spring and summer wood is most often even.

Picea abies and *Larix decidua* have almost the same annual ring structure (see Table XVIII and Figs. 36 and 37).

The total conductive cross section area in the spring wood is double as large as that of the ring porous types (comp. Tables XVII and XVIII).

The commencement of summer wood formation may averagely be considered to take place from the beginning of July (see Fig. 36).

Literature gives the following information about the time of the inception of summer wood formation in the different tree species:

Quercus robur: The middle of June (MER 1892c and ANTEVS 1914—17).

The middle of July (PRIESTLEY and SCOTT 1936).

Fraxinus excelsior: The middle of June (LODEWICK 1925, CHALK 1930 and PRIESTLEY 1936).

Picea abies: The middle of August (MER 1892c).

The end of July (WIELER 1898).

Picea rubra L.: The middle of July (REES 1929).

4. The Width of the Annual Ring.

In hardwoods the percentage of summer wood increases with the width of the annual ring, and in the conifers it decreases at the same rate (cf. R. HARTIG (1891) and ANTEVS (1917)).

According to WIKSTEN (1944, p. 457) the width of the transition zone between spring and summer wood in conifers (*Picea abies* and *Pinus silvestris*) increases with the width of the annual ring.

The Cause of the Difference between Spring and Summer Wood.

1. Literature.

Ever since the first half of last century botanists have tried to find the cause of the difference between spring and summer wood.

Literature offers many more or less hypothetic explanations. Some of the most important are the following:

a) DIFFERENCE IN NUTRITION.

SCHACHT (1856) and R. HARTIG (1891) think that the reason is that the cambium is better supplied with food substances at the height of the summer season and late in summer than early in summer, when the temperature still is relatively low and the assimilation has not yet reached full height.

WIELER (1887) and KLEBS (1914) also seek the reason in the difference of the food supply of the cambium. But in contrast to the above mentioned investigators they think that summer wood formation is due to declining food supplies.

ANDRÉ (1920) has shown by experiments that spring wood is only formed when there is an excess of nutrients and the water supply is abundant.

b) BARK TENSION.

KRAUS (1867), SACHS (1868), DE VRIES (1872, 1874, 1875, and 1876) and BURNS (1910) maintain that summer wood formation is due to increasing bark pressure on the wood cylinder, when this in the course of summer increases in circumference owing to wood increment.

KRABBE (1882 and 1884) and WIELER (1885 and 1887) have by experiments shown that this assumption is incorrect.

c) TURGOR.

RUSSOW (1881) seeks the reason of summer wood formation in declining turgor.

d) WATER CONTENT.

LUTZ (1895) thinks that summer wood formation is due to decreasing water content in the bark and the young wood regions.

e) MECHANICAL POINTS OF VIEW.

METZGER (1908) explains the difference between spring and summer wood from purely mechanical points of view.

f) TELEOLOGY

HABERLANDT (1884), STRASBURGER (1891), R. HARTIG (1894) and HOLTERMANN (1907) explain the difference from teleological points of view. The spring wood is wide porous, because the trees at this time of the year, when leaf expansion takes place, require great water supplies. Later in summer when the foliage has hardened and the request for water supply decreases so much and extensive water conductive tissue is no longer necessary. Therefore at this time more thick-walled wood elements are formed to strengthen ". . . die Festigkeit des Stammes" (HABERLANDT 1884, p. 638).

g) HORMONE EFFECT.

COSTER (1927) has in tropical countries made the observation that wood of the spring wood type is only formed as long as foliage is developing. When the leaves are fully expanded summer wood formation begins.

He advances the theory that wood formation is under influence of growth hormones issuing from the foliage. The difference between spring and summer wood he explains in this way, that other hormones are formed in the foliage while it is developing than in the fully developed leaves.

h) VASCULAR CONNECTION.

PRIESTLEY and SCOTT (1936) have undertaken some investigations of summer wood formation in the ring porous types. They found that only the large vessels in

the spring wood stand in direct connection with the leaf traces. The small vessels in summer wood on the other hand issue from the bud scales and the embryonal shoot- and leaf-organs in the new formed buds.

2. A Comparison between the Length of the Shoot Extension Period and the Difference between the Size and Number of the Vessels in Spring and Summer Wood.

When considering the material from the investigations carried on in the first year I come to the result, that the difference between the size and number of the vessels in spring and summer wood may possibly be explained by a corresponding difference between the length of the shoot extension in the individual tree species. To try out the theory I measured the length of the shoot extension period in 1945 in the species of trees mentioned in Table XIX. The measurements were all carried out on trees of good growth, and at 7—14 days interval I measured the elongation growth in respectively,

- a) the three uppermost vigorous top branches,
- b) and the three lowest vigorous lateral branches.

Then the length of the shoot extension period in each species was calculated by taking the mean figure for the duration of the shoot extension in both categories of branches. The results are recorded in Table XIX.

TABLE XIX. The Length of the Shoot Extension Period in 1945.

1	2	3	4		5	6
Tree Species	No. of Trees	Age	Average for		All branches (a + b) 2	days
			Top branches (a) days	Lower branches (b) days		
Hardwoods:						
a) Ring porous						
<i>Quercus robur</i>	7	10—15	35	20		27.5
<i>Fraxinus excelsior</i>	8	7—12	43	20		31.5
<i>Ulmus glabra</i>	6	10—20	45	40		42.5
b) Diffuse porous						
<i>Fagus sylvatica</i>	7	10—15	47	39		43
<i>Sorbus aucuparia</i>	2	c. 15	61	43		52
<i>Prunus avium</i>	1	c. 10	68	—		(60)
<i>Corylus avellana</i>	3	c. 10	68	56		62
<i>Acer pseudoplatanus</i>	9	10—20	77	53		65
<i>Alnus glutinosa</i>	5	10—15	92	48		70
<i>Betula pendula</i>	9	5—12	105	68		86.5
Conifers:						
<i>Picea abies</i>	5	10	70	45		57.5
<i>Larix decidua</i>	5	7	(110)	(70)		(90)

In Table XVII in column 11 is recorded how great the difference is between the total conductive cross section area of the Vessels in spring and summer wood respectively in the said hardwoods. The difference is recorded in per cent.

In Fig. 38 these percentages are given as ordinates, while the length of the shoot extension period (Table XIX, column 6) is given as abscissa.

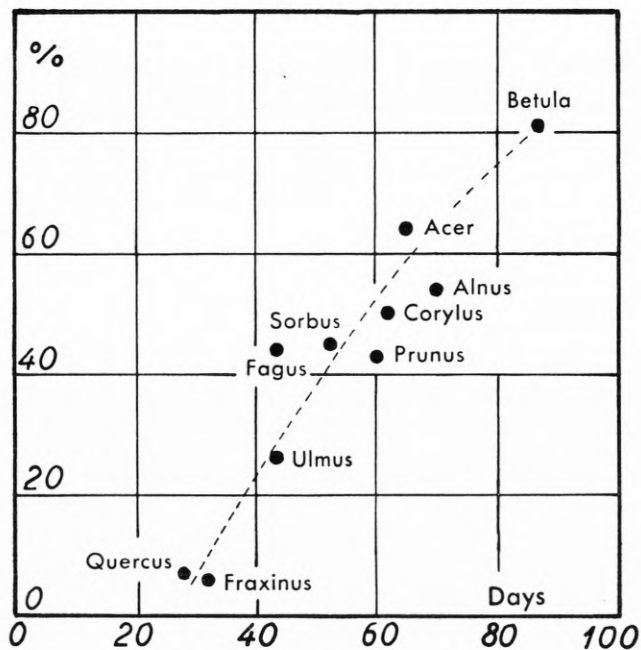


Fig. 38. A comparison between the mean length of the shoot extension period and the percentage relationship between the total conductive cross section area of the vessels in summer and spring wood.

It appears from the figure that there almost exists an inverse proportion between the length of the shoot extension period and the difference between the total conductive cross section area of vessels in spring wood and summer wood.

After this result there is reason to suppose that the size and the distribution of the vessels within the annual ring in the individual broad leaved trees, and thus one of the most essential differences between wood formation in spring and summer wood, is due to a difference in the length of the shoot extension period, comp. COSTER (1927). This explanation is confirmed by the fact that there, so to speak, is no difference between spring and summer wood in tropic tree species with leaves and shoots developing all the year round.

The reason of this connection may presumably be sought in:

- a) The close connection which according to PRIESTLEY and SCOTT (1936) exists between formation of vessels in the leaves and large vessels in the wood.
- b) Relatively larger hormone production during the last part of the summer in

trees with a long shoot- and leaf-developing period than in trees with a short one, cf. pp. 34—36.

c) Presumably it is also of importance how long time passes between the differentiation of the vessels in the young branches and lower down in the stem. A long interval in time (the diffuse porous) must be supposed to cause a more even distribution of vessels than a short interval (the ring porous), comp. the figures in Table XVII, column 11, with the time that passes between the beginning of wood formation at bud base and at breast height (Figs. 7 and 8).

XI. Water Transportation.

On the basis of the figures in Tables XVII and XVIII and HUBER and SCHMIDT'S (1936) figures for the velocity of the water flow some estimates have been made concerning the amount of transportation in *Quercus robur*, *Fraxinus excelsior*, *Fagus silvatica*, *Alnus glutinosa*, *Betula pendula*, *Acer pseudoplatanus*, *Picea abies* and *Larix decidua*.

TABLE XX. Calculation of Water Transportation in the Middle of the Day in the Outermost Annual Ring in a 20 cms Thick Stem, when the Annual Ring is 5 mm Wide (diameter increment = 1 cm).

1 Tree Species	2 Tree No.	3 Mean annual ring width mm.	4 Total con- ductive cross section area %	5 6 7 8 Water Transportation in the Middle of the Day at Breast Height			
				velocity m/hour	per cm ² annual ring cm ² /hour	in the whole outermost annual ring Liter/hour	relative for <i>Quercus robur</i> 100
Ring porous:							
<i>Quercus robur</i>	1, 2, 3, 5 and 7	4.9	8.2	43.6	358	10.74	100
<i>Fraxinus excelsior</i>	1, 2, 3, 6, 7 and 8	5.1	8.8	25.7	226	6.78	64
Diffuse porous:							
<i>Alnus glutinosa</i>	2, 3, 4 and 5	5.0	11.4	2.00	23	0.69	6
<i>Fagus silvatica</i>	1, 3, 4, 6 and 7	5.0	12.6	1.07	14	0.42 ¹	4
<i>Acer pseudoplatanus</i>	1 and 3	4.8	5.4	2.40	13	0.39	4
<i>Betula pendula</i>	3, 5 and 6	4.7	7.2	1.60	12	0.36	3
Conifers:							
<i>Picea abies</i>	3 and 6	5.0	39.4	(0.50)	(20)	(0.64)	(6)
<i>Larix decidua</i>	3 and 4	5.5	47.3	2.1	99	2.97	28

¹ Water transportation in the outermost annual ring in a 120-year-old *Fagus silvatica* quality class 2 is after corresponding calculations 0.66 liters/hour. DETLEV MÜLLER (1943, p. 161) has by other methods approximately estimated it at 0.7 liters/hour.

Water Transportation in the Outermost Annual Ring.

In Table XX is shown a calculation of the water transportation in the middle of the day through the outermost annual ring in a 20 cms thick stem when the annual ring is 5 mm wide.

The figures in column 2 refer to the trees described in Tables V—XIII. They are here selected in such a way, that the mean annual ring width is as close to 5 mm as possible (column 3).

The total conductive cross section area (column 4) is given in per cent of the cross section area of the whole annual ring. It is calculated after curves for the relative course of wood formation (Figs. 16, 18, 20, 22, 24, 26, 28 and 30) and curves for the total conductive cross section area in wood formed within various times of the growth period.

The velocity of flow (column 5) is taken after HUBER and SCHMIDT (1936).

In the ring porous species (*Quercus robur* and *Fraxinus excelsior*) the water transportation in the outermost annual ring is 10 to 30 time larger than in the diffuse porous (*Alnus glutinosa*, *Fagus silvatica*, *Acer pseudoplatanus* and *Betula pendula*).

As the conductive cross section area is approximately the same for both groups taken in sections the difference is chiefly due to the much greater velocity of flow in the ring porous species (column 5).

In *Picea abies* the velocity of flow must be supposed to be very small (see HUBER and SCHMIDT 1936, p. 411). Thanks to the large conductive cross section area the total water transportation in the outermost annual ring is nevertheless just as great as in the best yielding among the diffuse porous.

In *Larix decidua* the velocity of flow is approximately as in the diffuse porous types (*Acer pseudoplatanus* and *Alnus glutinosa*). But on account of the much larger conductive cross section area the water transportation in the outermost annual ring is 5 to 10 times larger.

Total Water Transportation.

In order to be able to calculate the total water transportation we must know how many annual rings are engaged in it.

According to RUMBOLD (1920), PRIESTLEY, SCOTT and MALINS (1933) and HUBER and SCHMIDT (1936) the water transportation in the ring porous species almost exclusively takes place in the outermost annual ring.

In the diffuse porous on the other hand it takes place through several annual rings. As to how many we have only uncertain information. WIELER (1888) states that in branches of *Fagus silvatica* 3.6, and in the stems of *Betula pendula* over 15 annual rings are water conductive. DETLEV MÜLLER (1943) has approximately estimated that in 120-year-old *Fagus silvatica* between 10 and 20 of the outermost annual rings are engaged in water transportation.

In June 1944 I have carried out the following investigations of how many annual rings participate in the water transportation in *Quercus robur*, *Fraxinus excelsior*, *Fagus silvatica*, *Acer pseudoplatanus* and *Betula pendula*.

At a week's interval a tree was felled within each species. The trees were 15 to 20 years old. They were all well-grown, stood in close stands and had medium sized crowns.

The trees were felled at about nine o'clock. They were felled in such a way, that they did not fall to the ground, but remained standing, leaning against neighbouring trees.

Immediately after the felling the trees were placed in containers with water stained with red ink.¹

The weather was each time warm with sunshine and a cloudless sky.

About 6 p.m. the stems were cut and examined.

The following annual rings participated in the water transportation:

Quercus robur and *Fraxinus excelsior* (ring porous):

1. Annual ring (under formation): All vessels.
2. — — : Most of the small and c. $\frac{1}{5}$ of the large vessels.
3. — — : C. one half of the small and a few of the large vessels.
4. — — : A few small vessels.

According to estimates roundly speaking 75 % of the total water transportation take place in the outermost annual ring.

Fagus silvatica, *Acer pseudoplatanus* and *Betula pendula* (diffuse porous):

Almost all vessels in all annual rings (up to 20). But the velocity of the water transportation decreases much inwards. It is 5 to 15 times greater in the outermost than in the innermost annual rings, comp. R. HARTIG (1888a, p. 223) and ANTEVS (1914—17, p. 353).

After measurements and curves water transportation in the outermost annual ring is calculated at:

<i>Fagus silvatica</i>	10.4 %	of the total water transportation
<i>Acer pseudoplatanus</i>	9.1 %	- - - - -
<i>Betula pendula</i>	8.9 %	- - - - -

After these results and the figures in column 7 in Table XX the total water transportation in the middle of the day in a 20 cms thick stem with 5 mm wide annual rings may be estimated at:

Ring porous:

<i>Quercus robur</i>	14.1	liter/hour
<i>Fraxinus excelsior</i>	9.1	—

Diffuse porous:

<i>Fagus silvatica</i>	4.0	—
<i>Acer pseudoplatanus</i>	4.3	—
<i>Betula pendula</i>	4.0	—

¹ First experiments were made with a solution of methyl blue which HUBER and SCHMIDT used (1936) in some of their experiments. The result was not, however, completely satisfactory as the colouring matter was strongly absorbed by the cell walls of the vessels and therefore took comparatively long time to enter the vessels. Diluted red ink rose considerably quicker.

We have too little information about the velocity of the flow at other hours of the day and night to undertake a calculation of the total transpiration during 24 hours.

HUBER and SCHMIDT (1936, Table 5) give some figures for the velocity of the flow in the evening in branches and stem. According to these figures the transpiration flow between 6 and 8 p.m. in a c. 20 cms thick stem with 5 mm wide annual rings may approximately be calculated at:

Ring porous:

<i>Quercus robur</i>	1.1 liter/hour
<i>Fraxinus excelsior</i>	2.2 —

Diffuse porous:

<i>Fagus sylvatica</i>	2.7 —
<i>Acer pseudoplatanus</i>	1.4 —

From the calculations appears that in the middle of the day the transpiration flow is two to three times greater in the ring porous than in the diffuse porous species. In the evening it is on the other hand almost alike within both groups.

This seems to indicate, that the water transportation in the ring porous types shows a greater adaptability towards the much increased transpiration in the middle of the day than in the diffuse porous types. The reason must be sought in the much larger vessels, the strong concentration of the transportation tissue (chiefly the outermost annual ring), and a wide margin in the velocity of flow.

From the point of view of production it presumably means that the ring porous types¹ utilize the warm, sunny hours of the day relatively better than the diffuse porous (the stomata keep open longer?). Possibly it is the reverse in the hours of morning and evening.

XII. Comparisons.

1. Hardwoods.

In Table XXI the above main results are collected in a graphic summary of the anatomic-physiological differences among the hardwoods.

Compared with Figs. 5—8 it appears that the ring porous species differ from the diffuse porous by:

- a) Much wider spring vessels and smaller and fewer summer vessels.
- b) Much higher top yield in water transportation.
- c) 75 % of the total water transportation take place in the outermost annual ring against only 9—10 % in the diffuse porous.

¹ The ring porous are all light trees (see DETLEV MÜLLER 1943, p. 166). After investigations by STÄLFELT (1924) and BOYSEN JENSEN (1932) the light leaves of the light trees may get a considerably higher production capacity by strong light (full daylight) than the leaves of the shade trees.

TABLE XXI. Graphic Summary of the Anatomical

1	2	3	4	5	6
Tree Species	Mean diameter of the vessels in spring wood	Tissue length	Percentage rela- tion between the total conductive cr. sect. area in summer and spring wood	Water Transporta- tion. Highest velo- city the middle of the day at breast height	The water trans- portation in the outermost annual ring in % of the total water trans- portation
	mm.		%	m/hour	%
Ring porous:					
<i>Fraxinus excelsior</i>	0.165	} > 1	6	25.7	} 75
<i>Quercus robur</i>	0.161		7	43.6	
<i>Ulmus glabra</i>	0.127		26	6.0	
Diffuse porous:					
<i>Carpinus betulus</i>	0.045	} < 0.5	34	1.25	—
<i>Tilia cordata</i>	0.036		38	—	—
<i>Prunus avium</i>	0.057		43	—	—
<i>Fagus sylvatica</i>	0.039		44	1.09	10.4
<i>Sorbus aucuparia</i>	0.034		45	—	—
<i>Corylus avellana</i>	0.026		50	—	—
<i>Alnus glutinosa</i>	0.041		54	2.0	—
<i>Acer pseudoplatanus</i>	0.062		64	2.4	9.1
<i>Aesculus hippocastanum</i> ...	0.026		75	0.80	—
<i>Betula pendula</i>	0.060	81	1.6	8.9	

The figures in column 3 are quoted after DETLEV MÜLLER (1943, Table 3).
The dates for leaf expansion in column 7 are quoted after BRUUN (1919).

- d) Averagely later leafing (except in elm).
- e) Shorter interval between bud break and complete leafing.
- f) Shorter shoot extension period (if no repeated shoots are formed).
- g) Much shorter interval between the commencement of wood formation at bud- and stem-base.
- h) More active wood formation in May and June.

TABLE XXII. Graphic Summary of the Anatomical-Physiological

1	2	3	4
Tree Species	Conduction Tissue. The mean cr. sect. area of the tracheids in spring wood	Percentage relation between the total conductive cr. sect. area in summer and spring wood	Water Transportation. The highest velocity in the middle of the day at breast height
	mm ²	%	m/hour
<i>Picea abies</i>	0.00088	34	(0.50)
<i>Larix decidua</i>	0.00114	46	2.1

* Short Shoot.

Physiological Differences among the Hardwoods.

7 Leafing and Shoot Extension			10 Periodicity of Wood Formation				13	14
Mean date of leafing	No. of Days between bud break and complete leafing	Length of shoot extension period Days	No. of Days between beginning of wood formation at bud base and at breast height Days	At breast height wood formation begins the following no. of days		Relative annual ring formation per July 1. %	Force-readiness in winter	
	Days			before bud break Days	after bud break Days			
5/6	18	32	2	8	..	58	} Difficult to force	
29/5	15	28	2	6	..	44		
—	—	43	2	0—3	..	—		
17/5	28	—	9	..	7	—	} Difficult to force	
—	—	—	11	..	6	—		
—	—	(60)	19	..	15	—		
11/5	14	43	16	..	14	40		
—	—	52	16	..	11	—		
—	..	62	27	..	26	—		
16/5	25	70	35	..	35	47	} Comparatively easy to force	
12/5	24	65	29	..	23	38		
9/5	—	—	27	..	22	—		
13/5	24	87	32	..	31	40		

The growth periodicity of the ring porous types seems to be more autonomously determined and the growth to have a more marked optimum than in the diffuse porous types.

In the typically ring porous types (*Quercus robur* and *Fraxinus excelsior*) the buds, irrespective of temperature, do not begin to move till May. But then things also happen in quick succession. Leafing proceeds quickly, shoot extension terminates in the course of relatively short time, and in branches as well as in stem comparatively much wood is formed in May and June.

Differences between *Picea abies* and *Larix decidua*.

5	6 Periodicity of Wood Formation		7	8	9
Length of the shoot extension period Days	No. Days between inception of wood formation at bud base and at breast height Days		At breast height wood formation begins the following no. of days		Relative annual ring formation per July 1 %
			before bud break Days	after bud break Days	
58	8		5	..	50
(90)	6		..	36*	50

Outside the growing period the ring porous (*Quercus robur* and *Fraxinus excelsior*) are very difficult to force, cf. LAKON (1912) and KÜHN (1916).

The diffuse porous types are more sensitive towards the increase in temperature in spring. If the latter is mild the buds begin to swell already in March. But it takes a long time before the growth really increases. Leafing, shoot extension, and wood formation begin at a slow rate. Wood formation takes a long time before it spreads in basipetal direction. In the stem between one third and one half of the annual ring only is formed in May and June

Outside the growth period the typical diffuse porous (*Acer pseudoplatanus*, *Aesculus hippocastanum* and *Betula pendula*) are comparatively easy to force.

Among the diffuse porous *Carpinus betulus*, *Tilia cordata*, *Prunus avium* and *Fagus silvatica* are nearest the ring porous. Particularly *Fagus silvatica* has a few qualities in common with them. Its growth periodicity thus seems to be autonomously determined. It develops fairly late in spring. Its shoot extension period is relatively short. Outside the growth period it is very difficult to force, cf. JOHANNSEN (1906), HOWARD (1906), MOLISH (1908 and 1909), WEBER (1911), LAKON (1912), and KÜHN (1916).

There is some reason with DETLEV MÜLLER (1943, p. 165) to believe that the diffuse porous types phylogenetically are older than the ring porous ones. "Ring porous condition is a higher development and more specialised."

In the anatomy and physiology of the ring and diffuse porous types a certain adaptation may be traced to the climatic conditions under which the trees have their greatest distribution.

The ring porous species chiefly grow within the area of summer green forests of hardwoods¹ (see DENGLER (1930, Table I)). In the warmest part of this area (*Castanetum*) they are conspicuous: *Castanea*, *Quercus*, *Carya*, *Morus*, *Robinia* and *Ailanthus*. With HUBER and SCHMIDT (1936, p. 404) they may be considered as outposts in the warm and relatively dry border areas towards the steppes where on account of their greater top yield in water transportation it is easier for them to grow than the diffuse porous.

To the North and in direction from the marked continental towards the Atlantic climate the ring porous decrease in species and in dominance. At the same time the diffuse porous species spread and particularly those which are nearest the ring porous types. In the intermediate and northern parts of the area of the summer green forests of hardwoods (*Fagetum*) the beech (*Fagus*) and the oak (*Quercus*) are dominant with an intermixture of *Fraxinus*, *Ulmus*, *Tilia*, *Carpinus*, *Acer*, and *Alnus*.

In the northernmost and coldest part of the area the ring porous are less conspicuous.

Within the area of conifers in the cold climates only diffuse porous trees are on the whole to be found. At the polar forest border there are of hardwoods only *Populus tremula*, *Salix* and *Betula pendula* (typically diffuse porous species).

¹ In the tropical countries there are almost no ring porous trees, cf. FORSAITH (1926, pp. 83—84).

On the whole the number of ring porous species is only small. CHALK (1937, p. 325) mentions that out of 1700 genera collected in Imperial Forestry Institute less than 3 % have species with ring porous wood.

2. Conifers.

In Table XXII a graphic summary is made of the most important anatomical-physiological differences between *Picea abies* and *Larix decidua*.

Physiologically they are nearest the diffuse porous species. They both show adaptation to a relatively cold and moist climate, which fact is confirmed through their distribution.

XIII. Summary.

1. During the resting stage in winter the cell walls of the cambium generally appear sharply and distinctly outlined under the microscope. In transverse sections the cell form is most often markedly rectangular.

2. When temperature rises in March or April the appearance of the cambium changes. The walls of the cells become semi-transparent and the protoplasm proceeds from a gel- to a sol-like condition. At the same time the radial cell walls begin to extend (size increment) and the cambial ring increases in width.

3. The change (the preliminary change of the cambium) begins at bud base and from here spreads in basipetal direction. In *Picea sitchensis* and *Pseudotsuga taxifolia* it starts at a mean temperature of 4° to 5° C. In *Pinus silvestris*, *Larix decidua*, *Picea abies*, *Betula pendula*, *Alnus glutinosa*, *Corylus avellana*, *Carpinus betulus*, *Ulmus glabra*, *Tilia cordata*, *Aesculus hippocastanum*, *Acer pseudoplatanus*, *Prunus avium* and *Sorbus aucuparia* it starts after a few warm spring days at the end of March or the beginning of April with a maximum temperature over 12° C. In *Fagus sylvatica*, *Quercus robur* and *Fraxinus excelsior* the change in the cambium does not set in till the last half of April. In the latter species the time seems to be more autonomously determined than in the former.

4. When the cambium is in the preliminary change it is sensitive to frost.

5. One to four weeks after the change has started in the cambium cell division begins. It starts at bud base and from here spreads in basipetal direction.

6. In the ring porous species cell division begins at bud base one to nine days before bud break. In the diffuse porous species with considerable shoot extension before bud break (*Sorbus aucuparia*, *Acer pseudoplatanus*, *Aesculus hippocastanum* and *Prunus avium*) it starts up to a week before bud break; in the other diffuse porous at the earliest two days before bud break.

In conifers it begins five to fifteen days before bud break.

7. Cell division spreads quicker in basipetal direction in the ring porous species than in the diffuse porous and the conifers.

In the ring porous and the evergreen conifers cell division begins in the lower part of the trunk some days before or at the latest simultaneously with bud break. In the diffuse porous and *Larix decidua*, on the other hand, it does not begin till after the leaves (the short shoots in *Larix decidua*) are completely or partly expanded.

8. In the roots cell division only takes place when the temperature of the soil has reached up between 10° to 13° C.

9. The elongation growth of the roots precedes their growth in thickness.

10. The reason that cambial activity begins at bud base and from there spreads in basipetal direction is that growth hormones are formed in the buds of the trees when they begin to swell in spring. From the buds (and inflorescence) the growth hormones proceed down through the branch-, stem- and root-cambium and stimulate it to a resumption of growth.

11. There is reason to assume that the change in the cambium before its preliminary change is due to a beginning downward progress of growth hormones from the swelling buds.

12. In the young branches the main part of the annual ring is formed within the period when the liveliest shoot extension takes place.

13. The length of the wood formation period increases gradually from the young branches and down into the stem, and a relatively greater part of the annual ring is formed later in summer.

14. There is a difference in the course of the wood formation in the stems of the various species of trees. They may be divided into three groups:

Fraxinus excelsior: Wood formation is lively from the very start. About one half of the annual ring are formed in May and June. After July there is only slight wood formation.

Picea abies and *Larix decidua*: Wood formation is lively from the start as in *Fraxinus excelsior*. About half of the annual ring is formed in May and June. After July wood formation is not particularly active.

Betula pendula, *Fagus silvatica*, *Alnus glutinosa*, *Acer pseudoplatanus* and (*Quercus robur*): Some time often elapses before wood formation actually becomes active. Only between one third and one half of the annual ring is formed in May and June. On the other hand wood formation is very lively in August. Between one third and one fourth of the annual ring is formed in this month and during the first days of September.

15. The less the trees grow in thickness the earlier in summer wood formation declines. The reason may be sought in external as well as in internal nutrition-physiological conditions.

16. In well-grown trees wood formation in the stem terminates in the last half of August or the beginning of September.

17. In the roots wood formation often continues into October.

18. In April, May, June, and July there is a distinct positive correlation between wood formation and temperature.

19. Only in *Picea abies* can it be proved with certainty that protracted drought retards wood formation.

20. The growth in thickness (apposition) of the cell walls terminates two to four weeks later than the cell division.

21. In the ring porous species (*Quercus robur*, *Fraxinus excelsior*, and *Ulmus*

glabra) summer wood formation begins about mid-June, in beech at the end of June, in *Alnus glutinosa* about mid-July, and in *Picea abies* and *Larix decidua* about the beginning of July.

22. The diameter of the spring vessels is approximately three times larger in the ring porous than in the diffuse porous species.

23. The total conductive cross section area for spring and summer wood in sections is averagely about equally large in the ring porous and the diffuse porous species. In conifers it is four to nine times greater than in hardwoods.

24. There exists an almost inverse proportionality between the length of the shoot extension period and the difference between the total conductive cross section area of the vessels in spring and summer wood.

The difference between the distribution of the vessels within the annual ring, and thus the difference between spring and summer wood in hardwoods, may therefore partly be referred to a difference in the length of the period of the shoot- and leaf-expansion.

25. In the ring porous species (*Quercus robur* and *Fraxinus excelsior*) the water transportation in the outermost annual ring is in the middle of the day ten to thirty times greater than in the diffuse porous species (*Alnus glutinosa*, *Fagus sylvatica*, *Acer pseudoplatanus* and *Betula pendula*).

26. The difference is due to the much greater velocity of flow in the ring porous species.

27. In *Picea abies* the water transportation in the outermost annual ring is in the middle of the day almost of the same size as in the diffuse porous species. In *Larix decidua* it is five to ten times greater.

28. In the ring porous species (*Quercus robur* and *Fraxinus excelsior*) the whole water transportation takes place in the four outermost annual rings. 75 % of the total water transportation, however, take place in the outermost annual ring.

29. In the diffuse porous species (*Fagus sylvatica*, *Acer pseudoplatanus*, and *Betula pendula*) the water transportation takes place through many annual rings (over twenty). But the velocity of the flow is five to fifteen times greater in the outermost than in the innermost annual rings. Approximately 10 % of the total water transportation take place in the outermost annual ring.

30. In the middle of the day the total transpiration flow is two to three times greater in the ring porous than in the diffuse porous trees. In evening and morning it is on the other hand alike within the two groups.

From the view of production this presumably means that the ring porous utilize the warm and sunny hours about noon relatively better than the diffuse porous. In the hours of the morning and evening the case is probably reversed.

31. In the anatomy and physiology of the ring and diffuse porous species a certain adaptation may be traced to the climatic conditions under which the trees have their greatest distribution.

The ring porous have their chief distribution within the area of the summer-green hardwood forests. In the warm and dry regions of the latter they dominate

as they thrive better here than the diffuse porous owing to the higher top yield in the water transportation.

Towards the North and in direction from the Continental towards the Atlantic climate the ring porous decrease in species and dominance, and simultaneously the diffuse porous gain ground, in the first line those that are nearest to the ring porous types. Within the area of conifers in cold climates there are so to speak diffuse porous trees only.

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