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The anatomical structure of the common fir (*Abies alba* Mill.) bark

II. Quantitative changes in bark tissues within the stem

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Abstract:

The regularities of the process of secondary sclerification of secondary phloem were investigated. A correlation was found between the number of sclereid layers and the age of the tree. A new sclereid layer forms within the secondary phloem on the average every 4–8 years. The process of formation of the successive layers is not uniform in its course. The differences concern mainly the structure of the successive sclereid layers and the duration of the process of their filling.

INTRODUCTION

The investigation of the quantitative changes in bark tissues, within the stem is a continuation of the studies on bark development which have been reported in the first part of this work (Golinowski 1971). The chief aim of these investigations was to establish the regularities of the process of secondary sclerification of secondary phloem. Studies on development established that: 1) the first layer of sclereids starts to form in a 3-year shoot; 2) the process of formation of this layer lasts 4–6 years; 3) the second sclereids layer begins to form in the 8-year-old shoot, 4) in 10-year shoots two layers of sclereids are found, 5) the 15-year shoot exhibits 3 layers and 6) the 20-year shoot — 4 layers of sclereids.

These data lead to the following hypothesis: if there exists a rhythmicity in the formation of the successive sclereid layers (as seems to be indicated by the above named results), there also should exist a close correlation between the number of sclereid layers and the age of the tree. In order to verify this hypothesis, the variability of the bark tissues within the stem at various ages (16, 30, 52, 63, 83 and 115 years) was analysed. A method was developed for measurement of the thickness of the layers of particular bark tissues and a method for graphic presentation of the results (diagrams 1–11).

MATERIAL AND METHODS

Investigation of the quantitative variability of the bark tissues within the stem was carried out on six trees from the section 101c, in the Forest District Kąśna Górna. Characteristic of the sample trees:

tree no. 1 —	age 16 yrs,	height 2.3 m,	Diagram 1	
,, ,, 2 —	,, 30 ,,	,, 7.2	Diagrams	2 and 3
,, ,, 3 —	,, 52 ,,	,, 20	,,	4 and 5
,, ,, 4 —	,, 63 ,,	,, 24	,,	6 and 7
,, ,, 5 —	,, 83 ,,	,, 30.2	,,	8 and 9
,, ,, 6 —	,, 115 ,,	,, 29	,,	10 and 11.

The quantitative studies were started on tree no. 5 in 1966. Material was collected in 1965 as follows. Before cutting down the tree, the northern side of the stem was marked. After felling stem segments were taken at 2-m intervals. On each segment four radii were measured, and of each of them the bark thickness (N, S, E and W), then the number of annual rings was counted. From the segments, 5 × 5 × 10-cm samples from all four sides were taken. The material was fixed in 80 per cent ethyl alcohol.

Cross sections of bark tissues 30–80 μ thick with adjacent fragments of secondary xylem were prepared with the use of a Reichert microtome. Glycerin slides were then prepared and negative pictures of them 8 times enlarged were taken in a "Krokus" enlarger. The negative pictures were found to give a very good differentiation of the zone of secondary phloem undergoing sclerification, and the phloem layer which does not undergo this process. The pictures also allow precise delimitation of other bark tissues. The sclereids forming tangential layers within secondary phloem are light in colour in contrast to the phloem tissues not undergoing sclerification. The layers of sclereids and other tissues were transposed onto tracing paper and their width was measured. On the basis of the results obtained a method of graphic analysis of the thickness of the bark tissues within the stem was developed (diagrams 1–11).

For each side a diagram was plotted. The successive tree heights at which segments were taken were laid off on the axis of ordinates in a 1:50 scale (trees nos 1 and 2) and in a 1:100 scale (trees nos 3–6). On the axis of abscissae the thickness of the bark tissue layers distinguished on the negative photographs was cut off in a 8:1 scale. The ordinate axis demarcates schematically the border between xylem and cambium. The axis of abscissae gives the characteristic of the bark tissues at the successive investigated levels of the stem. The rectangles with diagonals denote secondary phloem layers undergoing sclerification. The space between the ordinate axis and the first sclereid layers is occupied by secondary cambium, vascular bundles and fragments of crushed and torn nonconducting phloem. There are zones of secondary phloem between the sclereid layers, which do not undergo sclerification. The hatched area running in the perpendicular plane denotes the peridermis together witht the desquamating cork. The distance between the last sclereid layer and the periderm indicates the width of the zone occupied by the primary cortex tissues.

Samples from the remaining trees were taken in October 1967 from the same stand as tree no 5. The following changes were introduced in material collection: from trees nos 1 and 2, segments were taken at 0.5-m distances, whereas from trees nos. 3, 4 and 6 they were spaced by 1 m. On each segment the width of the particular annual rings in the four quadrants was additionally precisely measured in order to obtain an accurate characteristic of the increment in thickness of the stem on the analysed sections. The annual ring increments are shown in graphs representing a longitudinal section of the stem, where on the axis of ordinates the heights at which the particular segments were taken are laid off in a 1:50 scale (trees nos 1 and 2) and in a 1:100 scale (trees nos 3–6), the axis of abscissae shows the width of the successive annual rings in a 1:5 scale.

The diagrams of annual rings on the N-S and E-W axes are placed next to one another so that the vertical axis of ordinates represents schematically the morphological axis of the stem. On the right from this line, the sum of annual rings is laid off in the S and W directions, whereas, on the left side the sum of annual rings in N and E direction is marked. Then the annual increments for 5 years were joined in vertical plane to give a scheme of the course of the given xylem increments on the longitudinal axis of the stem. The diagrams thus obtained are not symmetrical and owing to this they show the differences in the course of growth in various directions.

The corresponding diagrams of the longitudinal stem section and analyses of the bark tissues are placed next to one another with a common height scale. On each diagram the annual increment of the stem is given in the middle and on both sides two diagrams representing the bark. Thus, the graphically presented results of measurements make possible the comparison of the size and course of the annual xylem growth, giving at the same time a characteristic in detail of the adjacent bark tissues in which among other things the width of the sclereid layers and their distribution within the stem were taken into account. The diagrams are about three times reduced.

RESULTS

The numerical results are listed in the following tables and supplemented by information concerning the process of sclerification.

Abbreviations used in Tables 1–6: *Sc* – sclereid, *ScL* – sclereid layer, *SPh* – secondary phloem, *PC* – primary cortex, *RS* – resin space, *RC* – resin canal

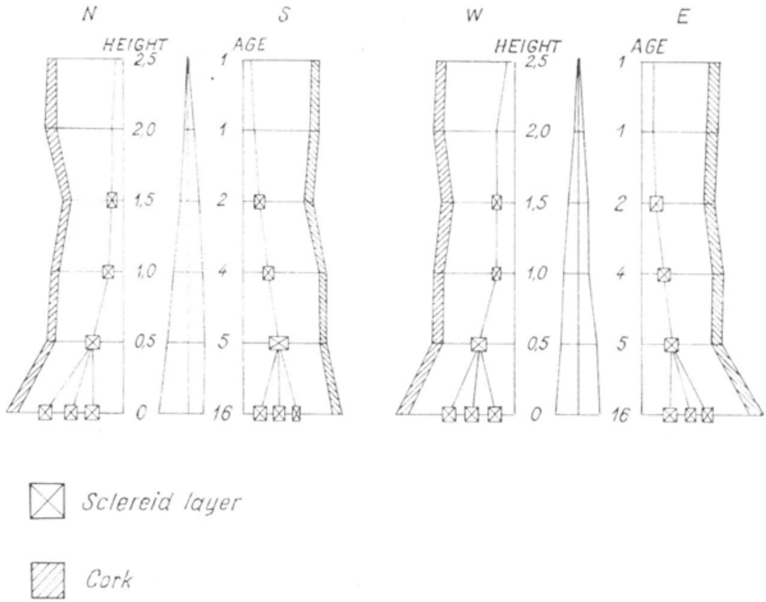


Fig. 1. Diagram of stem and bark tissues of 16-year-old fir (*Abies alba* Mill). Height scale ca 1:100, Stem thickness scale ca 1:10. Bark thickness scale ca 4:1

Table 1

Tree no. 1, age 16 years, height 2.3 m (diagram 1)

Height, m	Age of cross section, years	No. of sclereid layers	Directions in which sclereids are most numerous		Dimensions of resin canals on cross section	Remarks
			SPh	*PC*		
1.5	2	—	S	S	0.2×0.08	On the border between *SPh* and *PC* parenchyma small groups of *Sc* sporadically occur
1	4	1	S, E	S	0.3×0.1	Continuous *ScL*, intensive division in *PC*
0.5	5	1	S	S	0.6×0.1	On S side under *ScL* large groups of *Sc* are formed within the 4th annual ring of *SPh*
0	16	3	N	N, W	0.4×0.1	Inner *Sc* discontinuous. In *SPh* numerous *RS*

Within the tree investigated two zones were distinguished:

1) zone of root neck. Sclereid layers frequently coalesce, this indicating progressing sclerification processes in tissue between sclereid layers. In secondary phloem numerous resin spaces. In tissues

between cambial zone and 3rd sclereid layer there are wide intracellular spaces. Within primary cortex thin layers of rhytidome. Outer cork cell layers desquamate;

2) zone of stem. Progressing processes of 1st and 2nd sclereid formation. In primary cortex tissues intensive parenchymal cell divisions. Under periderm single groups of sclereids.

Table 2

Tree no. 2, age 30 years, height 7,2 m.
(diagrams 2, 3, plate I)

Height, m	Age of cross section, years	No. of sclereid layers	Directions in which sclereids are most numerous		Dimensions of resin canals on cross section	Remarks
			SPh	*PC*		
5	3	—	N, W	E, W	0.4×0.1	At border of *SPh* and *PC* single groups of *Sc*
4.5	4	1	E, W	W	0.4×0.1	*Sc* form within 1st and 2nd ring of *SPh*
4	4	1	S ,W	E	0.5×0.1	In early phloem formed in 3rd year numerous intercellular spaces form
3.5	5	1	E, W	E, W	0.4×0.1	On S side *ScL* discontinuous
3	6	1	W, S	W	0.6×0.15	*ScL* spreads and sometimes intrudes on 3rd ring of *SPh*
2.5	8	2	N, S	N, W	0.5×0.1	2nd *ScL* discontinuous, it forms in 5th ring of *SPh*
2	9	2	N, S	S	0.75×0.2	On E side large *RC*. Under enlarged canals outer *ScL* undergoes enzymatic breakdown
1.5	11	2	S	S	0.6×0.16	2nd *ScL* within rings of *SPh* formed in 5, 6 and 7th year
1	14	3	N, S	S, W	0.66×0.16	3rd *ScL* formed in 11th ring of *SPh*
0.5	16	3	N	N	0.6×0.1	On all sides well filled *ScL*
0	30	6	S, E	S, E	1.2×0.25	In *SPh* numerous *RS*, on S side rhytido-me

Analysis of the structure and distribution of the bark tissues within the stem allowed to distinguich three zones:

1) zone of rhytidome (up to 0.5 m). Shallow cracks in the bark. The bark tissues undergo sclerification. Thin layers of rhytidome separate. Secondary processes of sclerification of the tissues between the sclereid layers. In the secondary phloem numerous resin spaces;

2) zone of secondary phloem sclerification (0.5—5 m). Bark smooth. Sporadical desquamating cork cell layers. Outer sclereid layer continuous. Primary cortex tissues undergo sclerification;

3) zone of intensive parenchymal cell divisions 4—7 m. Second and third zone are not distinctly delimited.

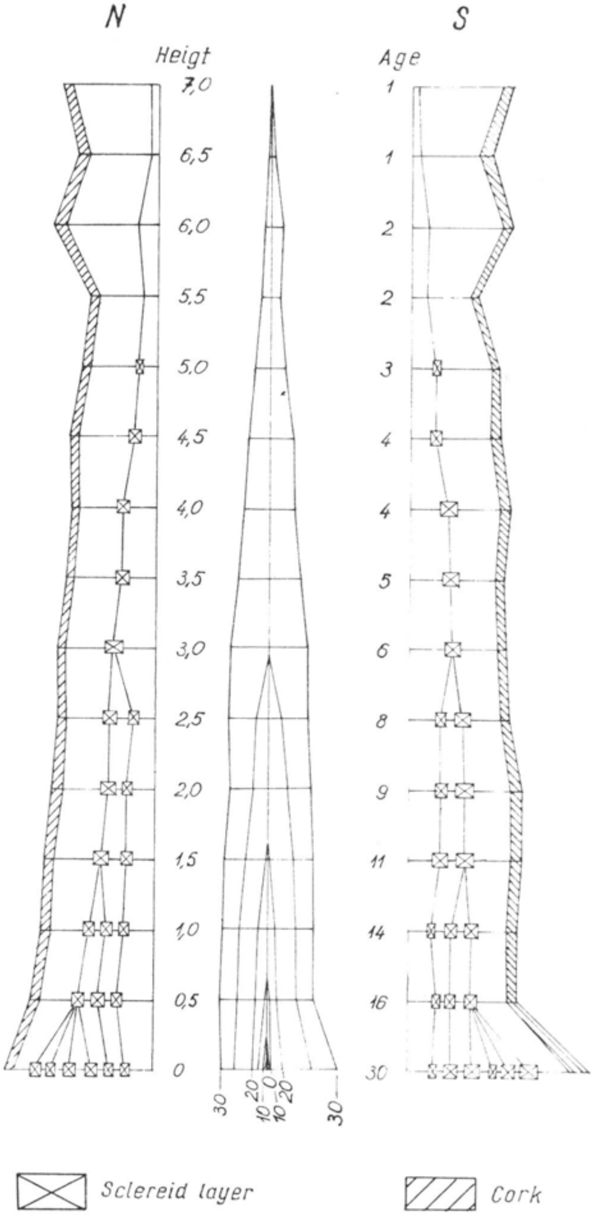


Fig. 2. Diagram of stem and bark tissues of 30-year-old fir (on N and S sides). Scale as in fig. 1

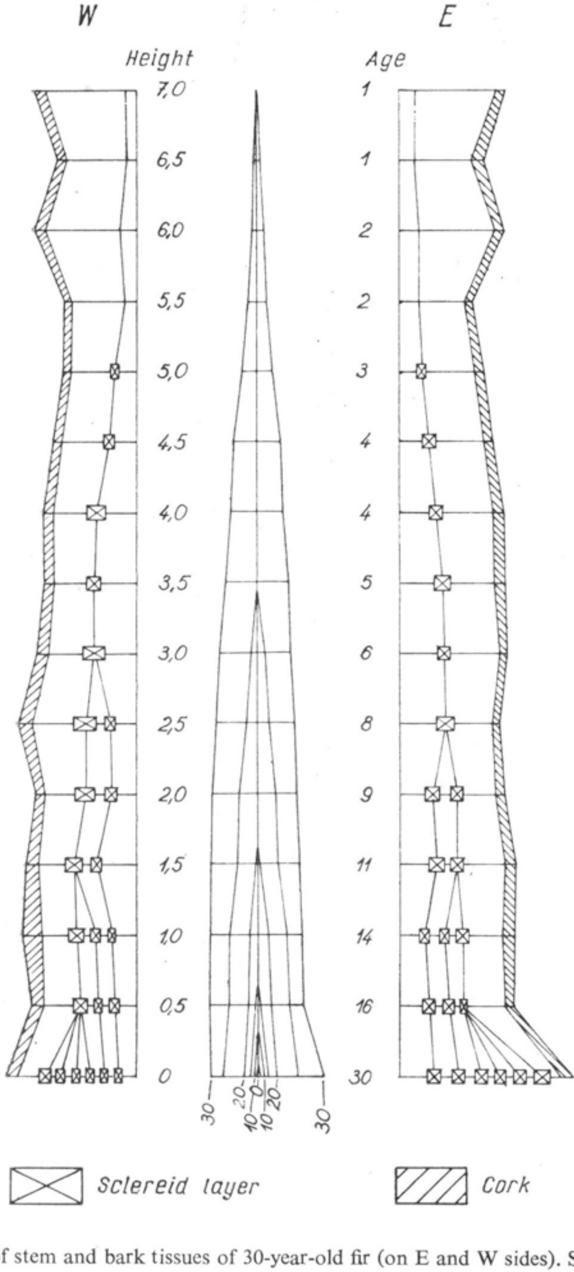


Fig. 3. Diagram of stem and bark tissues of 30-year-old fir (on E and W sides). Scales as in fig. 1

Table 3

Tree no. 3, age 52 years, height 20 m (diagrams 4, 5, plate II)

Height, m	Age of cross section, years	No of sclereid layers	Directions in which sclereids are most numerous		Dimensions of resin canals on cross section	Remarks
			SPh	*PC*		
1	2	3	4	5	6	7
19	3	1	N	—	0.32×0.1	On border of *SPh* and *PC* single groups of *Sc*
18	6	1	N, S	S	0.5×0.1	On all sides continuous *ScL*. On S side thin rhytidome layer
17	10	2	E	E	0.8×0.16	2nd *ScL* discontinuous. On E side sporadic *Sc* groups in 8th ring of *SPh*
16	13	3	E	E	0.86×0.15	3rd *ScL* forms within 9th and 10th *SPh* annual ring. On E side in 3rd *ScL* numerous *RS*
15	15	3	E, S	S	0.8×0.1	First *ScL* continuous on all sides. Filling of 2nd and 3rd *ScL* advances. In *PC* numerous *RS*, particularly on S side
14	16	3	S, E	S, E	0.9×0.2	In E drirection numerous *RS* between *Sc* groups of 2nd layer. Intensively advancing process of filling of this layer
13	17	4	E, N	E, N	1.5×0.4	Formation of 4th *ScL* is most advanced on E and N sides. On E side *RC* 3.2×0.9 mm. Under canal complete disappearance of 1st *ScL*
12	19	4	N. S	S, W	1.1×0.3	On N and S sides well developed 4th *ScL*. Owing to crushing and secondary sclerification in many places the two outer *ScL* are coalesced. On E side *RS* 3×0.7 mm
11	20	4	N, S	S, W	1×0.3	On W and N sides numerous *RS* in 17th and 18th ring of *SPh*. On W side rhytidome involving outer *PC* layers
10	22	5	N, S	S	1.4×0.3	On N and S sides well developed 5th *ScL*. On N side *RC* 3.1×1 mm occupies space between periderm and outer *ScL*
9	25	5	E, W	W	1.1×0.3	On all sides distinct *ScL*. 4th *ScL* continuous, 5th best filled on E side. On N side *RC* 2.8×1 mm
8	26	5	S. W	S	0.8×0.2	On E and W sides numerous *RS* in 22nd and 23rd *SPh* ring. On N and E side large outer *ScL* coalesced

(c.d. ɿabl. 3)

1	2	3	4	5	6	7
7	28	5	E, W	E	0.8×0.2	On all sides numerous *RS* in 25th and 26th *SPh* ring. Two last formed *ScL* discontinuous
6	29	6	E, N	N	1×0.3	In 25 and 26th *SPh* ring 6th *ScL* is forming. In this layer between *Sc* groups numerous *RS*
5	30	6	N, S	N	1.3×0.3	On S side numerous small groups of *Sc* in tissues between 4th and 6th *ScL*
4	34	7	N	N	1×0.2	The two newly formed *ScL* are discontinuous. On N and E sides in 33 and 34th *SPh* ring numerous *RS*
3	35	7	N	N	3.1×0.6	In 7th *ScL* numerous *RS*
2	38	8	N	N	1.4×0.2	In many places outer *ScL* are coalesced. On S side sporadic *RS* in 36 and 37th *SPh* ring
1	43	9	N	N	2.1×0.4	In 7, 8 and 9th *ScL* *RS*, particularly on W side
0	52	10	N, E	E	5×1.6	On N, S and W sides in entire *SPh* numerous *RS*. Sclerification of tissues between *ScL* progresses

In 52-year-old tree three zones could be distinguished within the bark:

1) zone of rhytidome (up to 0.5 m). In bark longitudinal cracks. Sclereid layers irregular in structure. Within entire secondary phloem very numerous resin spaces indicating an intensive process of secondary sclerification of tissues between sclereid layers. Within primary cortex inner periderms separating thin rhytidome layers. Bark tissues undergo secondary sclerification;

2) smooth bark zone (0.5–9 m). Sclereid layers regular. The two newly formed sclereid layers are discontinuous with numerous resin spaces. Outer sclereid layers continuous and undergo secondary processes of thickening. Sporadic thin layers of rhytidome separating outer primary cortex tissues;

3) apical zone (above 9 m). Bark smooth. Sporadic desquamating cork cell layers. Sclereid layers torn owing to increase in girth. The diagrams show considerable increment in primary cortex tissues. Resin canals enlarge. Primary cortex tissues undergo sclerification.

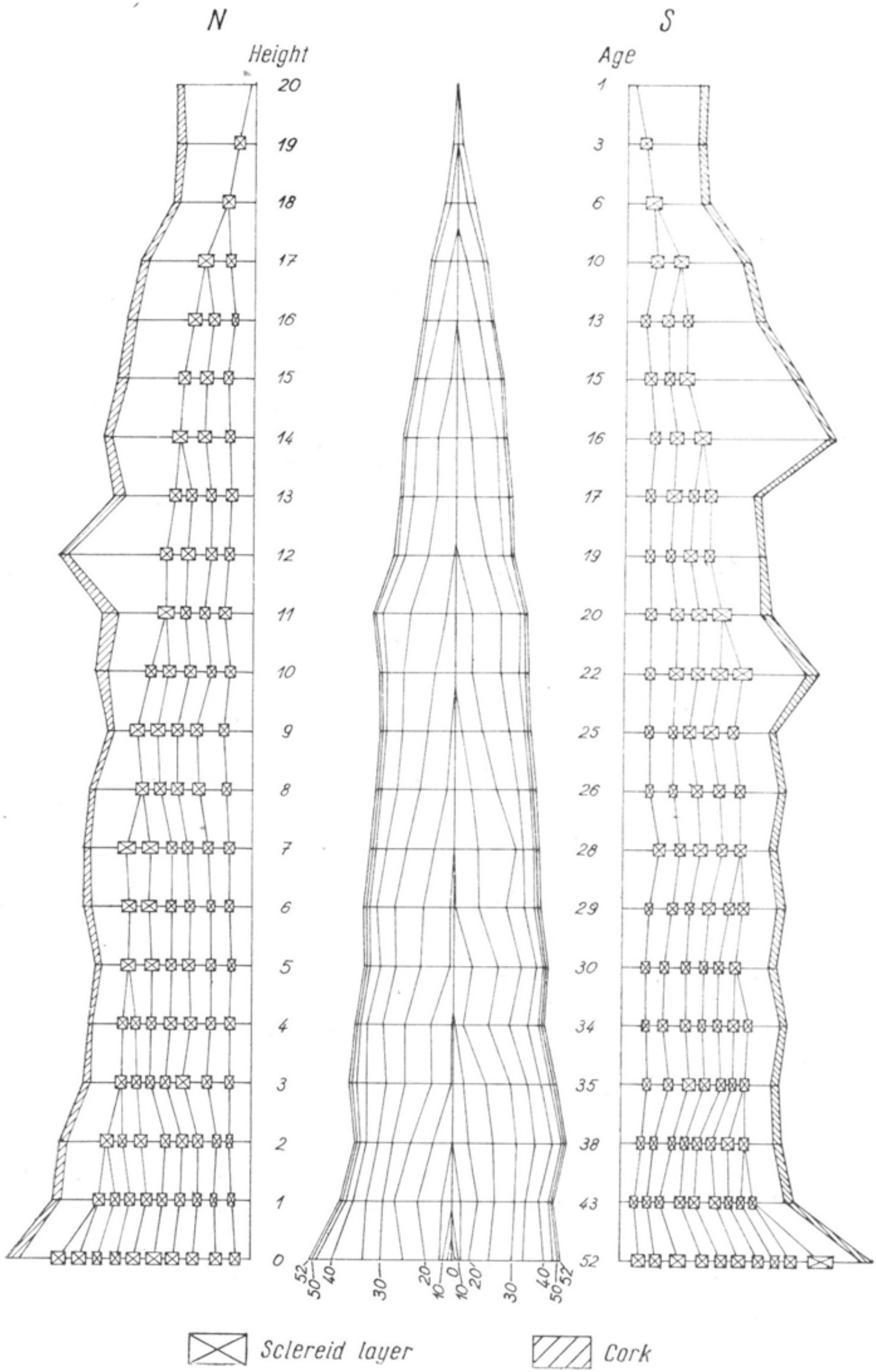


Fig. 4. Diagram of stem and bark tissues of 52-year-old fir (N and S sides). Height scale ca 1:200. Stem thickness scale ca 1:10. Bark thickness scale ca 4:1

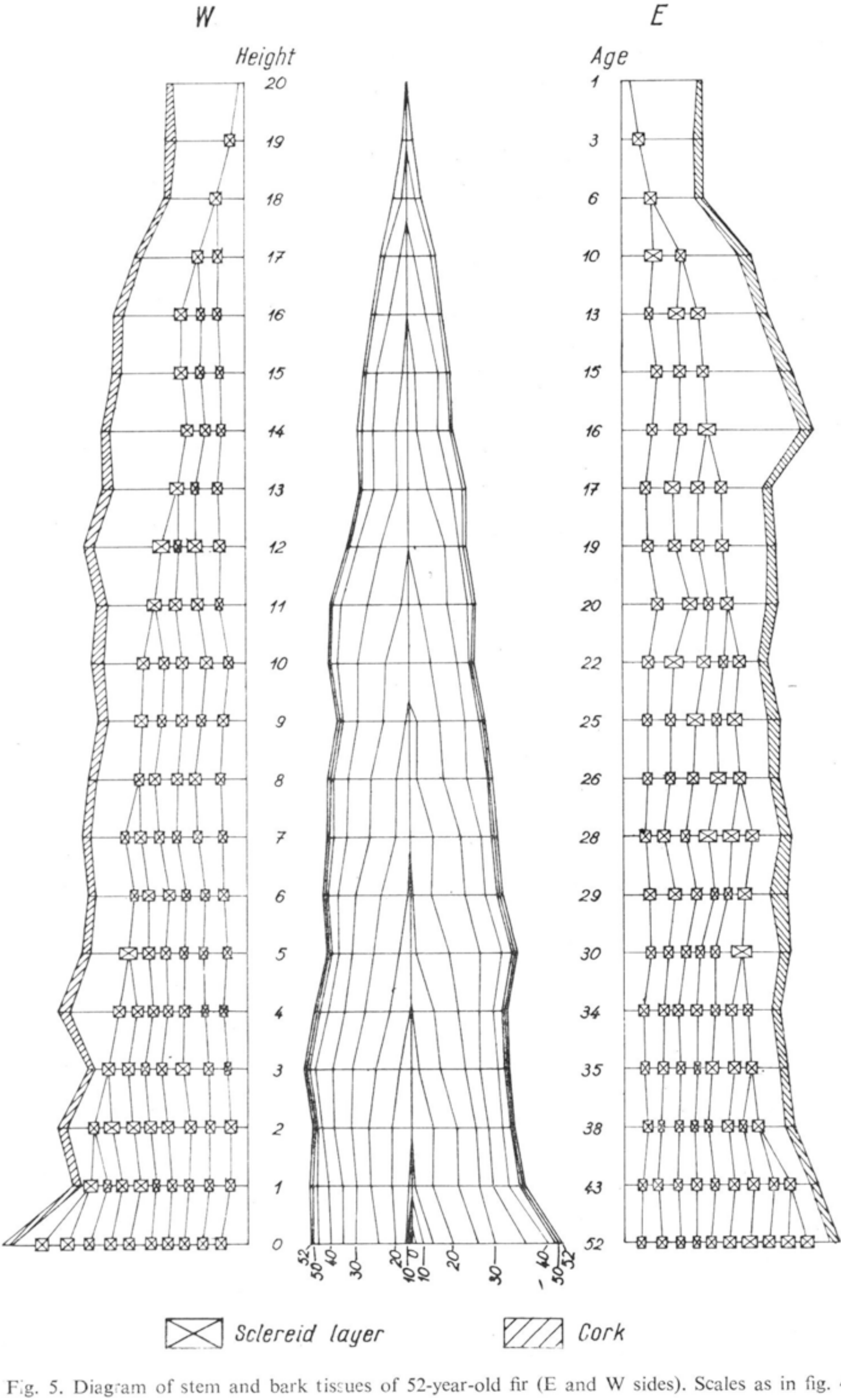


Fig. 5. Diagram of stem and bark tissues of 52-year-old fir (E and W sides). Scales as in fig. 4

Table 4

Tree no. 4, age 63 years, height 24 m (diagrams 6,7)

Height, m	Age of cross section, years	No. of sclereid layers	Directions in which sclereids are most numerous		Dimensions of resin canals on cross section	Remarks
			SPh	*PC*		
1	2	3	4	5	6	7
23	2	1	N	N	0.28×0.25	At border of *SPh* and *PC* single groups of *Sc*
22	3	1	S, E	S, E	0.7×0.3	On all sides well filled *ScL*. In 2nd *SPh* ring *RS* and intercellular spaces
21	9	2	S, E	S, E	1×0.3	1 st *ScL* wide and irregular, formed within 1st and 2nd *SPh* ring. 2 nd *ScL* discontinuous, numerous *RS*. On N side *RC* 2.4×0.5 mm
20	12	2	S	S, W	1×0.3	Wide irregular *ScL*. 2nd *ScL* formed within 6, 7 and 8th *SPh* ring. In 2nd *ScL* *RS*. On E side *RC* 2.5×0.6 mm
19	14	3	N, E	S, W	0.7×0.3	3rd *ScL* formed of *Sc* groups in 11th *SPh* ring. Within 11 and 12th ring *RS*
18	18	4	N, E	N, W	0.8×0.2	In 14 and 15th *SPh* annual rings irregular *Sc*. groups and *RS*. All *ScL* have an irregular structure, *RS* occur between them
17	19	4	S	S, W	1,2×0.3	*ScL* irregular. On S and W sides in all these layers *RS*. On W side large *RC* 1.6×0.5 mm
16	21	4	W	W	1×0.3	On W side of *PC* numerous *RS*. Intensive sclerification progresses in *PC* tissue. On N and E sides *ScL* are regular
15	24	5	N, W	N, W	0.8×0.2	On N and W sides *ScL* are regular. On S and E sides in 3, 4 and 5th *ScL* *RS*. On all sides *RC*
14	26	5	N	N	1.2×0.3	*ScL* regular. On N side in *PC* and *SPh*, *RS*. On E side *RC* 4.5×1.5 mm
13	27	5	N, W	N, W	0.7×0.2	On N side inner periderm separates *RC*. Two inner *ScL* noncontinuous. In 23 and 24th *SPh* rings *RS* and intercellular spaces
12	28	6	N, W	E	0.8×0.2	6th *ScL* forms irregular groups in 23 and 24th *SPh* annual rings
11	30	6	W	N	1.2×0.3	6th *ScL* is best filled on N and W sides. On S side inner periderm separates *RC*. The contribution of *PC* in the bark structure decreases distinctly
10	32	6	E, W	S	0.8×0.2	On all sides 6th *ScL* is distinctly visible. On S side secondary sclerification on *SPh* occurs in 4 outer *ScL*

(c.d. tabl. 4)

1	2	3	4	5	6	7
9	34	7	W	W	0.7×0.3	On W side, in *SPh* and *PC* very numerous small *Sc* groups. On E side in *SPh* numerous *RS*
8	36	7	E, W	E, W	0.5×0.2	*ScL* regular. On all sides in zone from 2 to 5th *ScL* secondary sclerification progresses. Numerous *RS*
7	36	7	E, S	N, E	1.2×0.2	7th *ScL* well filled on N and S sides. *ScL* regular. Secondary sclerification of tissues between *ScL* progresses
6	37	7	N, S	E	1.2×0.3	In *SPh* and *PC* tissues secondary sclerification progresses. On E side *RC* 3×0.5 mm
5	39	8	N	N, S	0.5×0.1	In bark tissues secondary sclerification advances on N side in zone from 3–7th *ScL*. Numerous *RS*. On S side inner periderm separates *RC*
4	41	8	N	N, S	1.3×0.1	On all sides *ScL* regular and well filled. Secondary sclerification of *SPh* only on E side
3	43	9	N, S	N, S	0.8×0.1	On N and S sides inner periderm separates *RC*. *ScL* regular. In *PC* and outer zone of *SPh* secondary sclerification advances
2	46	9	N, E	N, E	0.9×0.2	In *PC* tissues and outer *SPh* zone numerous small *Sc* groups resulting from secondary sclerification of these tissues
1	49	10	E, S	E, S	1.6×0.3	*ScL* regular. In outer bark tissue numerous small groups of *Sc*. On Sside *RC* 4×0.6 mm
0	63	13	N, S	N, S		On all sides secondary sclerification progresses. In rhytidome *ScL* can be distinguished and *PC* zone with enlarged *RC*

Three zones were distinguished within the stem:

1) zone of rhytidome (up to 1 m). Numerous cracks in bark. Rhytidome involves primary cortex tissues and outer secondary phloem layers. Periderm consists of thin-and thick walled cork cells. Under inner periderm numerous resin canals.In rhytidome sclereid layers and primary cortex zone with enlarged resin canals can be distinguished. Sclereid layers regular. Within secondary phloem secondary sclerification of tissues between sclereid layers progresses. This process is preceded by the formation of numerous resin cells irregularly distributed, most frequently situated in central zone of secondary phloem;

2) smooth bark zone with some few almost round scales (1–13 m) Rhytidome constitutes generally fragments of primary cortex parenchyma, containing periphereal resin canals. The latter filled with cork tissues. Sclereid layers regular. Two last layers discontinuous. In tissues between sclereid layers frequent small groups of sclereids;

3) apical zone (above 13 m). Outer sclereid layer continuous, inner layers usually discontinuous and irregular. In this stem zone secondary phloem rings are large. In late phloem the transitional zone consists of 4–7 layers of sieve cells. In primary cortex parenchyma intensive cell division. Resin canals greatly enlarged. Diagrams show increase in girth of primary cortex tissues.

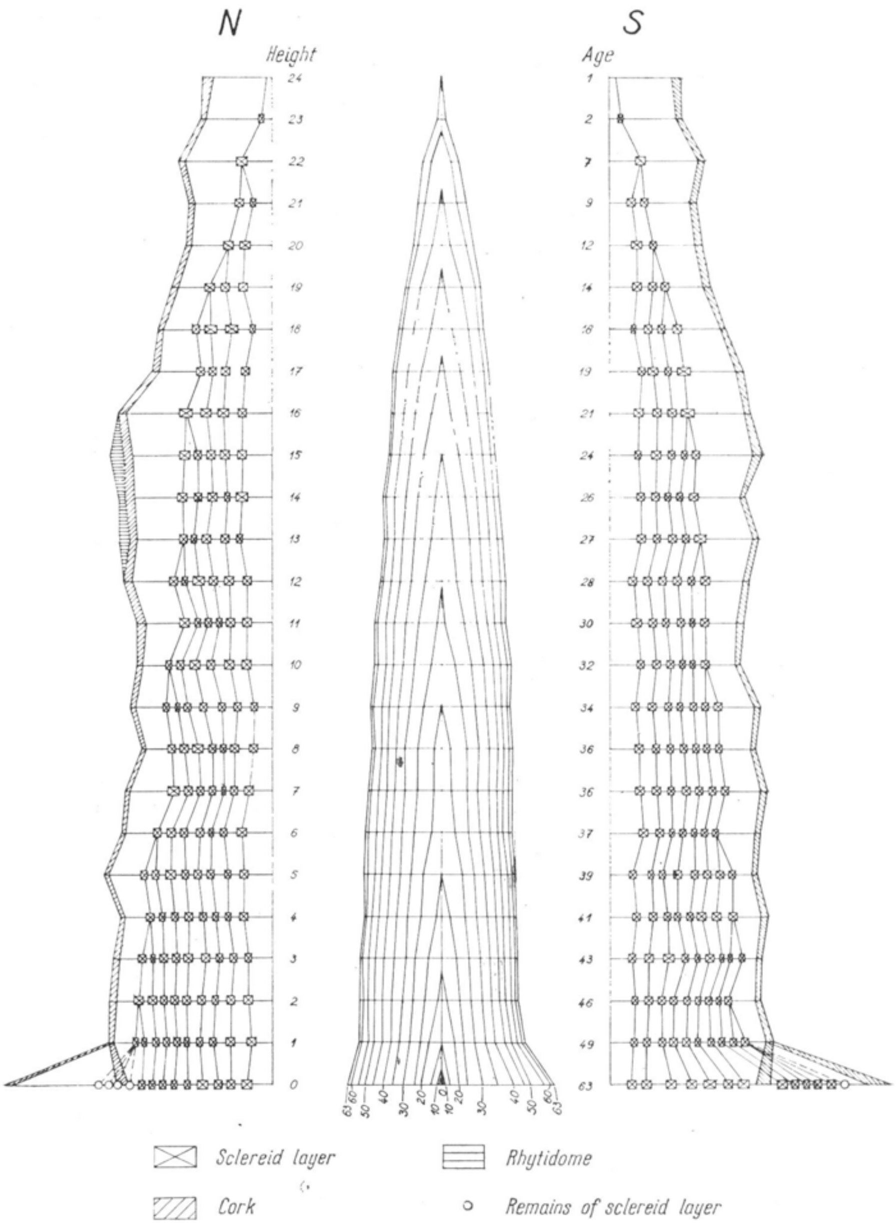


Fig. 6. Diagram of stem and bark tissues of 63-year-old fir (N and S sides). Scales as in fig. 4

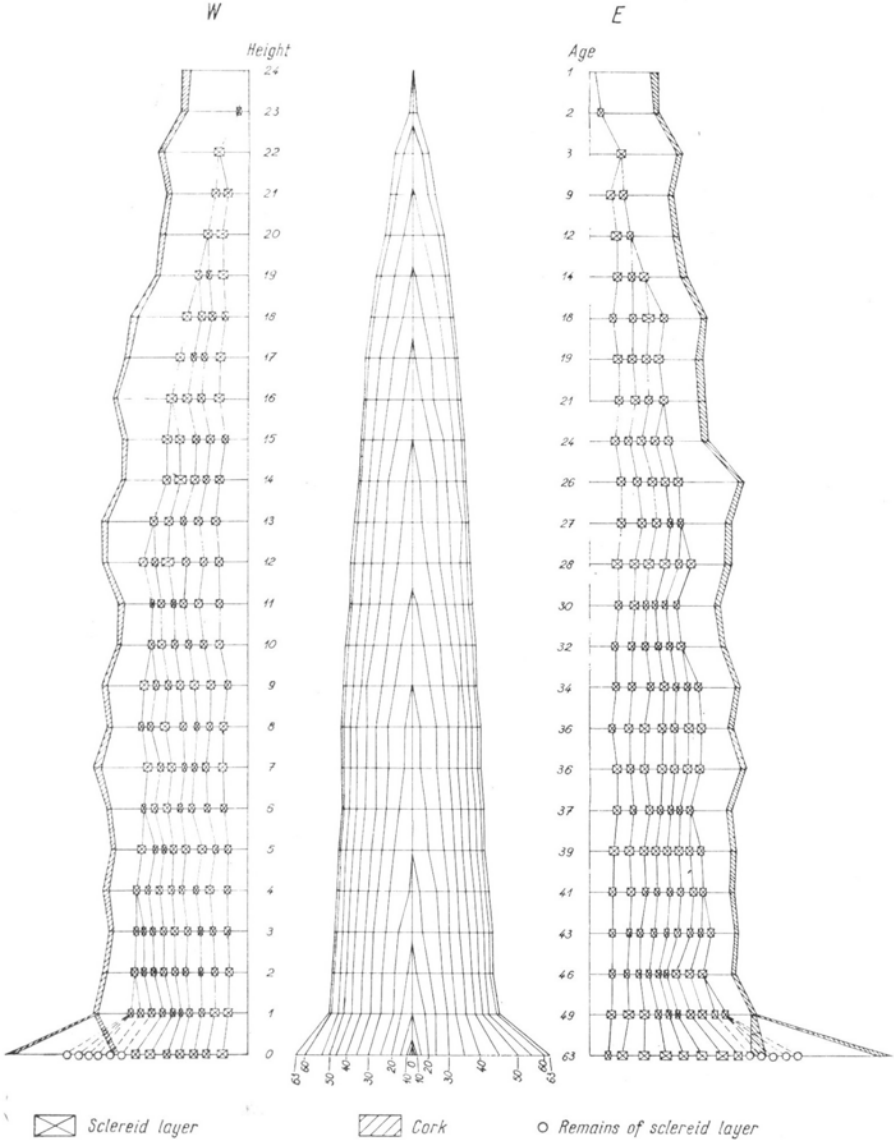


Fig. 7. Diagram of stem and bark tissues of 63-year-old fir (E and W sides). Scale as in fig. 4

Table 5

Tree no. 5, age 83 years, height 30 m (diagrams 8, 9)

Height, m	Age of cross section, yrs	No. of sclereid layers	Directions in which sclereids are most numerous		Dimensions of resin canals on cross section	Remarks
			SPh	*PC*		
1	2	3	4	5	6	7
30	6	1	N, S	N, S	0.5×0.2	*ScL* irregular and discontinuous formed of single *Sc* groups in 1st and 2nd *SPh* ring. In this layer numerous intercellular spaces
28	10	2	N, E	E	1.2×0.3	*ScL* irregular and discontinuous. In *SPh* numerous *RS*. On W side *RC* 2.1×0.5 mm
26	20	4	N, E	N, E	1.2×0.3	*ScL* very irregular. In outer zone of *SPh* large groups of *Sc*. 4th *ScL* formed of rarely distributed large *Sc* groups
24	29	6	N, S	S	2.5×0.5	*ScL* very irregular. In *SPh RS*. Sec. sclerification of *SPh* progresses. On N side *RC* 4×1 mm. On S side *RC* filled with cork tissue
22	37	7	S	N	1.6×0.3	Inner *ScL* consist of *Sc* groups of almost tetrahedral shape. Surface area of largest section of largest group exceeds 0.25 mm^2
20	46	9	S	E	1.5×0.3	*ScL* continuous and regular. *Sc* groups reach 1×0.5 mm size. On E side rhytidome 3 mm wide
18	50	10	S	S	1.2×0.2	On W side *Sc* forming 9th layer reach a 1.2×0.7 mm size. Sec. sclerification of tissues between primary *ScL* advances
16	55	11	S, E	E	1.2×0.2	*ScL* regular. On E side internal periderms form which separate thin layers of *PC* tissues. Under inner periderm secondary *RC*
14	58	12	S, E	W	1×0.2	In *SPh* sec. sclerification advances. On W side rhytidome forms separating enlarged *RC* from *SPh* tissues
12	60	12	S	W	1.2×0.3	*ScL* regular. In 3 inner layers numerous *RS*. 8, 9 and 10th *ScL* contain very large *Sc* groups
10	61	12	N	N	1.2×0.2	*ScL* regular. In *SPh* formed in the last 15–20 years v. numerous small *Sc* groups. Filling of inner *ScL* advances
8	66	13	W	W	1×0.2	On S, E and W sides rhytidome is formed involving *SPh* tissues. Under inner periderm numerous secondary *RC*

(c.d. tabl. 5)

1	2	3	4	5	6	7
6	69	14	W	W	1×0.2	*ScL* regular. Filling of 4 inner *ScL* advances
4	73	15	W	W	1.1×0.2	On E side rhytidome involving *PC* tissues and outer zone of *SPh*. Inner periderm consisting of thin- and thick- walled cork cells
2	75	15	W, N	N	1.5×0.3	*ScL* regular. On S side rhytidome involving *PC* and *SPh* tissues. Primary *RC* filled with thinwalled cork cells
0	83	17	S, W	S, W		Rhytidome involving *PC* and *SPh* tissues. Inner *ScL* well filled and distinctly delimited

On the basis of the morphological and anatomical structure of the bark tissues three zones were distinguished:

1) zone of rhytidome (up to 2 m). Irregular deep cracks in bark. Rhytidome involves primary cortex and secondary phloem tissues. Inner sclereid layers well filled and distinctly delimited;

2) smooth bark zone with some few almost round scales (2–20 m). Rhytidome involves thin primary cortex layers. It mostly separates peripherally situated resin canals. Sclereid layers regularly distributed. Inner layers consist of large groups of sclereids with surface area on cross section exceeding 0.5 mm^2;

3) apical zone (above 20 m). Its characteristic is the same as for tree no. 4 (table 4).

Table 6

Tree no. 6, age 115 years, height 29 m (diagrams 10, 11, plate III)

Height, m	Age of cross section, yrs	No. of sclereid layers	Directions in which sclereids are most numerous		Dimensions of resin canals on cross section	Remarks
			SPh	*PC*		
1	2	3	4	5	6	7
28	2	1	W	—	0.5×0.1	At border of *SPh* and *PC* single groups of *Sc*
27	10	2	E	W	1×0.2	*ScL* discontinuous, within them numerous *RS*. Under enlarged *RC* complete disappearance of outer *ScL*
26	16	3	N	N	1.3×0.3	In *SPh RS*. *ScL* irregular and discontinuous. On N side rhytidome is distinct involving *PC* tissues. Under inner periderm numerous secondary *RC*
25	23	5	N	N	1.2×0.3	Inner *ScL* discontinuous. On N and W sides advancing sec. sclerification of outer *SPh* layers and *PC* tissues

(c.d. tabl. 6)

1	2	3	4	5	6	7
24	29	6	S, W	S	1.2×0.2	*ScL* regular. Filling of two inner layers progresses. In *PC* numerous *Sc*
23	33	7	S	S, E	1.2×0.3	In *PC* tissues and outer *SPh* zone numerous *Sc* formed in the process of sec. sclerification of these tissues
22	39	8	S, E	S, E	1.2×0.2	Filling of 3 inner layers progresses. On all sides *ScL* pronounced
21	42	8	S, E	S, E	1.3×0.3	On S and E side *ScL* well filled and distinctly outlined. On S side *RC* 3.1×1.2 mm
20	48	10	S	S, W	1×0.2	On S and W sides rhytidome involving *PC* tissues and outer *SPh* zone. Under inner periderm secondary *RC* 0.6×0.3 mm
19	53	11	S	S	1.2×0.2	Filling of inner *ScL* progressing. Within these layers numerous *RS*
18	58	12	S, E	N	1.3×0.3	In inner *ScL* large groups of *Sc*. On S and W sides *RC* 3×0.8 mm
17	60	12	N	N	1.8×0.3	*ScL* distinct. On N side rhytidome involves *PC* tissues. Under rhytidome enlarged *RC* 4×1 mm
16	62	12	N	N	1×0.2	Inner *ScL* poorly filled. On all sides rhytidome. Under inner periderm secondary *RC* 0.3×0.3 mm
15	63	13	S, E	S, E	0.8×0.1	On N side *ScL* distinct. On remaining sides rhytidome. At site of inner periderm formation *ScL* enzymatically broken down
14	64	14	S	S	—	On all sides rhytidome involves *PC* tissues and outer *SPh* layers. In rhytidome *ScL* distinctly outlined
13	68	14	S	S	0.8×0.1	*ScL* regular and distinctly outlined. Layers 7–11 generally form continuous line on cross section
12	68	14	S, E	S	0.8×0.1	*ScL* regular. Layers 13 and 14 discontinuous. Filling progresses. Within these layers numerous *RS*
11	69	14	S	S	0.9×0.2	*ScL* 12, 13, 14 discontinuous. Filling is progressing
10	70	14	S, W	S	×	On all sides under inner periderm numerous secondary *RC*

(c.d. tabl. 6)

1	2	3	4	5	6	7
9	72	14	S. W	W	1.8×0.3	*ScL* 7–11 very regular and well filled. On N and S sides enlarged functioning primary *RC*
8	75	15	S	S	1×0.2	*ScL* regular. Advancing secondary sclerification of outer bark layers
7	79	16	N	N	—	Rhytidome on entire periphery. On N side two inner periderms are formed.
6	79	16	N, W	N	—	The outer one separates *PC* tissues in which an enlarged *RC* is present, the inner one separates 7–8 inner *ScL* of *SPh*. Under periderm inner secondary *RC* 0.4×0.4 mm
5	80	16	N, W	N, W	—	*ScL* regular. Inner periderms consist of thin- and thickwalled cork cells
4	83	17	S, W	S, W	—	*ScL* 10–15 regular. Filling of inner layers and sec. sclerification of other tissues progress. On S side secondary *RC* up to 0.6××0.5 mm
3	84	17	S, E	S	—	*ScL* 10–13 very regular. Inner layers consist of Sc groups of various size
2	86	17	S, W	S, W	—	*ScL* 9–14 very regular. On S side most numerous *RC*. Advancing sec. sclerification
1	94	19	S, E	S, E	—	*ScL* 10–15 regular. On S side most numerous secondary *RC* up to 0.7×0.6 mm
0	115	23	S, W	S, W	—	*ScL* well filled and regular, easily distinguishable in rhytidome. Under inner periderm numerous *RC*

In apical part of stem, up to the age of 50 years the bark structure is similar to that in the previously described trees. Plate III shows the outer appearance of the bark at various levels of the tree examined. Within the stem three zones were distinguished:

1) zone of rhytidome (up to 8 m). Numerous cracks in the bark. Rhytidome involves primary cortex and secondary phloem tissues. Under inner periderm numerous secondary resin canals. Sclereid layer 8–14 within the entire zone regular and exhibit good filling. Sclerification of tissues between sclereid layers progresses;

2) smooth bark zone (8–20 m). On bark surface sporadical longitudinal cracks, more frequently separating roundish scales. Rhytidome generally involves primary cortex tissues. In several cases it also involved the outer secondary phloem tissues. Inner sclereid layers continuous and well filled, sometimes secondary thickening may be observed. The inner layers are built of sclereid groups of unequal size. Some of these groups increase in volume;

3) apical zone (above 20 m). The diagrams show an intensive increment in secondary phloem and primary cortex parenchymal tissues. The resin canals enlarge. The cork cell layers desquamate.

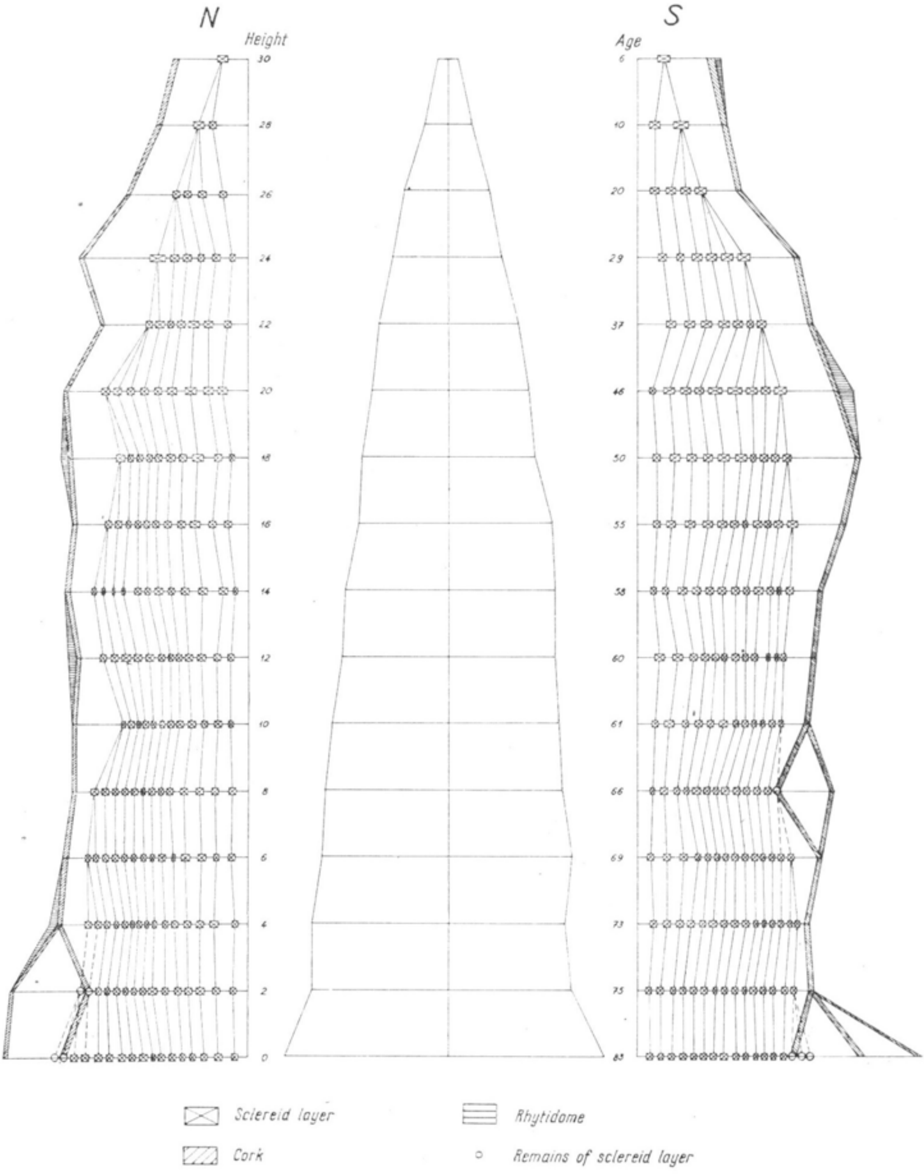


Fig. 8. Diagram of stem and bark tissues of 83-year-old fir (N and S sides). Scales as in fig. 4

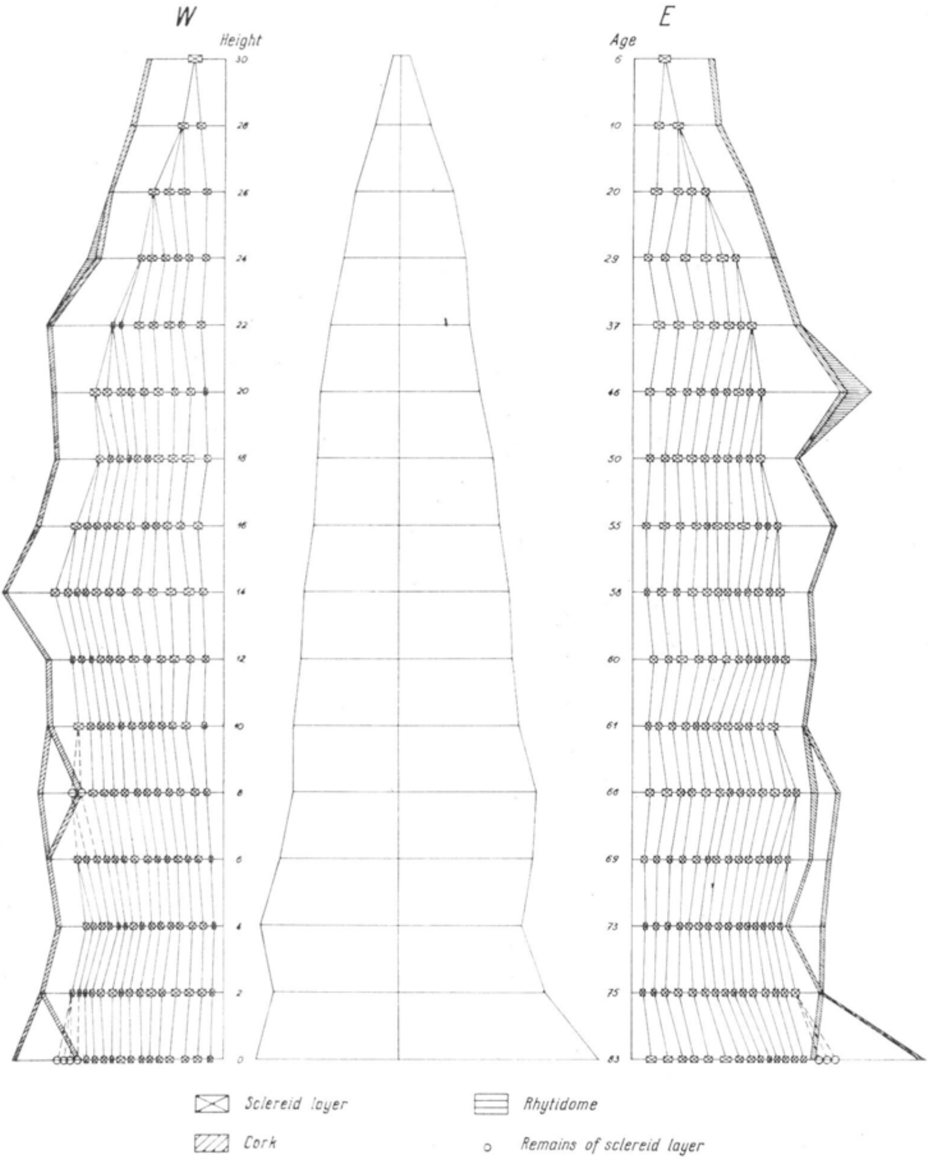


Fig. 9. Diagram of stem and bark tissues of 83-year-old fir (E and W sides). Scales as in fig. 4

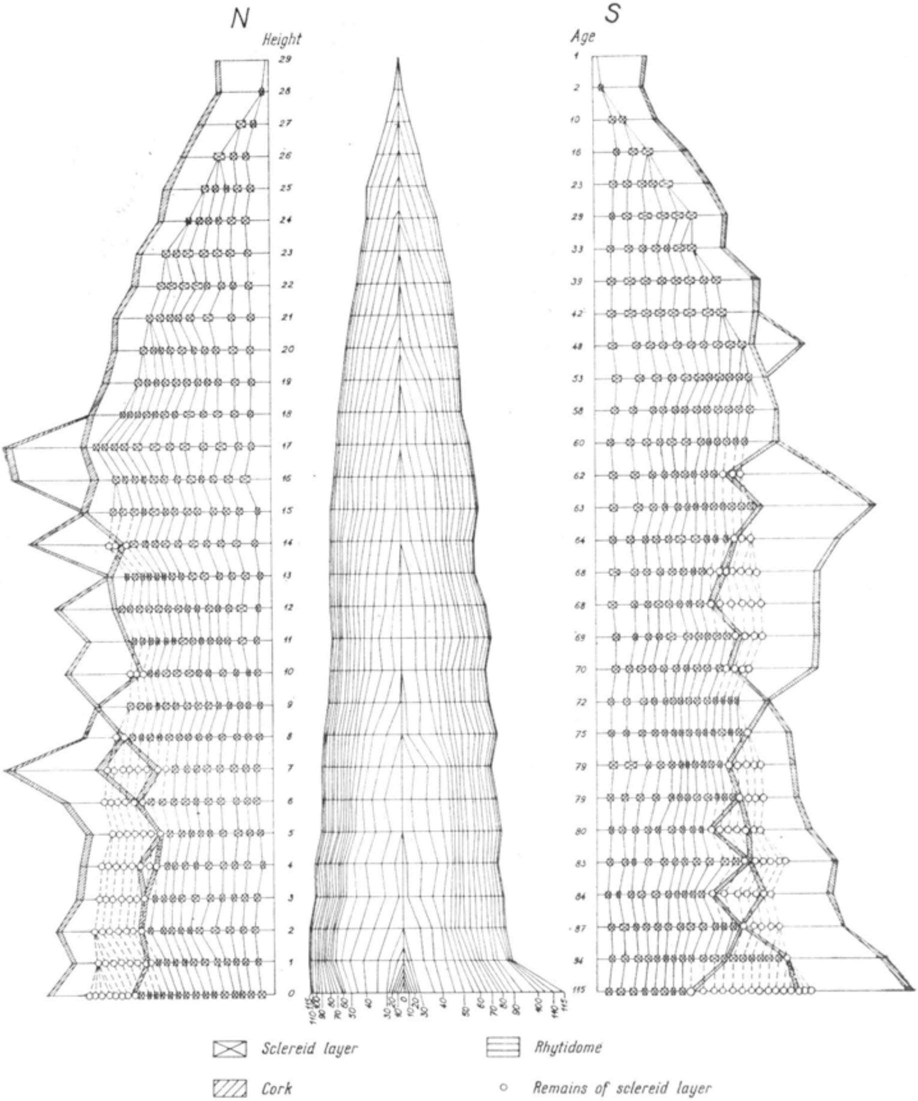


Fig. 10. Diagram of stem and bark tissues of 115-year-old fir (N and S sides). Scales as in fig. **4**

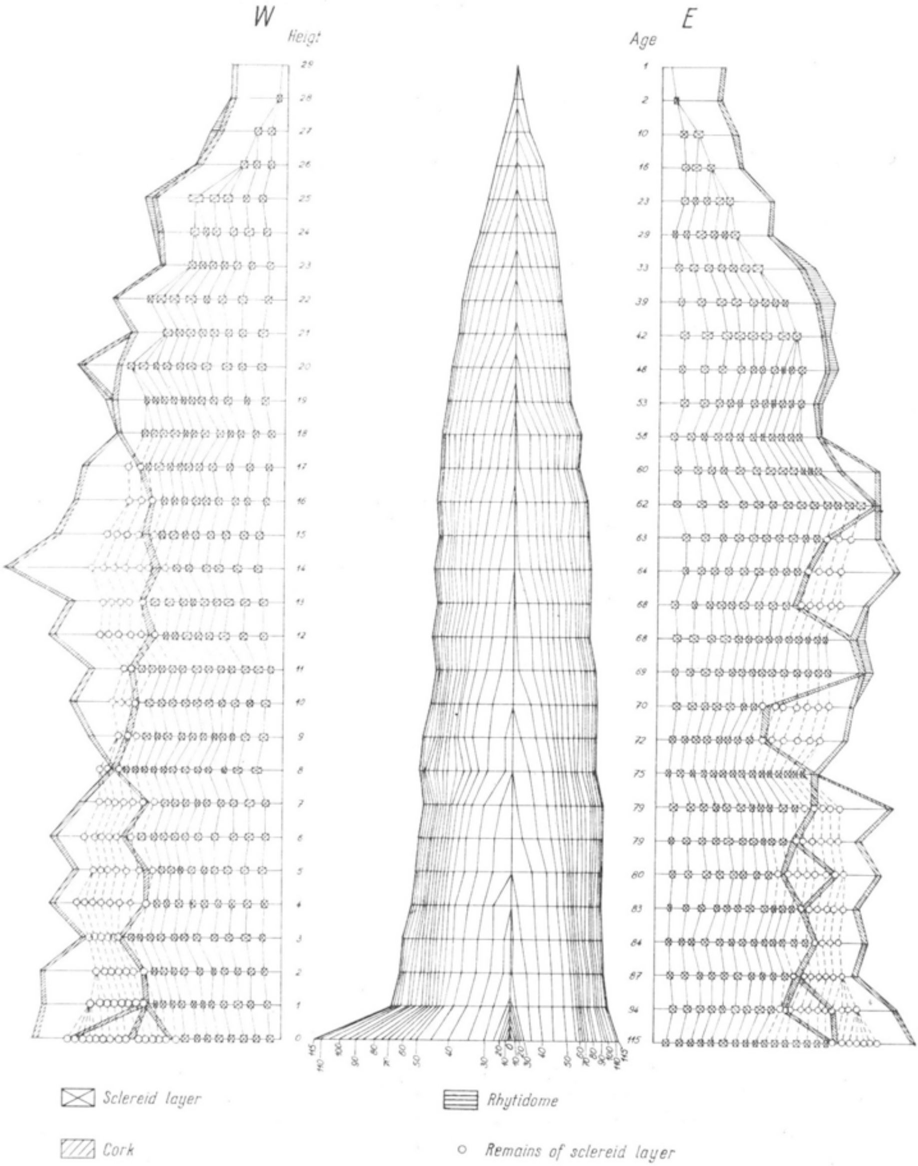


Fig. 11. Diagram of stem and bark tissues of 115-year-old fir (E and W sides). Scales as in fig. 4

EXPLANATIONS OF THE PLATES I–III

Plate I

Characteristic of bark tissues of 30-year-old fir. Negative photographs of cross section. × 8.

1. Root neck,	age 30 yrs	7. Height 3 m	age 6 yrs
2. Height 0,5 m	,, 16 ,,	8. ,, 3,5 m	,, 5 ,,
3. ,, 1 m	,, 14 ,,	9. ,, 4 m	,, 4 ,,
4. ,, 1,5 m	,, 11 ,,	10. ,, 4,5 m	,, 4 ,,
5. ,, 2 m	,, 9 ,,	11. ,, 5 m	,, 3 ,,
6. ,, 2,5 m	,, 8 ,,	12. ,, 5,5 m	,, 2 ,,

Plate II

Characteristic of bark tissues of 52-years-old fir. Negative photographs of cross sections. × 8.

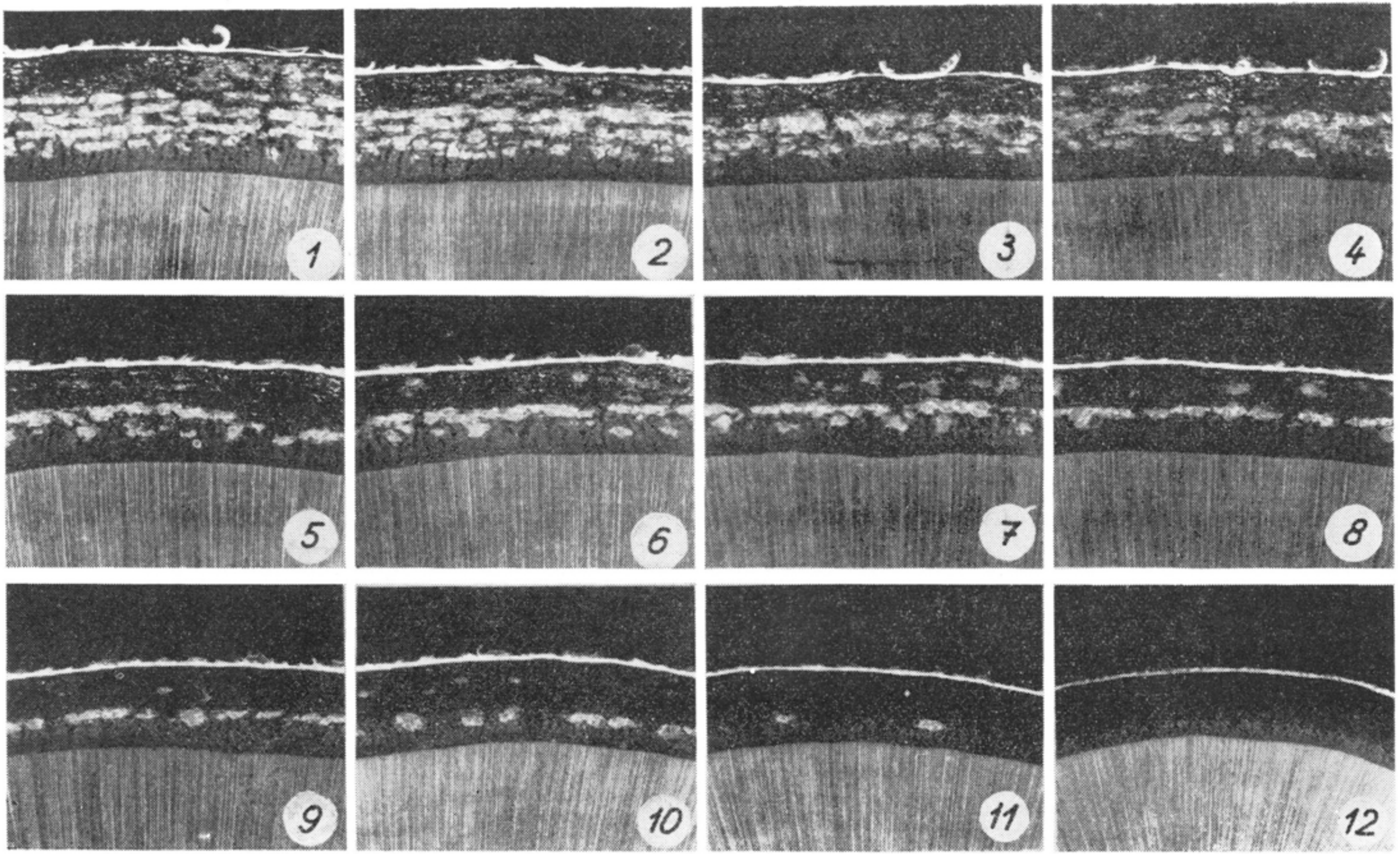
1. Root neck,	age 52 yrs	11. Height 10	age 22 yrs
2. Height 1 m	,, 43 ,,	12. ,, 11 m	,, 20 ,,
3. ,, 2 m	,, 38 .,	13. ,, 12 m	,, 19 ,,
4. ,, 3 m	,, 35 ,,	14. ,, 13 m	,, 17 ,,
5. ,, 4 m	,, 34 ,,	15. ,, 14 m	,, 16 ,,
6. ,, 5 m	,, 30 ,,	16. ,, 15 m	,, 15 ,,
7. ,, 6 m	,, 29 ,,	17. ,, 16 m	,, 13 ,,
8. ,, 7 m	,, 28 ,,	18. ,, 17 m	,, 10 ,,
9. ,, 8 m	,, 26 ,,	19. ,, 18 m	,, 6 ,,
10. ,, 9 m	,, 25 ,,	20. ,, 19 m	,, 3 ,,

Plate III

Outer appearance of 115-years-old fir bark

1. Bark in root neck zone on E side,
2. Bark in root neck zone on S side
3. Bark at 6 m height on N side (age 79 years).
4. Bark at 12 m height on N side (age 68 years).
5. Bark at 18 m height on N side (age 58 years).
6. Bark at 24 m height on N side (age 29 years).

Plate I



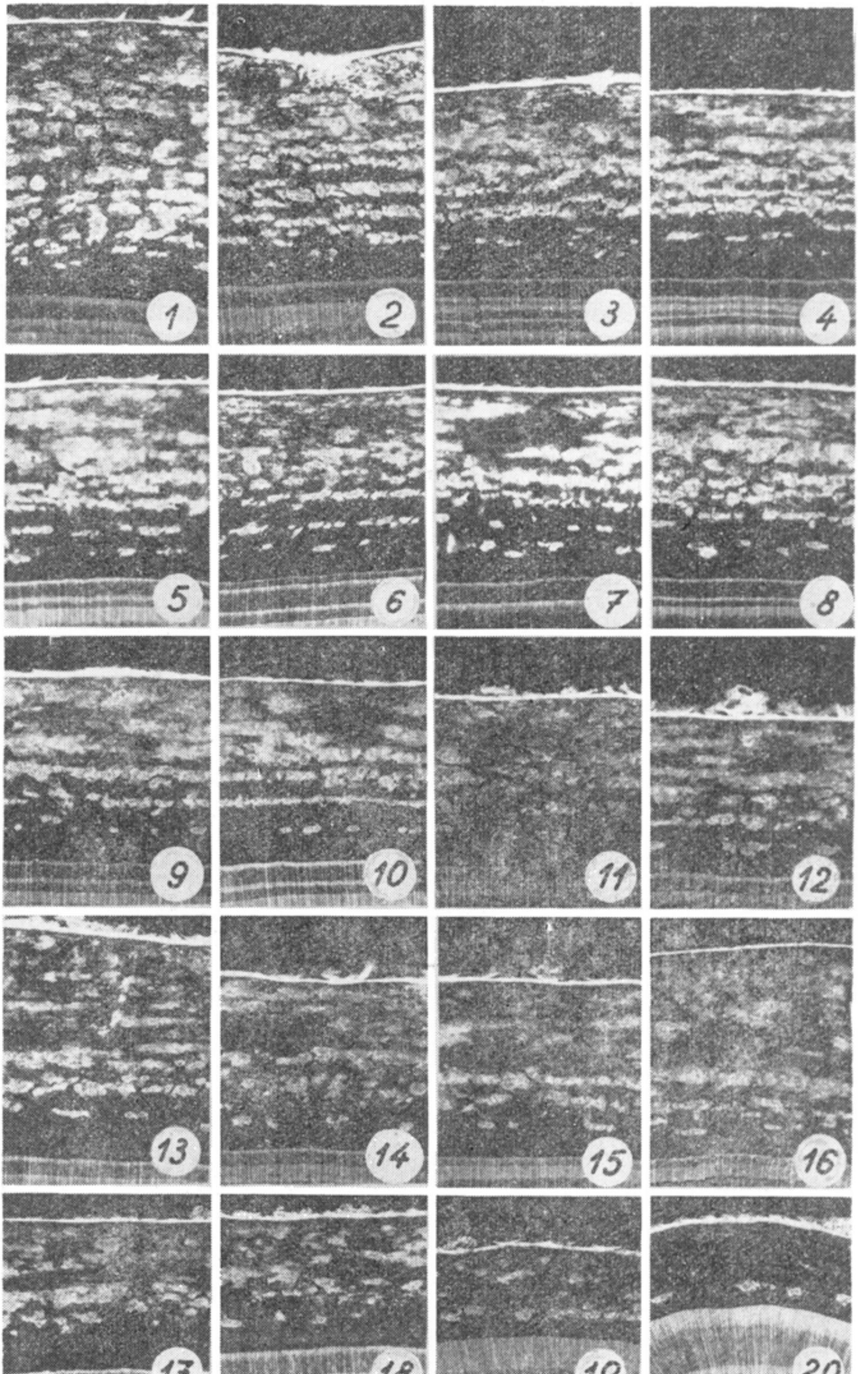

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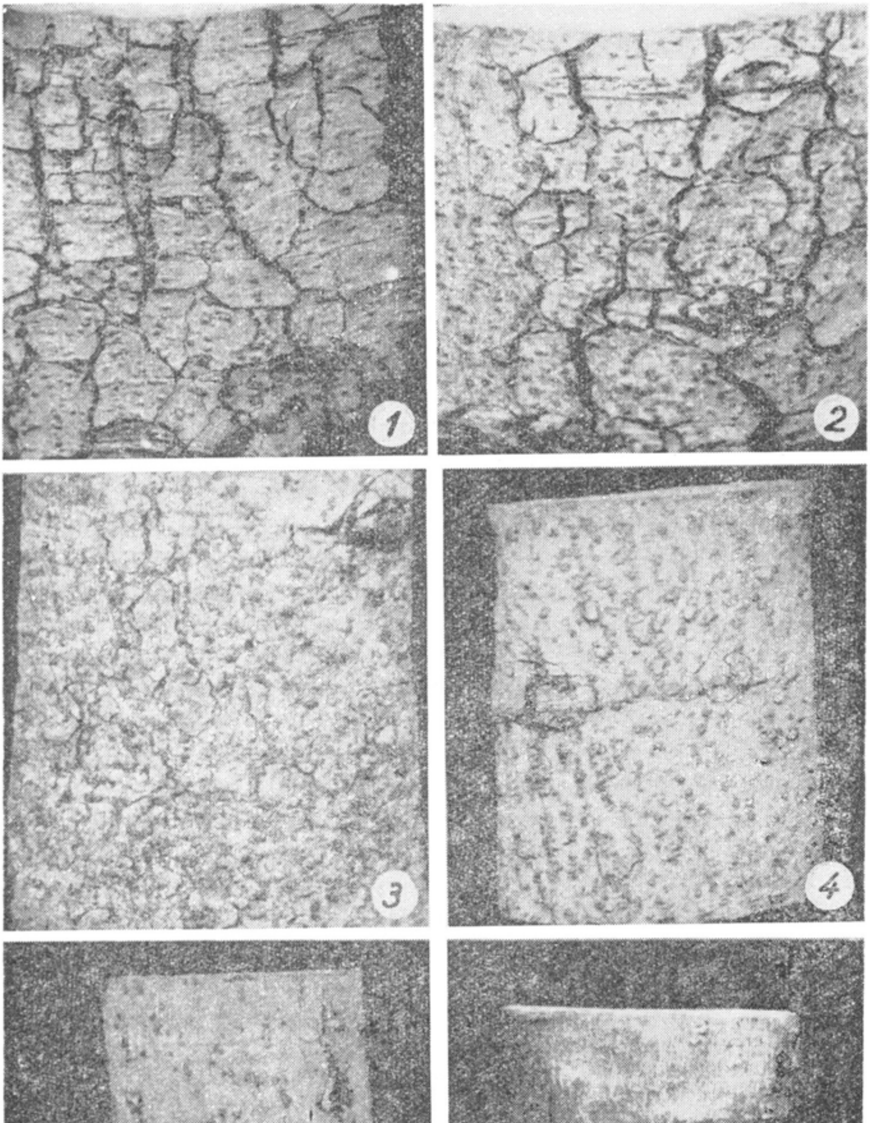
Plate III



DISCUSSION AND CONCLUSIONS

The changes occurring in secondary phloem lead to the formation of more or less regular sclereid layers (Plates I and II). Holdheide (1951) and Chang (1964) report that sclereids may sometimes form tangential discontinuous strands in *Abies*.

In the material examined a rhythmicity in the formation of successive sclereid layers was noted. It was found that within the secondary phloem a new sclereid layer develops on the average every 4–8 years (Figures 1–11).

The process of successive sclereid layer formation within the secondary phloem is not uniform. The differences concern mainly the structure of the successive sclereid layers and the duration of their development (filling).

The first sclereid layer constitutes the border between secondary phloem and primary cortex. It starts to form in the 3-year-old stem. The process of its formation lasts on the average 4–6 years. This layer is continuous but of uneven thickness. The sclereids forming this layer vary in shape.

The sclereid layers 2–5 (counting from outside) are irregular in structure. The process of their filling may last up to 15 years (average 10 years). These layers consist both of sclereids of irregular shape and of spherical ones. In the tissues lying between the sclereid layers secondary sclerification occurs. The sclereids formed between these layers are small and do not form tangential strands. Sometimes bridges may be seen joining the sclereids of two neighbouring layers.

The sclereid layers 6–12 (sometimes to 15) are regular. They are of nearly the same width on almost their entire length. Sclereidal bridges joining the layers occur here very seldom. The process of filling of these layers lasts up to 15 years. The sclereids forming these layers are mostly of almost tetrahedral shape.

The sclereid layers beginning with the 12th one are less regular. The process of one layer formation lasts here up to 30 years. The successive layers from at 5–10-year intervals. The sclereid groups in these layers are large. The surface area of the cross section of a single group may exceed 0.5 mm^2. Secondary sclerification of the tissues between the layers is observed.

The width of the sclereid layer is closely connected with that of the secondary phloem annual ring. Within wider secondary phloem rings the sclereid layers are also wider and vice versa.

A frequent correlation was also observed between the annual xylem ring and the width of the sclereid layer. During development of wide rings of xylem, a narrow sclereid layer forms, and on the contrary, when the xylem ring is narrow it frequently corresponds to a wide sclereid layer.

These observations seem to indicate that the regularity in the occurrence of sclereid layers is the expression of some obscure biophysical and biochemical processes occurring in the bark of the fir (*Abies alba* Mill).

In the primary cortex tissues, secondary processes take place connected with the growth of the stem in girth: 1) growth and division of parenchyma (this newly formed tissue fills the spaces left after crushing and tearing of primary tissues); 2) enlargement of the primary resin canals owing to the division of epithelial cells; 3) sclerification of the primary cortex parenchyma.

Parenchyma cell division is most intensive in the apical part of the tree (stems up to 20-years old) The enlargement of the resin canals is inhibited only when the inner periderm separating the resin canal from the inner tissues is formed. Enlargement of the resin canals is preceded by processes of enzymatic breakdown of sclereids both in the primary cortex and in the outer sclereid layers of secondary phloem. The first sclereids formed within the primary cortex were observed in a two-year-old stem. An intensive process of primary cortex sclerification occurs in stems aged 8–10 yeras.

In the fir examined, phellogen forming the outer periderm functions for a very long time (Golinowski 1968). Outer periderm was observed on a 75-year old cross section. In the apical part of the tree (stem aged up to 25 years) phellogen is very active forming yearly 2–8 cork cell layers. In this part of the stem desqumation of the outer cork cell layers is observed.

The development of inner periderm comprising the peripheral primary cortex layers was observed in 20–30 -year-old stems. Inner periderm formation is preceded by enzymatic processes of sclereid breakdown. In 20–70-year-old stems frequently the development of inner periderm was observed isolating a resin canal. In stems older than 60 years, inner periderm was observed within the secondary phloem. Formation of this type of periderm is preceded by enzymatic breakdown of sclereids forming the outer sclereid layers of secondary phloem. On the inner side of the periderm formed within secondary phloem, secondary resin canals are formed. After development of the epithelium such a canal is capable of enlargement, its diameter, however, on the cross section does not exceed 0.5 mm. In bark tissues older than 80 years, two or even three successively formed inner periderms could be seen. Under each of these, formed within the secondary phloem secondary resin canals occur, the larger the deeper they lie under the epidermis. Phelloid cells contribute largely to the structure of the inner periderm, forming sometimes strands of 3–5 cell layers.

Changes in the inner structure of bark tissues find their reflection in the outer appearance of the bark (Plate III). On the basis of the investigations performed three zones were distinguished within the stem:

1) Rhytidome zone. Deep longitudinal cracks in the bark, corresponding to the formation of inner periderm and dying of the separated outer tissues.

2) Smooth bark zone. Longitudinal cracks occur sporadically on the surface of the bark, more frequently desquamating roundish scales are observed. Rhytidome mostly involves primary cortex tissues. The outer sclereid layers are regular. The two or three latest formed sclereid layers are discontinuous. The process of secondary sclerification (filling) of these layers progresses.

3) Apical layer. The inner sclereid layer is continuous, the outer ones are irregularly arranged. In this zone of the stem the secondary phloem annual rings are

large. In the primary cortex parenchyma intensive cell division occurs. The resin canals greatly enlarge. In the periderm desquamation of the outer cork cell layers is observed.

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Budowa anatomiczna kory jodły pospolitej (Abies alba Mill.)

II. Zmiany ilościowe tkanek korowych w obrębie pnia

Streszczenie

Badania ilościowe miały na celu przede wszystkim ustalenie prawidłowości procesu wtórnej skleryfikacji łyka wtórnego. Na podstawie wyników uzyskanych w badaniach rozwojowych przyjąłem następującą hipotezę: jeżeli istnieje rytmika tworzenia kolejnych warstw sklereidów (na co wskazują uzyskane wyniki — Golinowski 1971), to powinna istnieć także ścisła współzależność pomiędzy liczbą warstw sklereidów i wiekiem drzewa. W celu sprawdzenia tej hipotezy wykonałem analizę zmienności tkanek korowych w obrębie pnia drzew o różnym wieku (16, 30, 52, 63, 83, 115 lat). Opracowałem metodę pomiaru grubości warstw poszczególnych tkanek korowych oraz metodę graficznego przedstawienia uzyskanych wyników.

W badanym materiale stwierdziłem istnienie rytmiki w wytwarzaniu kolejnych warstw sklereidów. Ustaliłem, że na terenie łyka wtórnego przeciętnie co 4 do 8 lat powstaje nowa warstwa sklereidów. Proces tworzenia kolejnych warstw ma niejednakowy przebieg. Różnice dotyczą głównie struktury kolejnych warstw sklereidów oraz długości trwania procesu ich wypełniania się.

Pierwsza warstwa sklereidów stanowi granicę pomiędzy łykiem wtórnym i korą pierwotną. Zaczyna się tworzyć w pędzie 3-letnim. Proces tworzenia tej warstwy trwa przeciętnie od 4 do 6 lat. Warstwa ta jest ciągła i posiada niejednakową grubość. Sklereidy tworzące ją odznaczają się różnorodnymi kształtami.

Warstwy sklereidów od 2-5 (licząc od zewnątrz) posiadają nieregularną budowę. Proces ich wypełniania może trwać do 15 lat (przeciętnie 10 lat). Warstwy te budują zarówno sklereidy o kształtach nieregularnych, jak również sklereidy o kształcie zbliżonym do kulistego.

Warstwy od 6 do 12 (niekiedy do 15) mają regularną budowę. Na całej długości posiadają prawie jednakową szerokość. Bardzo rzadko występują tutaj mostki sklereidalne łączące sąsiadujące warstwy. Proces wypełniania warstwy trwa do 15 lat. Sklereidy tworzące warstwy w przeważającej ilości posiadają kształty zbliżone do prostopadłościanów.

Warstwy sklereidów od 12 wzwyż odznaczają się mniejszą regularnością budowy. Proces powstawania warstwy trwa tutaj do 30 lat. Kolejne warstwy tworzą się w odstępach od 5 do 10 lat.