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Abies lasiocarpa (Hook.) Nutt. (sub-alpine fir) trees of comparable vigor growing in eastern British Columbia were studied in order to determine the effects of cork bark disease on phellogen and vascular cambium activity.

Diseased trees form hard deeply fissured rhytidome several inches thick over large areas of the bole when phellogens that produce large increments of phellem form successively deeper in cortical and secondary phloem tissues. Expansion of the secondary xylem cylinder causes cracks to form in the rhytidome.

Non-infested trees and areas above and below infested sites may retain their superficial phellogen for nearly 200 years and possess relatively thin layers of cork with a smooth surface texture.

Phellem cells from diseased areas contain numerous fungal

hyphae. Those from adjacent smooth bark areas and healthy trees are filled with phenolic compounds but are of different dimensions and lack hyphae. In addition infested areas show denser wood, significantly shorter tracheids, sieve cells and fusiform initials, greater frequency of fusiform initials dividing by anticlinical partitions, higher rate of new fusiform initial loss, and greater number of vertical albuminous cells. New ray initials are formed from declining fusiform initials in control and diseased trees.

Effects of Cork Bark Disease on Cambial Activity and Secondary Tissues in *Abies lasiocarpa* (Hook.) Nutt.

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
MATERIALS AND METHODS	4
OBSERVATIONS	10
Periderm Development	10
Secondary Xylem	13
Secondary Phloem	16
Vascular Cambium	23
DISCUSSION	37
Periderm	37
Secondary Xylem	38
Secondary Phloem	40
Vascular Cambium	42
SUMMARY	50
BIBLIOGRAPHY	54
APPENDICES	57

LIST OF TABLES

Table		Page
1	Bole description of ten specimens of Abies lasiocarpa (Hook.) Hutt. sampled.	5
2	Mean thickness of dead bark and dimensions of component phellem cells.	11
3	Analysis of secondary xylem produced in 1968 by ten specimens of A. lasiocarpa.	14
4	Analysis of secondary phloem produced in 1968 by ten specimens of A. lasiocarpa.	18
5	Analysis of dormant vascular cambium in ten specimens of A. lasiocarpa subsequent to the 1968 growing season.	24
6	Frequency of anciclinal division in fusiform initials from six alpine fir specimens as inferred from secondary xylem and phloem.	26
7	Fate of daughter fusiform initials formed during the 1968 growing season in six alpine fir specimens as inferred from cell wall configurations in secondary xylem.	28
8	Fate of daughter fusiform initials formed during the 1968 growing season in six alpine fir specimens as inferred from cell wall configurations in secondary phloem.	29
9	Description of ray initial formation in six alpine fir specimens during the 1968 growing season as inferred from the secondary xylem record.	32

Table		Page
10	Description of ray initial formation in six alpine fir specimens during the 1968 growing season as inferred from the secondary phloem record.	33

LIST OF FIGURES

Figure		Page
1	Distribution map of alpine fir.	57
2	Map showing the two alpine fir collection sites.	57
3	Smooth bark control tree showing two sampling wounds.	58
4	Cork bark fir (A. lasiocarpa var. arizonica) bole.	58
5	Alpine fir bole covered with cork bark.	58
6	Bark thickness of cork bark area and smooth bark area 12 inches below.	58
7	Smooth bark control and cork bark bearing tree.	58
8	Two cork bark cankers on an alpine fir bole.	58
9	Irregular distribution pattern of cork bark areas.	58
10	Cross section of cork bark rhytidome composed of many cork increments.	59
11	Cross section of cork bark rhytidome composed of increments of dead cork cells and dead secondary phloem.	59
12	Cross section of control tree periderm.	59
13	Cross section of A. lasiocarpa var. arizonica periderm.	59
14	Cross section of part of control tree periderm.	59

Figure		Page
15	Cross section of cork bark phellem containing fungal hyphae.	59
16	Tangential section of control tree phellogen showing each component cell with a nucleus and vacuole.	60
17	Tangential section of cork bark phellogen showing starch grains in component cells.	60
18	Tangential section of control tree phellem.	60
19	Tangential section of cork bark tree phellem showing fungal hyphae.	60
20	Cross section of 1968 xylem increment in control tree number 1.	61
21	Cross section of 1968 xylem increment under cork bark of tree number 9.	61
22	Cross section of alpine fir secondary xylem with traumatic resin canals.	61
23	Secondary xylem cross section showing irregular outline of increment beneath cracks in cork bark.	61
24	Cross section of control tree cambial zone with record of a recent anticlinal division.	62
25	Cross section of canker cambial zone showing the record of fusiform initial loss and intrusion of the fusiform initial from an adjacent tier.	62
26	Cross section of 1968 phloem increment in control tree number 3.	62

Figure		Page
27	Cross section of 1968 phloem increment under cork bark of tree number 7.	62
28	Tangential section of nonfunctional phloem with sclereids, small resin cells in rays and crystal containing parenchyma strands.	63
29	Tangential section of older nonfunctional phloem with enlarged resin cells.	63
30	Cross section of cambial zone and adjacent vascular tissues of canker tree sclereids.	63
31	Cross section of cambial zone and adjacent vascular tissues of control tree with phloem ray and parenchyma strands.	63
32	Percentage of fusiform initials undergoing anticlinal division during the 1968 growing season in control trees, cankers, and smooth bark areas below cankers.	64
33	Radial section of control tree cambial zone and adjacent secondary phloem with a radial plate of vertical albuminous cells.	65
34	Radial section of control tree cambial zone with last two remaining segments of fusiform initial producing a radial plate in adjacent phloem.	65
35	Control tree cambial zone and adjacent secondary phloem with radial plate and sieve cells with sieve area.	65
36	Tangential section of cambial zone with fusiform initials and ray initials.	65

Figure		Page
37	Tangential section of secondary phloem in control tree produced near end of 1968 growing season.	66
38	Cambial zone adjacent to secondary phloem shown in Figure 37.	66
39	Photomicrograph showing secondary xylem temporally related to secondary phloem shown in Figure 37.	66
40-43	Radial section of vascular ray and ray initials.	67
44-48	Serial tangential sections through control tree secondary phloem illustrating preliminary steps in ray initial formation.	68
49	Photomicrograph of tangential section through cambial zone producing cells shown in Figures 44-48 and 50-54.	68
50-54	Every fifth serial tangential section through xylem temporally related to phloem is shown in Figures 44-48.	68
55	Diagramatic presentation of selected patterns of fusiform initial activity which occurred in control and diseased trees during the 1968 growing season.	69

EFFECTS OF CORK BARK DISEASE ON CAMBIAL ACTIVITY AND SECONDARY TISSUES IN ABIES LASIOCARPA (HOOK.) NUTT.

INTRODUCTION

Abies lasiocarpa (Hook.) Nutt. (alpine or sub-alpine fir) normally grows in the Canadian and Hudsonian zones at 2,000 feet to timberline in the north and from 10,500 feet to timberline in the southern part of its range. Although commonly found in sub-alpine valleys and on slopes and ridges from southeastern Alaska through British Columbia, western Alberta, Montana, Wyoming and into Arizona and New Mexico (Figure 1), merchantable stands of alpine fir are mostly restricted to the central interior of British Columbia at an elevation of 2,000 to 2,500 feet. In this area, more than 238 million board feet were harvested for dimension lumber and pulp in 1968 (McBride, 1970).

Kennedy and Wilson (1954a) noted that alpine fir exists in two forms in the interior of British Columbia as well as throughout the Canadian Cascade Mountains. One form was described as having its entire stem covered with firm, smooth bark about one inch thick while the other type was depicted as possessing deeply fissured corky bark, reaching several inches in thickness over large areas of the bole.

The cork bark condition may manifest itself as isolated thick bark swellings circumscribing boles and branches of trees of all ages.

The protuberances are restricted infrequently to only one side of the axis. Young developing cankers are generally traversed by longitudinal fissures whereas more established cork bark areas also exhibit numerous short horizontal cracks which intersect with those vertically oriented. It is not uncommon for the same tree to display both extremes of the cork bark condition as well as intermediate stages.

Such bark does not resemble that of cork bark fir, Abies lasiocarpa var. arizonica (Merr.) Lemm. which is found only in New Mexico, Arizona and southern Colorado. This accepted genetic variant has uniformly soft, corky, ash-gray bark covering the entire bole (Figure 4).

Recently Kuijt (1969) described the pattern of development of cork bark on normal smooth bark trees and proposed that a fungus, Gelatinosporium abietinum Peck, is instrumental in causing the transition. A progressive decrease in size of contiguous swellings up or down the trunk led him to suggest that the cork bark disease can spread in either direction. He also noted that new cork bark cankers arise isolated between pre-existing ones.

It has been shown that wood subjacent to areas of cork bark is more dense than wood from normal trees and that the tracheids are significantly shorter (Kennedy and Wilson, 1954a, b). Are there commensurate differences in wood from cork bark and smooth bark areas of the same tree and, if so, are they comparable to disparities

in xylem from cork bark trees and normal trees? What is responsible for the shorter tracheids subjacent to cork bark cankers? Do cork bark and adjacent smooth bark areas show differences in the secondary phloem? Is cork bark solely a result of increased phellogen activity or is there a concommitant surge in secondary phloem production? Is the activity of the vascular cambium affected by the formation of cork bark?

This study will attempt to answer these questions and thereby elucidate the activity of the vascular cambium and the development of secondary tissues of alpine fir trees afflicted with cork bark disease.

MATERIALS AND METHODS

Samples of the vascular cambium and adjacent secondary tissues were collected from the boles of alpine fir trees growing at an elevation of approximately 5,000 feet along the Ottertail river (50°17'N, 116°23'W) in Yoho National Park, British Columbia. Sixteen trees were sampled at weekly intervals from June 12, 1968 to August 30, 1968 and again on May 30, 1969. In addition, ten trees at about 5,200 feet on Mt. King were sampled on June 10, 1968. At both locations (Figure 2), one half of the trees studied possessed one or more thick bark cankers along the lower six feet of their boles whereas the remaining trees had thin smooth bark (Figures 3, 5, 6, 7, 8 and 9). Of the 26 trees sampled for this study, only ten, comparable in age and vigor according to secondary xylem production, provided the data presented. Smooth bark control trees numbered 1-5 were from 162 to 184 years old as determined from increment borings and measured 7.4 to 8.5 inches in diameter four feet from the ground (Table 1).

For every collection after the first one, a core of tissues was removed from each of the control trees at breast height and a few centimeters to the side of the previous sampling wound. A similar procedure was used in obtaining plugs of tissues from trees possessing cork bark except that samples were taken from the cankers and also from smooth bark areas 12 inches directly above and/or below the cankers sampled. Two trees were sampled at areas 180 degrees from

Table 1. Bole description of ten specimens of Abies lasiocarpa (Hook.) Nutt. sampled.

Position of sample area on bole	Tree number	Bole diameter at sample area (in)	Tree age at lowest smooth bark area
Four feet from base	1	8.5	184
Four feet from base	2	8.0	162
Four feet from base	3	7.4	163
Four feet from base	4	8.4	189
Four feet from base	5	8.5	175
Canker 4'6" from base		12.7	
Smooth bark 3'3" from base	6	8.7	187
Smooth bark 5'7" from base		8.4	
Canker 5'8" from base		14.3	
Smooth bark 4'1" from base	7	9.1	201
Smooth bark 7'4" from base		8.4	
Canker 3'1" from base		15.1	
Smooth bark 4'8" from base	8	8.8	193
One-half canker 5' from base		8.5	
Smooth bark 180° from canker	9	8.5	144
Smooth bark 3'6" from base		6.8	
One-half canker 4' from base		9.9	
Smooth bark 180° from canker	10	9.9	179
Smooth bark 2'8" from base		8.2	

cankers which were formed on only one side of the bole.

Because of the similarity in names, it was considered advisable to compare the structure of the cork bark disease cankers with the bark of cork bark fir of the southwestern United States. Hence, samples of cork bark fir (Figure 4) were obtained from the San Francisco Mountains in Arizona in March, 1969.

To obtain cores of tissues, a Skil model 203 Power-Pack drill equipped with a 1-1/4 inch hole saw and powered by a ten volt direct current Eveready nickel-cadmium rechargeable battery was used to make a circular incision at least 1/2 inch into the secondary xylem. A hole 1/8 inch in diameter was then drilled through the center of the core to facilitate fixation and infiltration. Then each sample was removed from the tree by cutting away rectangular areas of tissue on two opposing sides of the initial circular cut and forcing a narrow chisel under the plug at an obtuse angle. Petrolatum was applied to the exposed surfaces of the well in the trunk to prevent fungal attack. Figure 3 shows two wounds subsequent to removal of samples.

Cores of tissues obtained in the above manner were fixed in Navashin's III, dehydrated with tertiary butyl alcohol and infiltrated with paraffin as described in Johansen (1940) and Sass (1958) except that the time intervals between all solution changes were extended to 24 hours. Each infiltrated plug was then cooled, cut into four one-centimeter square blocks with an electric jigsaw, and subsequently

infiltrated for 24 hours in a partial vacuum with two changes of 61° Tissuemat. Softening of the embedded tissues was achieved by exposing the surface to be sectioned and soaking overnight in a solution of glycerin and detergent (Alcorn and Ark, 1953). Tangential and transverse sections 15 microns thick were stained with safranin and hematoxylin. Tannic acid and lacmoid were employed for staining radial sections which were cut at thicknesses varying from 10 to 20 microns. The presence of tannins and starch was determined by treating transverse and radial sections with ferrous sulphate and IKI, respectively. Transverse sections of smooth and cork bark were treated with KOH and stained with chlorzinc-iodide so that the occurrence of suberin could be ascertained (Johansen, 1940).

Elements of the secondary tissues and interjacent vascular cambium of alpine fir are organized in radial rows which extend from various depths in the secondary xylem into the previous year's increment of secondary phloem where radial alignment is lost due to crushing. Tracheids or sieve cells at the beginning of xylem and phloem increments produced in 1968 were considered to be approximate replicas of the parental fusiform initials in the spring of the same year. Observations of successive serial tangential sections allowed subsequent secondary xylem and phloem cells in the same radial rows to be viewed as replicates of the fusiform initials at later periods in the growing season. Studying serial tangential sections of radial rows

extending through the 1968 increments of xylem and phloem made it possible to indirectly witness cambial activity in alpine fir stems for the entire 1968 growing season.

Eight by ten prints were made from 35 millimeter negatives of serial tangential sections through the secondary tissues in a manner similar to that described by Smith (1967). Data concerning the formation and loss of fusiform and ray initials were obtained primarily from the prints but frequent microscopic observations were made also. All longitudinal measurements were made from tangential sections and in the case of xylem elements, also from slides of macerated wood. Mean tracheid, sieve cell and ray heights were obtained from elements located near the middle of 1968 xylem and phloem increments. Cross sections provided all width dimensions. Unless otherwise stated, each figure in subsequent tables represents a mean based on a sample number of 50. Student's "T" test (Snedecor and Cochran, 1967) was used to determined if significant differences exist between data obtained from control trees, cankers and smooth bark areas below cankers.

In order to use the 1968 phloem increment as a record of one year's growth, it was first necessary to determine its limits. In alpine fir, the last phloem cells produced during one growing season are easily crushed and are smaller than the first cells produced the

the following growing season. This pattern of development allowed the limits of the 1968 phloem increment to be accurately determined (Figures 26, 27).

OBSERVATIONS

Periderm Development

Although the place of origin of the first phellogen in stems is quite variable, in Abies it originates in the hypodermis, a layer of cells just below the epidermis (Chang, 1954a). The first periderm has been shown to be retained for as long as 100 years in some specimens of Abies lasiocarpa (Chang, 1954a), but it is eventually replaced by deep periderm layers which differentiate repeatedly but rarely annually, deeper in the cortex and eventually in the secondary phloem (Esau, 1965). These subsequent layers of nonliving phellem separate variable amounts of cortex or secondary phloem from the subjacent living tissues. Alternating layers of deep phellem and dead tissues isolated by the phellem are collectively called rhytidome.

Cork bark was found to be mostly rhytidome but adjacent smooth bark areas and bark of control trees possessed only a single superficial periderm at the areas sampled for this study.

Phellogen cells from control trees and smooth bark areas of canker bearing trees are nearly isodiametric in tangential view but are radially flattened (Figures 14, 16). A small spherical nucleus and usually one large dark vacuole whose contents give a staining reaction characteristic of tannins, are present in each cell (Figure 16). Cork cambium cells from cork bark accumulate large quantities

of starch and appear more nearly square in tangential section, but otherwise resemble phellogen cells from adjacent smooth bark (Figure 17).

Control trees have layers of suberized cork 21 to 64 cells thick but only a one to three cell layer of phelloderm (Figures 12, 14). Smooth bark areas above and below cankers have an amount of phelloderm similar to that of control trees, but the cork thickness ranged from 27 to 87 cells. Layers of 40 to 120 suberized phellem cells irregularly alternating with small amounts of crushed secondary phloem containing numerous sclereids were found to make up the bulk of cork bark which averaged 5.03 centimeters in thickness on trees studied (Figure 11; Table 2). The phelloderm of the most recent periderm was from one to three cells thick. Regularly distributed bands of darkly staining late cork cells which divide the empty phellem cells into layers, suggests that each phellogen might function for several years in the process of forming cork bark (Figures 10, 11).

Table 2. Mean thickness of dead bark and dimensions of component phellem cells.

Source of sample	Thickness of dead bark (cm)	Dimensions of phellem cells (μ)		
		radial	tangential	vertical
Controls	0.067	14.0	55.8	59.1
Cankers	5.030	27.9	38.4	56.2
Below cankers	0.623	15.2	50.3	58.7

Phellem cells from control trees (Figure 18) average 14 microns by 55.8 microns in radial and tangential dimensions, respectively, and 56.2 microns high. Cork cells from smooth bark areas have similar dimensions but those from cork bark averaged 27.9 microns and 38.4 microns in their radial and tangential measurements and 56.2 microns in height (Table 2). Vertical and tangential dimensions of cork cells appear to be a reflection of phellogen cell size (Figures 16-19) but radial expansion accounts for final radial dimensions.

Soft spongy dead bark of A. lasiocarpa var. arizonica averages 0.56 centimeter in thickness on samples collected and was found to be composed entirely of many layers of thin-walled, empty cork cells with slightly suberized walls (Figure 12). Their dimensions are greater than those of comparable cells from control trees and cork bark of diseased trees. Trees utilized for this study possessed only superficial cork.

Fungal hyphae were ubiquitous in cork bark (Figures 15, 19) but were not observed in the functional phellogen or secondary phloem of cankers and only rarely in phellem of adjacent smooth bark and control trees. Although hyphae encountered in tissues from different trees appeared similar, no attempt was made to show that they represented the same fungus.

Secondary Xylem

Wood of alpine fir is composed of relatively few cell types. Tracheids, a small amount of terminal parenchyma strands, and, infrequently, traumatic resin canals make up the vertical system. Secondary xylem from control trees (Figure 20), cankers (Figure 21) and adjacent smooth bark regions appear similar in cross section except for fewer continuous tiers of tracheids in cankers.

The mean number of cells in each radial row of the 1968 xylem increment is 16.2 for control trees, 15.4 for cankers, 15.3, 17.2 and 15.0 for smooth bark areas below, above and 180 degrees from cankers, respectively (Table 3). Width of the increment averages 435 microns in cankers and 530 microns in control trees. Mean width at smooth bark areas below cankers averages 483.9 microns (Table 3). Trees displaying cork bark show no significant difference in the amount of wood produced in 1968 beneath the thick bark of cankers and smooth bark 12 inches down the bole, in terms of cells per radial row ($t = 0.067$, $df = 8$) or increment width ($t = 0.113$, $df = 8$). Nor is there a significant difference between the number of xylem cells per tier in control trees and smooth bark regions below cork bark areas ($t = 0.698$, $df = 8$) or control trees and cork bark areas ($t = 0.592$, $df = 8$).

The cylinder of wood subjacent to cork bark may become slightly ridged beneath cracks in the rhytidome so that it appears polygonal in cross section. Figure 23 shows the irregular outline that annual rings

Table 3. Analysis of secondary xylem produced in 1968 by ten specimens of A. lasiocarpa. Each figure represents a mean of 50 measurements.

Source of sample	Tree number	Width of 1968 xylem increment		Thickness of tracheid walls microns		Length of tracheids (mm)	Number of rays per mm^2	Height of rays	
		cells	μ	early wood	late wood			cells	μ
Control	1	17.6	576	2.34	3.01	3.15	41.3	10.4	143
	2	15.4	483	2.28	3.41	2.87	42.9	10.2	139
	3	18.8	601	2.37	3.07	2.95	43.7	8.1	112
	4	13.6	470	2.26	3.29	3.00	46.4	8.8	126
	5	15.7	520	2.19	3.40	3.23	38.2	9.5	131
$\overline{\overline{X}}$ =		16.2	530	2.29	3.24	3.04	42.5	9.4	
Canker	6	15.0	447	2.30	3.21	2.23	43.7	8.3	118
	7	18.7	503	2.39	3.39	2.17	42.8	9.0	130
	8	12.3	369	2.33	3.47	2.10	38.9	8.5	122
	9	16.7	464	2.21	3.13	2.30	44.6	8.8	127
	10	14.2	392	2.27	3.71	2.38	39.9	8.6	121
$\overline{\overline{X}}$ =		15.4	435	2.30	3.38	2.24	42.0	8.6	
12" below canker	6	16.4	531	2.28	3.85	2.97	38.0	9.2	125
	7	17.7	574	2.18	3.47	2.87	35.7	10.5	145
	8	12.1	372	2.21	3.27	2.83	44.0	8.0	113
	9	16.2	500	2.35	3.38	3.20	41.3	8.1	116
	10	14.0	441	2.27	3.04	3.01	39.7	9.7	146
$\overline{\overline{X}}$ =		15.3	483	2.26	3.40	2.98	39.7	9.1	
12" above canker	6	17.0	522	2.22	3.67	3.09	42.9	9.0	117
	7	17.4	537	2.27	3.03	3.00	38.3	9.2	122
180^{o} from canker	9	14.9	490	2.31	3.34	3.14	37.7	8.1	120
	10	15.0	466	2.24	3.72	3.08	45.8	9.6	144

can assume underneath cork bark.

Kennedy and Wilson (1954a) have shown that tracheids comprising the outermost increments of alpine fir wood from 120-year-old smooth bark trees ten inches in diameter average 3.2 millimeters in length, while tracheids from beneath cankers on trees similar in size average only 2.4 millimeters. This study substantiates the above findings and discloses that no significant difference exists between the mean length of tracheids from control trees and those from smooth bark areas 12 inches below cankers on trees of nearly the same size and age ($t = 0.648$, $df = 8$). Tracheids from the various smooth bark areas are approximately of the same length. They average 3.04 millimeters in control trees, 2.98 millimeters at smooth bark areas below cankers, 3.05 millimeters at smooth bark areas above cankers and 3.11 millimeters at areas opposite cankers located on only one side of the bole (Table 3). However, tracheids from cork bark regions average 2.24 millimeters and are significantly shorter than tracheids from smooth bark regions below cankers ($t = 9.07$, $df = 8$) and tracheids from control trees ($t = 9.75$, $df = 8$).

Tangential cell wall thicknesses are similar for early wood tracheids from control trees (2.29 microns), cork bark regions (2.30 microns) and contiguous smooth bark areas above (2.25 microns), below (2.26 microns) and opposite (2.28 microns) cork bark cankers (Table 3). The thicker walls of late wood tracheids are of nearly the

same width regardless of source of sample. Those from wood subjacent to cork bark possess walls which average 3.38 microns thick, while walls of late wood tracheids in control trees and smooth bark locations above and below cork bark average 3.24 microns, 3.35 microns and 3.40 microns, respectively.

Traumatic resin canals (Figure 22) were observed in the late wood of control trees 1, 3 and 4 and in late wood of cankers and smooth bark regions of trees 6, 7, 8 and 10.

The radial system of alpine fir wood consists of uniseriate rays which are composed of ray parenchyma cells only and ray tracheids were not observed in any of the trees utilized for this study. Fusiform rays do not occur in grand or balsam fir (Chang, 1954a, b) and were not found in alpine fir.

Wood from cankers and smooth bark areas below cankers show no significant differences in ray number ($t = 1.25$, $df = 8$) or height ($t = 0.61$, $df = 8$). Rays average 42 per square millimeter of xylem under cork bark. Control trees average 42.5 per square millimeter and smooth bark areas below cankers average 39.7. Ray height averages 8.6 cells for cankers, 9.1 cells for areas below cankers and 9.4 for control trees (Table 3).

Secondary Phloem

Vertical elements of functional alpine fir phloem consist of sieve

cells, phloem parenchyma strands and vertical albuminous cells arranged in radial rows. Fusiform parenchyma cells were not observed in alpine fir phloem. Sclereids and crystals are confined to nonfunctional phloem.

The number of secondary phloem cells produced in each radial row during the 1968 growing season by control trees is not significantly different from the number produced in cankers ($t = 0.173$, $df = 8$) or smooth bark regions below cankers ($t = 0.713$, $df = 8$). Cork bark and smooth bark regions 12 inches below show no significant difference in number of cells per radial row in 1968 phloem increments ($t = 0.081$, $df = 8$) (Figures 26, 27). Control trees produce an average of 7.46 cells in each row; cork bark regions average 7.80 and smooth bark areas below cankers average 7.86 (Table 4). Although the 1968 phloem increment is slightly narrower in cankers than smooth bark areas 12 inches towards the tree base (177.76 microns vs. 181.17 microns), the difference is not significant ($t = 0.398$, $df = 8$). The increment in control trees averages 184.43 microns, a value not significantly different from either of those listed above. Approximately six of seven cells in each radial row of the 1968 increment in control and diseased trees are sieve cells (Table 4).

Sieve cells in control trees have a mean length of 2.77 millimeters while in smooth bark areas below cankers they average 2.69 millimeters. There is no significant difference between the above

Table 4. Analysis of secondary phloem produced in 1968 by ten specimens of A. lasiocarpa. Each figure represents a mean of 50 measurements.

Source of sample	Tree number	Cells per radial row	Sieve cells per radial row	Seive cell length (mm)	Number of rays per mm^2	Height of rays in cells	Number of radial plates per mm^2
Control	1	7.4	6.3	2.82	41.3	12.3	4.2
	2	7.3	6.1	2.64	42.9	12.0	4.8
	3	8.5	7.3	2.73	43.7	9.8	3.4
	4	7.1	6.0	2.81	46.4	10.7	2.8
	5	7.0	6.0	2.87	38.2	11.2	5.7
$\overline{\overline{X}}$ =		7.5	6.3	2.77	42.5	11.2	4.2
Canker	6	7.6	6.4	1.92	43.7	10.3	9.2
	7	10.0	8.7	1.86	42.8	11.0	7.8
	8	7.0	6.0	1.73	38.9	10.4	9.4
	9	7.2	6.1	2.06	44.6	10.7	8.0
	10	7.2	6.0	2.15	39.9	10.2	10.4
$\overline{\overline{X}}$ =		7.8	6.6	1.94	41.9	10.5	9.0
12" below canker	6	7.5	6.3	2.68	38.0	10.8	5.6
	7	9.7	8.1	2.59	35.7	12.3	5.2
	8	7.0	6.0	2.66	44.0	9.7	3.6
	9	7.1	6.0	2.83	41.3	10.0	4.3
	10	8.0	6.8	2.67	39.7	11.6	3.4
$\overline{\overline{X}}$ =		7.9	6.6	2.69	39.7	10.9	4.4
12" above canker	6	7.3	6.2	2.77	42.9	11.2	5.8
	7	7.1	6.0	2.83	38.3	10.8	4.7
180° from canker	9	6.9	6.0	2.64	37.7	9.8	4.0
	10	7.4	6.2	2.83	45.8	11.1	4.3

values ($t = 1.45$, $df = 8$). A significant difference does exist between the mean length of sieve cells in cankers ($x = 1.94$ mm) and control trees ($t = 10.31$, $df = 8$) and cankers and smooth bark areas below cankers ($t = 9.32$, $df = 8$). Average length of sieve cells from control trees is 0.27 millimeters less than the mean length of tracheids in the same radial tier. The differences in length between sieve cells and tracheids in cankers and smooth bark areas below cankers average 0.30 millimeter and 0.28 millimeter, respectively.

A wavy and more or less continuous band of parenchyma strands (Figures 24-27) was produced near the middle of the 1968 growing season in phloem of control trees and smooth and cork bark regions of diseased trees. Phloem parenchyma strands are approximately the same length as adjacent sieve cells in the same radial row and are subdivided into a variable number of short rectangular segments except for the tapered end cells (Figure 47). As seen in cross section, the cells are rectangular or square near the cambium but appear rounded and enlarged in the older phloem (Figures 24, 27). Contents of the segments making up a strand give staining reactions characteristic of lipids, tannins, resins and starch. Many of the parenchyma strand cells in nonfunctional phloem amass numerous rectangular to rhomboidal crystals (Figure 28) which Srivastava (1963) has suggested are calcium oxalate.

Parenchyma strand cells in nonfunctional phloem may

differentiate into sclereids or persist as living cells until cut off by deep phellogen. Sclereids occur in the 1967 and older phloem but only rarely in 1968 phloem (Figures 28, 30). There are no obvious differences in number, composition or position of parenchyma strands and sclereids or quantity of crystals in the phloem of control and diseased trees. Nonfunctional phloem of cork bark areas appears crushed to a greater degree than does phloem of smooth bark. Figure 30 illustrates radial rows bent nearly 45 degrees from their normal direction. Polarity of samples was not maintained during processing and thus direction of bend cannot be determined. Such distortion does not exist in phloem of smooth bark.

Nontanniferous parenchyma strands appearing in radial sections as plates of cells (Figure 33) are present in functional secondary phloem of control trees and smooth and cork bark areas of diseased trees. Bannan (1953) and Srivastava (1963) have described radial plates as phloem products of subdivided declining fusiform initials. In old stems of Thuja occidentalis, declining fusiform initials produce radially contiguous cells in the phloem but only sporadic cells in the xylem (Bannan, 1953). In the case of alpine fir, derivatives are produced only to the phloem side. Differentiation of some of the initial segments results in production of lower radial plates. Figures 34 and 35 illustrate radial plates two cells high which were produced by the last two remaining segments of declining fusiform initials.

Albuminous cells comprising radial plates and at margins of phloem rays contain little or no starch as indicated by the IKI staining reaction. Most submarginal and rarely marginal phloem ray cells contain numerous starch grains. Parts of radial plates extending into nonfunctional phloem are collapsed and thus can be distinguished from phloem rays.

There is no significant difference in number of radial plates in control trees and smooth bark areas of diseased trees ($t = 1.11$, $df = 8$). However, the number of radial plates in smooth and cork bark of the same tree are significantly different ($t = 7.0$, $df = 8$). There is also a significant difference in number of radial plates in control trees and cork bark areas of diseased trees. As seen in tangential section of phloem produced near the end of the 1968 growing season, the mean number of radial plates per square millimeter is 4.18 for control trees, 8.96 for cankers and 4.42 for smooth bark regions below cankers.

The radial system of functional A. lasiocarpa phloem consists of uniseriate rays made up of procumbent ray parenchyma and erect ray albuminous cells (Figures 42, 43). Secondary phloem from cankers and smooth bark areas below cankers show no significant differences in ray number ($t = 1.25$, $df = 8$) or ray height ($t = 0.48$, $df = 8$). As viewed in tangential sections, rays from cork bark areas average 41.9 per square millimeter of phloem. Control trees average 42.5 per

square millimeter and smooth bark areas below cankers average 39.7. Ray height averages 10.5 cells for cankers, 10.9 cells for areas below cankers and 11.2 for control trees (Table 4).

Rays in alpine fir are usually higher in phloem than in temporally related xylem. Phloem rays from control trees average 11.2 cells in height, but the same rays in xylem have an average height of 9.4 cells. Rays from canker areas average 10.5 cells in phloem and 8.6 cells in xylem. Smooth bark areas below cankers have phloem rays 10.9 cells high but xylem rays average only 9.1 cells (Tables 3, 4). Figures 37-39 show tangential sections through the same tiers of cells in phloem, cambium and xylem tissues of a control tree sampled on July 17, 1968. Xylem and phloem tissues are temporally related as evidenced by records of anticlinal divisions in areas of both sections not included in the photographs. The "3" and "8" in Figure 37 refer to the number of cells comprising phloem rays at the end of the arrows. Figure 38 shows initials producing the two rays to be composed of 3 and 8 cells, respectively. However, in xylem both rays are lower as indicated by the "2" and "5" (Figure 39).

Nonfunctional phloem contains resin cells similar to those described in grand fir by Saigo (1969). Many submarginal ray cells in two-year-old alpine fir phloem contain small amounts of resins (Figure 28). With age, more resins accumulate in some ray cells so that in older phloem large resin filled cells are present (Figure 29). No

obvious difference in number of resin cells in control and diseased trees was observed.

Vascular Cambium

On June 12, 1968 mitosis was occurring in the cambial zone of the ten trees listed in Table 5. One precocious sieve cell is present in most radial rows; however, secondary xylem is not yet differentiated. By June 26, 1968 the vascular cambium obtained a maximum mean with 7.4 cells under cork bark, 7.9 beneath smooth bark 12 inches below cankers and 7.5 in control trees. Few initials underwent mitosis after July 24 and the entire 1968 xylem and phloem increments were differentiated by August 15. At the end of the 1968 growing season, dormant cambial zones averaged 4.56 cells in width under cork bark, 4.74 beneath smooth bark below cankers and 4.36 in control trees. No significant differences exist between any of these values. Figures 24 and 25 show the cambial zones from a control tree and a canker as they appeared on July 12, 1968.

Vascular cambium of alpine fir is composed of long tapering fusiform initials, segmented declining fusiform initials and uniseriate ray initials (Figures 38, 49). Fusiform initials under cork bark are significantly shorter than those under smooth bark 12 inches down the bole ($t = 7.0$, $df = 8$). They average 1.87 millimeters under cork bark and 2.61 millimeter under smooth bark 12 inches below (Table 5).

Table 5. Analysis of dormant vascular cambium in ten specimens of A. lasiocarpa subsequent to the 1968 growing season. Each figure represents a mean of 50 measurements.

Source of sample	Tree number	Zone width (cells)	Fusiform initial length (mm)	Number of ray initials per mm^2	Ray initial height (cells)	Number of declining fusiform per mm^2
Control	1	4.1	2.74	41.3	12.5	4.2
	2	5.0	2.53	42.9	12.1	4.8
	3	4.4	2.66	43.7	10.2	3.4
	4	4.2	2.77	46.4	10.0	2.8
	5	4.1	2.69	38.2	11.7	5.7
$\overline{\overline{X}}$ =		4.4	2.68	42.5	11.3	4.2
Canker	6	5.2	1.90	43.7	10.4	9.2
	7	4.3	1.81	42.8	11.1	7.8
	8	4.2	1.69	38.9	10.6	9.4
	9	4.7	1.97	44.6	10.9	8.0
	10	4.4	1.98	39.9	10.4	10.4
$\overline{\overline{X}}$ =		4.6	1.87	42.0	10.7	9.0
12" below canker	6	5.3	2.64	38.0	11.0	5.6
	7	5.1	2.47	35.7	12.5	5.2
	8	4.4	2.56	44.0	9.8	3.6
	9	4.7	2.77	41.3	10.1	4.3
	10	4.2	2.60	39.7	11.8	3.4
$\overline{\overline{X}}$ =		4.7	2.61	39.7	15.0	4.4
12" above canker	6	4.9	2.68	42.9	11.4	5.8
	7	4.3	2.72	38.3	10.9	4.7
180^{o} from canker	9	3.9	2.58	37.7	10.0	4.0
	10	4.2	2.82	45.8	11.5	4.3

Fusiform initials from control trees have a mean length of 2.68 millimeters and are not significantly different in length from initials under smooth bark of diseased trees but are significantly different from ones in cankers.

According to cell wall configurations in secondary phloem, secondary xylem and vascular cambium, 41% of the fusiform initials subjacent to cork bark divided anticlinally at least once during the 1968 growing season (Figure 32; Table 6). Fusiform initials in cankers divided anticlinally at a rate significantly greater than that of initials in adjacent smooth bark areas ($t = 6.65$, $df = 4$) and control trees ($t = 7.09$, $df = 4$). The percentage of fusiform initials from control trees and smooth bark areas 12 inches below cankers that divided anticlinally is 17.6 and 15.6, respectively (Figure 32; Table 6). A record of an anticlinal division can be seen in Figure 24. Few initials in cankers underwent two successive anticlinal divisions in 1968 but fewer initials from smooth bark areas divided twice (Table 6).

Anticlinal partitions varied from nearly transverse to quite oblique but generally were of the pseudotransverse type. Except in cases where ray initials were cut from ends, partitions were usually situated near the middle of the dividing initial.

Under smooth bark areas 12 inches below cankers, an average of 7.3 out of 47 fusiform initials divided to give 15.3 daughter initials of which 8.7 or 55.5% were retained in the cambium. Similar values

Table 6. Frequency of anticlinal division in fusiform initials from six alpine fir specimens as inferred from secondary xylem and phloem.

Source of sample	Tree number	Number of tiers studied	Number of divisions observed	Initials dividing by anticlinal division					
				once		twice		total	
				no.	%	no.	%	no.	%
Control	1	45	9	9	20	0	0	9	20
	2	51	8	8	17	0	0	8	17
	3	49	9	7	14	1	2	8	16
$\overline{\overline{X}}$ =		48.3	8.7	8	17	.3	.7	8.3	17.6
Canker	6	58	29	21	36	4	7	25	43
	7	49	21	15	31	3	6	18	37
	8	48	26	16	33	5	10	21	43
$\overline{\overline{X}}$ =		51.7	25.3	17	33	4	7.6	21.3	41
12" below canker	6	54	10	8	15	1	2	9	17
	7	46	8	6	13	1	2	7	15
	8	41	6	6	15	0	0	6	15
$\overline{\overline{X}}$ =		47	8	6.7	14.3	.7	1.3	7.3	15.6

were observed for control trees. For every 51.7 initials subjacent to cork bark, 21.3 produced 46.7 daughter cells of which 12 or 25.3% were retained (Tables 6, 7, 8). Although more daughter cells were produced under cork bark, a greater percentage survived under smooth bark and the actual numbers retained in the two areas are not significantly different ($t = 1.21$, $df = 4$).

The fate of daughter cells resulting from anticlinal division of fusiform initials cannot clearly be determined by using only xylem or phloem. From observations of control tree xylem, 50.7% of the daughter fusiform initials produced during the 1968 growing season continued to function as initials while the remainder abruptly differentiated into elements of the secondary tissues (Figures 50-54; Table 7). The same tiers of cells in secondary phloem indicate a similar number of daughter initials retained in the cambium but showed no record of sudden differentiation of entire fusiform initials. Instead, the secondary phloem record indicates that 49.3% of the daughter initials became segmented and produced radial plates of vertical albuminous cells (Figures 44-48; Table 8). The number of declining fusiform initials in dormant vascular cambia of cankers is 2.7 times the number from adjacent smooth bark areas and control trees (Table 5). Declining fusiform initials which produced radial plates did not form cells in the xylem. Low declining fusiform initials can be separated from ray initials only on the basis of the products they do or

Table 7. Fate of daughter fusiform initials formed during the 1968 growing season in six alpine fir specimens as inferred from cell wall configurations in secondary xylem.

Source of sample	Tree number	Daughter fusiform initials: retained no.	retained %	differentiated no.	differentiated %	segmented no.	segmented %	total number produced
Control	1	10	56	8	44	0	0	18
	2	7	44	9	56	0	0	16
	3	9	53	8	47	0	0	17
	$\overline{\overline{X}}$ =	8.7	51	8.3	49	0	0	17
Canker	6	24	44	27	50	3	6	54
	7	12	31	27	69	0	0	39
	8	24	51	21	45	2	4	47
	$\overline{\overline{X}}$ =	20	42	25	55	1.7	3	47
12" below canker	6	16	63	6	32	1	5	19
	7	6	53	7	47	0	0	15
	8	4	50	6	50	0	0	12
	$\overline{\overline{X}}$ =	8.7	55	6.3	43	0.3	2	15

Table 8. Fate of daughter fusiform initials formed during the 1968 growing season in six alpine fir specimens as inferred from cell wall configurations in secondary phloem.

Source of sample	Tree number	Daughter fusiform initials						
		retained		differentiated		segmented		total number produced
		no.	%	no.	%	no.	%	
Control	1	10	56	0	0	8	44	18
	2	7	44	0	0	9	56	16
	3	9	53	0	0	8	47	17
$\bar{\bar{X}}$ =		8.7	51	0	0	8.3	49	17
Canker	6	24	44	0	0	30	56	54
	7	12	31	0	0	27	69	39
	8	24	51	0	0	23	49	47
$\bar{\bar{X}}$ =		20	42	0	0	26.6	58	46.6
12" below canker	6	16	63	0	0	7	37	19
	7	6	53	0	0	7	47	15
	8	4	50	0	0	6	50	12
$\bar{\bar{X}}$ =		8.7	55	0	0	6.6	45	15.3

do not produce. A low declining fusiform initial of radial plate-producing initial (rpi) is shown toward the top of Figure 38. It was producing a radial plate two albuminous cells high in the phloem (Figure 37) but was not producing xylem derivatives as denoted by the question mark in Figure 39. The vertical albuminous cell (va) at the bottom of Figure 37 is part of a radial plate. The initial producing it had differentiated as evidenced by the lack of an initial in the cambium (Figure 38).

The average number of ray initials observed in tangential section is nearly the same for control trees ($x = 42.5$) and smooth ($x = 39.8$) and cork bark areas ($x = 41.9$) of diseased trees (Table 5). No significant difference exists between any of the three values. Significant differences do not exist between the average heights of ray initials from control tree, cankers or smooth bark areas below cankers. Ray initial height averages 15, 10.7 and 11.3 cells in cankers, smooth bark areas below cankers and control trees, respectively.

As inferred from secondary phloem, rays under smooth and cork bark of diseased trees and smooth bark of control trees increased in height by an average of 0.46, 0.41 and 0.44 cells, respectively, during the 1968 growing season by transverse anticlinal divisions of the ray initials.

Conflicting data on origin or ray initials in the vascular cambium of alpine fir were obtained when both xylem and phloem were used as

records of past cambial development. Evidence from secondary xylem suggests that most new ray initials originate as small cells cut off from the ends and sides of fusiform initials (Figure 36; Table 9). Cell wall configurations in the secondary phloem of the same tiers indicate that nearly all ray initials develop from declining fusiform initials with few new ray initials arising from tips and sides of fusiform initials (Figure 36; Table 10). All the segments of subdivided fusiform initials may differentiate simultaneously into vertical albuminous strands and be lost from the cambium, but more often several of the initial segments continue to shorten and produce ray-like derivatives exclusively in the secondary phloem. Ultimately the initials differentiate and are lost from the cambium or become further subdivided and commence to produce rays in the xylem as well as in phloem. Since these events take place over several growing seasons, only parts of the entire process are recorded in the 1968 phloem increments. Older phloem increments in A. lasiocarpa are crushed and distorted and therefore it was necessary to assume that declining fusiform initials present in the cambium at the beginning of the 1968 growing season originated as described above. Observation of their differentiation or conversion to ray initials allowed the complete process of ray formation to be determined. Figures 44-54 represent sections through the same tiers of cells in phloem, cambium and xylem tissues of a control tree. Figures 44-48 illustrate serial tangential sections

Table 9. Description of ray initial formation in six alpine fir specimens during the 1968 growing season as inferred from the secondary xylem record.

Source of sample	Tree number	Number of ray initials formed	Number of ray initials formed via: terminal division	lateral division	segmentation of fusiform initial
Control	1	4	3	1	0
	2	2	1	1	0
	3	4	2	2	0
$\bar{\bar{X}}$ =		3.3	2	1.3	0
Canker	6	1	1	0	0
	7	6	4	2	0
	8	3	2	1	0
$\bar{\bar{X}}$ =		3.3	2.3	1	0
12" below canker	6	3	2	1	0
	7	2	1	1	0
	8	2	2	0	0
$\bar{\bar{X}}$ =		2.3	1.7	0.7	0

Table 10. Description of ray initial formation in six alpine fir specimens during the 1968 growing season as inferred from the secondary phloem record.

Source of sample	Tree number	Number of ray initials formed	Number of ray initials formed via: terminal division	lateral division	segmentation of fusiform initial
Control	1	4	0	0	4
	2	2	0	0	2
	3	4	0	0	4
$\bar{\bar{X}}$ =		3.3	0	0	3.3
Canker	6	1	0	0	1
	7	6	1	0	5
	8	3	1	0	2
$\bar{\bar{X}}$ =		3.3	.7	0	2.7
12" below canker	6	3	0	0	3
	7	2	0	0	2
	8	2	0	0	2
$\bar{\bar{X}}$ =		2.3	0	0	2.3

of phloem adjacent to the cambial zone which is represented by Figure 49. Figures 50-54 are photographs of every fifth serial section from xylem next to the cambial zone.

Phloem and xylem records of a fusiform initial undergoing a pseudotransverse anticlinal division are seen in Figures 45 and 53. Subsequent segmentation and decline are shown in Figures 46, 47 and 52. Figures 48 and 49 illustrate the loss of all but three segments from the cambium. As can be seen in Figures 50 and 51, no record of the declining fusiform initial is apparent in the xylem.

Although significantly more declining fusiform initials occur beneath cork bark than smooth bark 12 inches below ($x = 9.0$ vs. $x = 4.4$; $t = 7.0$, $df = 8$), apparently fewer develop into ray initials as evidenced by a comparable number of ray initials in cambia beneath cork and smooth bark (Table 5).

Two instances of high ray initials being bisected by intruding fusiform initials were observed in both xylem and phloem tissues of a control tree.

Figure 55 is a diagramatic presentation of selected patterns of fusiform initial activity which occurred in control and diseased trees during the 1968 growing season.

Figure 55a represents an initial which divided once anticlinally and both daughter cells survived. This type of activity was observed in control trees, cankers and below cankers seven, five and eight

times, respectively.

More often one daughter initial became segmented and commenced to produce a radial plate in the phloem as is shown by "b." Such a pattern was observed ten times in control trees, six times in smooth bark areas below cankers and 26 times in cankers.

In a number of cases both daughter initials became segmented as illustrated by "g." This pattern of activity was noted seven times in controls, six times below cankers and 21 times in cankers. Often submarginal segments of subdivided fusiform initials were lost so that several smaller isolated strands were produced as in the case of the lower daughter initial in "g."

The history of an initial which produced three daughter fusiform initials by means of successive anticlinal divisions is represented by "f." Two of the daughter initials were retained and one became segmented. One such case was found in control trees, two were found in areas below cankers and 12 were observed in cankers. Initial "h" did not divide anticlinally during the 1968 growing season. This was the case with 82.4% of initials in control trees, 59% of those in cankers and 84.4% of those in areas below cankers (Table 6).

"C" represents a segmented fusiform initial which differentiated into part of a radial plate and was lost from the cambium. This type of activity was recorded 16 times in control trees, 72 times in cankers and 13 times in areas below cankers.

"D" depicts the remaining segments of a declining fusiform initial taking on the function of a ray initial. This activity was observed nine times in controls, eight times in cankers and seven times in areas below cankers. Distinction between the last remaining segments of a subdivided fusiform initial and a newly formed ray initial is made on the basis of cells produced or not produced in the xylem. If the segments are not producing xylem derivatives they are considered to be part of a declining fusiform initial; however, with the commencement of xylem ray production the segments are referred to as ray initials. If the information from the activity of initials "b, " "f" and "g" (formation of subdivided fusiform initials) is combined with that obtained from initial "d" (conversion of part of a segmented fusiform initial to a ray initial), the principle method of ray initial formation in alpine fir is obtained. According to the phloem record over 92% of all new ray initials were formed by this method (Table 10).

Initials "e" and "f" illustrate the other method of ray initial formation in alpine fir. Here, new ray initials are cut off ends and sides of fusiform initials. Only 8% of all new rays were formed by this method as indicated by phloem analysis.

DISCUSSION

Periderm

The first formed cork cambium in alpine fir is normally replaced by a deeper seated phellogen within the first 100 years of secondary growth according to Chang (1954a); however, some slow growing specimens in the Canadian Rockies still retain the first phellogen after 200 years of growth. This extended longevity is probably related to the very slow increase in bole circumference.

Cork bark results when successive cork cambia which produce large increments of phellem, form deeper in cortical and eventually phloem tissues of smooth bark trees. This is the genetically determined pattern of rhytidome formation in many trees (Esau, 1965); however, in the process of canker formation, hard brittle dead bark is not sloughed off but is retained and develops deep fissures as the xylem cylinder expands.

Populus tremuloides Michx. in the Lake States has smooth bark but sometimes forms a thicker rough bark over large areas of the bole. In this case, a fungus, Macrophoma tumefaciens Shear, has been shown to bring about this more massive rhytidome formation (Kaufert, 1936).

Fungal hyphae are ubiquitous in cork bark of alpine fir and Kuijt (1969) has pointed out that cankers spread up, down and around

a tree bole in a manner similar to many pathological conditions. However, to date Koch's postulates have not been satisfied and it is not possible to give fungi a positive cause and effect role.

Kennedy and Wilson (1954a) inferred that cork bark is a genetically determined trait. This does not seem plausible if the irregular pattern of cork bark formation is considered. Though A. lasiocarpa var. arizonica and rhytidome producing specimens of alpine fir have both been called "cork-bark fir," only the former possesses bark with a texture similar to that of commercial cork. Bark produced on alpine fir trees with "cork bark disease" is very thick, hard and brittle.

Secondary Xylem

Tracheids in 1968 increments subjacent to cork bark of five trees averaging 181 years in age are 0.74 millimeter shorter than tracheids from smooth bark areas 12 inches below and 0.80 millimeter shorter than tracheids from five control trees with an average age of 175 years. These data agree with those presented by Kennedy and Wilson (1954a). They found that tracheids in the outer increment of 122-year-old smooth bark trees average 3.20 millimeters and those under cork bark of trees 190 years in age average 2.38 millimeters or a difference of 0.82 millimeter. These workers did not study older smooth bark trees or smooth bark areas below cankers. Average

tracheid length in areas adjacent to cork bark is similar to that of control trees. Thus tracheid length is not constant throughout the 1968 increment of a canker bearing tree as might be inferred from Kennedy and Wilson's (1954a) work, but instead is a function of bark type.

Wood under cork bark has a higher specific gravity than wood from control trees (Kennedy and Wilson, 1954b). Differences in cell length, cell wall thickness or a combination of both could account for differences in wood density. This study revealed no significant differences in wall thickness or lacunar diameter of tracheids comprising wood under cork bark and smooth bark. Wood subjacent to cork bark is composed of shorter cells and thus has more cell wall material per unit volume than wood from smooth bark areas below cankers and from control trees. It can be concluded that the density variability in alpine fir trees studied is a function of cell length.

Balsam woolly aphids bring about a decrease in mean tracheid length (3.77 mm to 2.14 mm) and a doubling of xylem ray number in grand fir (Doerksen, 1964). Although tracheids under cork bark are considerably shorter than those under smooth bark, ray number is essentially the same under both types of bark.

Xylem increments subjacent to cork bark do not significantly differ qualitatively or quantitatively from those under adjacent smooth bark or from control trees except for form.

Secondary Phloem

Chang (1954a, b) found that sieve cells average 2.35 millimeters long in grand and balsam fir whereas Saigo (1969) reported them to average 3.0 millimeters in healthy grand fir trees. Sieve cells in 1968 increments of five smooth bark alpine fir trees averaging 181 years in age were found to have an average length of 2.77 millimeters, or 0.27 millimeter shorter than tracheids in the same radial tiers and produced at about the same time during the growing season. Sieve cells from cork bark average 0.30 millimeter shorter than tracheids in the same tiers, and the difference for smooth bark areas below cankers is 0.29 millimeter.

Sieve cells from cork bark average 0.83 millimeter shorter than those from control trees and 0.75 millimeter shorter than sieve cells from smooth bark below cankers. These values closely approximate differences in length of tracheids from the same areas.

Tracheids generally elongate more than sieve cells in the process of differentiating from mother cells (Esau, 1965). Thus in slow growing alpine fir, it appears that tracheids elongate, on the average 0.30 millimeter more than sieve cells.

Ten slow growing alpine fir trees (five healthy and five diseased trees) produced between six and seven sieve cells and one or two phloem parenchyma strands in each radial row of the 1968 phloem increment, regardless of bark thickness. Healthy, more vigorous

balsam fir (Chang, 1954a) and grand fir (Chang, 1954b; Saigo, 1969) produce a comparable number of each cell type. Canker formation cannot be attributed to increased secondary phloem production.

Thuga occidentalis phloem subjected to radial pressure shows fewer thick-walled fibers with reduced lignin content than does phloem from normal areas (Bannan, 1957). Fibers were not observed in phloem of control or diseased alpine fir trees. Sclereids do occur in phloem of cankers, smooth bark areas below cankers and control trees. No obvious differences in number or size of sclereids in phloem from the three sources were noted.

Although phloem ray number is similar to xylem ray number in alpine fir, rays in wood are significantly lower than those in phloem. This condition exists under cankers and smooth bark of diseased trees and smooth bark of control trees. In most members of the Pinaceae, initials that produce marginal ray albuminous cells form ray tracheids at the margins of xylem rays (Esau, 1965); however, Abies lacks ray tracheids (Phillips, 1948).

Vertical albuminous cells were found to be more numerous in cork bark than in adjacent smooth bark or control trees. Bannan (1953) and Srivastava (1963) have described radial plates of albuminous cells as phloem products of declining fusiform initials. Since their number is a function of declining fusiform initial number, quantitative disparaties will be considered in the following section.

Vascular Cambium

Fungi observed in cork bark do not modify the temporal pattern of cambial activity or vascular tissue differentiation. Maximum and minimum widths of the cambial zone and time of cambial activity inception and cessation are similar for control trees, cankers and areas above and below cankers.

Shorter length of tracheids and sieve cells subjacent to cork bark might be a reflection of shorter fusiform initials or the result of less elongation of differentiating xylem and phloem mother cells.

The first possibility seems to be more plausible. Fusiform initials from cork bark areas average 0.74 millimeter shorter than initials from adjacent smooth bark areas and 0.81 millimeter shorter than those from control trees. These differences are comparable to disparaties in length of sieve cells or length of tracheids from control trees, cankers and areas below cankers.

Bannan (1957) has shown that as a consequence of an accelerated rate of anticlinal division, the average length of fusiform initials becomes markedly reduced. Such an explanation may be in order in the case of alpine fir. The frequency of anticlinal division of fusiform initials under cork bark is over twice that of initials under nearby smooth bark or smooth bark of control trees. Smith (1967) has shown that 13.3% of the fusiform initials in grand fir divided anticlinally prior

to infestation by balsam woolly aphid but 58% divided after infestation. A marked reduction in mean initial length accompanied the increase in rate of anticlinal division.

Although the rate of anticlinal division in normal alpine fir and in grand fir (Smith, 1967) are similar (17.7% and 13.3%), the values for other species of Abies might vary considerably. Alpine fir utilized for this study were much slower growing trees than the grand fir studied by Smith. In Pinus, Picea and Pseudotsuga, small annual xylem increments show a higher rate of anticlinal division than do wider increments. In addition, the frequency of anticlinal division of fusiform initials varies from species to species (Whalley, 1950), among individuals of the same species (Bannan, 1950) and in different areas of a given stem (Bannan, 1957). Bannan (1953) found that where radial growth is achieved against resistance, the effect of the increased pressure on the cambium is to stimulate anticlinal divisions to several times the normal rate.

The possibility exists that cork bark has a girdling effect on the expanding cylinder of secondary xylem and brings about a build up of abnormal pressures which effect a higher rate of anticlinal divisions. Crushing of nonfunctional phloem in cork bark suggests that pressures do develop.

Fungi found in cork bark may produce a growth promoting substance which stimulates fusiform initials to divide at abnormal

rates. Balch et al. (1964) have given a similar explanation for the increase in anticlinal divisions in balsam woolly aphid infested balsam fir. Certainly much more work needs to be done before any definite conclusions with regard to the cause of increased anticlinal divisions under cork bark can be drawn.

In conifers, more new fusiform initials are produced than are needed for circumferential expansion of the vascular cambium and are lost (Bannan, 1950, 1956; Bannan and Bayly, 1956; Srivastava, 1963). Bannan (1950) found that subsequent to anticlinal division, in 26.4% of the cases observed, both daughter initials were lost from the cambium of Chamaecyparis within a year. In 43.3% of the cases one daughter cell persisted and in 30.3% both persisted. Corresponding figures for Thuja (Bannan, 1956) and aphid infested A. grandis (Smith, 1967) are 8%, 48%, 44% and 36%, 32%, 32%, respectively.

Under cork bark of slow growing alpine fir trees following 33% of the anticlinal divisions observed, both daughter cells were lost by the end of the 1968 growing season, in 41% one persisted and in 8% both persisted. Values for adjacent smooth bark and control trees are 27%, 27%, 36% and 28%, 40%, 28%, respectively. Since initials which divided twice do not fit into any of the three categories, they are not included in the figures and thus the sum of the values does not equal 100%.

Data from this study agree with Smith's (1967) in that an increase in anticlinal division rate tends to decrease the chances of both

daughter initials surviving and increases the probability that they both will be lost.

Loss of fusiform initials in some cases appears to be related to tree vigor. In T. occidentalis survival rate is greater when large increments of xylem are produced than when small ones are formed. In some slow growing specimens, the rate of production and rate of loss were found to be equal (Bannan, 1960).

Smith (1967) noted a higher rate of anticlinal division in aphid infested balsam fir trees led to a net decrease in number of fusiform initials. Before infestation there were fewer anticlinal divisions but a net increase in number of fusiform initials. Bannan and Bayly (1956) noted that the rate of decline of fusiform initial increases with a greater frequency of anticlinal divisions.

The same trend was observed in alpine fir trees. In three control trees (numbers 1, 2, 3), a total of 25 fusiform initials divided anticlinally 26 times to give 51 daughter initials of which 25 became segmented and/or lost. Thus there was a net gain of one initial during the 1968 growing season. Cankers on trees 6, 7 and 8 during the same period showed 64 initials dividing to give 140 daughter cells. Only 60 were retained for a net loss of four initials. Areas below the same cankers showed a net gain of four cells. Here 22 initials divided 24 times to give 45 daughter cells of which 26 survived.

Although there was a net loss of initials under cork bark and a

net gain under adjacent smooth bark and in control trees, the differences are not great enough to be considered significant. Since in all three areas the rate of fusiform initial production was nearly equal to rate of loss, bark thickness and rate of anticlinal division do not effect a significant net change in number of fusiform initials present in the vascular cambium. A slow growth is probably the regulating factor.

Loss of fusiform initials occurs by two methods in T. occidentalis. A few of the excess initials differentiate into vertical elements but the majority become transversely subdivided with various proportions of the segments becoming ray initials. Segments not forming ray initials differentiate into elements of the secondary tissues (Bannan, 1953).

According to the secondary phloem record, loss of fusiform initials from alpine fir cambia takes place mainly by the latter of the two methods. Secondary xylem shows little record of segmentation; instead, radial tiers of tracheids come to an abrupt end as if the fusiform initials producing them had lapsed into maturity.

Bannan (1953) has shown that as a rule xylem and phloem elements in dying rows in Thuja do not conform exactly with regard to cell length or occurrence of segmentation. He found evidence of subdivision in phloem when none was present in xylem. In such cases he proposed that the fusiform initial producing a dying tier underwent subdivision before the final periclinal division and subsequent

differentiation into phloem parenchyma, while the earlier formed periclinally dividing xylem mother cells differentiated into tracheids.

Ray initials arise from segmented fusiform initials in a number of conifers (Bannan, 1950, 1953; Grillos and Smith, 1959; Srivastava, 1963). Radial plates (radial files of phloem cells marking the transition from elongated elements to shortened elements) were observed in a number of conifers by Chrysler (1913). He recognized that they represent a passing phase in the origin of rays.

In alpine fir radial plates are not always indicative of ray initial formation. In many cases, segmented fusiform initials producing radial plates lapse into maturity without forming ray initials. Bannan (1953) and Srivastava (1963) have interpreted radial plates in a similar fashion.

The xylem record indicates that new ray initials in grand fir are cut off the ends and sides of fusiform initials (Smith, 1967). Barghorn (1940) described various modes of ray initial origin in conifers but suggested that most new ray initials originate from the apex or side of fusiform initials.

Advocators of segmented fusiform initials as a source of new ray initials for the most part have used phloem record whereas xylem has been employed by those suggesting that ray initials are cut off of fusiform initials. Alpine fir phloem record indicates the former method while xylem suggests the latter.

A high rate of periclinal division in a given initial effects a complete xylem and phloem record of cambium activity; however, a low rate can lead to an incomplete record in xylem but not phloem (Bannan, 1953). The latter observation is applicable to alpine fir utilized for this study. The xylem record in the slow growing trees studied is incomplete. Xylem derivatives are not normally produced by segmented fusiform initials so that instead of a record revealing gradation from vertically elongated cells to radially extended cells, there is an abrupt ending of dying tiers of tracheids. Later in the growing season one or more of the segments of a declining fusiform initial may commence to function as ray initials and produce contiguous cells in the xylem. Thus the first tangential sections of 1968 xylem seldom show a record of fusiform initials which became segmented during the last part of the previous growing season. The sudden appearance of xylem rays in the latter part of the 1968 increment suggests that ray initials were derived from ends or sides of intruding fusiform initials. However, the record of activity left in phloem by the same initials indicate that most new ray initials in alpine fir are formed from segmented fusiform initials. Records of two ray initials being cut off from tips of fusiform initials were left in secondary phloem. Approximately the same number of new ray initials were formed by the two methods in control trees, subjacent to cork bark and adjacent smooth bark. So it appears that bark thickness and

frequency of fusiform initials dividing anticlinally have no quantitative or qualitative effect on ray initial formation in A. lasiocarpa.

Initials producing marginal ray albuminous cells leave no xylem record. Whether this phenomenon is a function of tree vigor or is ubiquitous in the species remains to be seen.

A study of xylem and phloem of more vigorous trees needs to be undertaken before an unequivocable picture of ray initial formation in alpine fir can be determined.

SUMMARY

Ten alpine fir trees of comparable vigor growing in eastern British Columbia were sampled on a weekly basis to determined the structure of cork bark and its effects on cambial activity and vascular tissue production. Five of the trees studied were smooth bark controls and five trees possessed varying amounts of cork bark on their boles. The latter trees were sampled at cork bark regions and nearby smooth bark areas. Samples of A. lasiocarpa var. arizonica were obtained from Arizona so that a comparison with bark from canker bearing trees could be made. All samples were processed by standard microtechnique procedures.

Control trees may retain their superficial phellogen for over 200 years and possess relatively thin layers of cork with a smooth surface texture. Smooth bark areas near cork bark show the same type of structure and activity. Rough cork bark results when the phellogen is stimulated to produce large increments of phellem. Such cork cambia are regularly replaced by others forming successively deeper in cortical and secondary phloem tissues. As a result cork bark consists primarily of phellem with varying amounts of dead secondary phloem. Dead bark is not sloughed off so that it accumulates to a thickness of several inches. Expansion of the secondary xylem cylinder causes deep fissures to develop. Cells comprising

cork cambia from cork bark areas and smooth bark areas are of different dimensions and give dissimilar staining reactions.

Fungal hyphae are ubiquitous in dead cork bark but not in adjacent living tissues. Kuijt (1969) has also observed fungi in phellem cells. Hyphae are rarely seen in phellem of control trees and smooth bark of canker bearing trees. Fungi may be a cause or effect of cork bark.

Cork bark fir from Arizona possess thin-walled phellem cells which do not remotely resemble the thick-walled cells of cork bark cankers.

Width of wood increments under cork bark is not significantly different from that under adjacent smooth bark. Tracheids from canker areas are significantly shorter than those of adjacent smooth bark areas and control trees. Since cell wall thickness varies little between the three sources, it is thought that a greater density of wood under cork bark can be attributed to shorter tracheid length. Wood anatomy in other respects is similar in control and canker bearing trees.

The amount of secondary phloem produced at cankers is essentially the same as the amount produced at adjacent smooth bark areas and in control trees of approximately the same vigor. Cork bark formation is not caused or accompanied by increased secondary phloem production. Sieve cells in cork bark are significantly shorter than

those from adjacent smooth bark and from control trees. Radial plates of albuminous cells are significantly more numerous in cork bark phloem than in adjacent smooth bark or control tree phloem.

Vascular rays average nearly two cells lower in xylem than in phloem of control and canker bearing trees. Apparently ray initials fail to produce xylem ray derivatives opposite marginal ray albuminous cells. Other aspects of secondary phloem anatomy are similar in the three sample sources.

Shortened tracheids and sieve cells of cankers are reflections of fusiform initial length. Fusiform initials beneath cork bark are significantly shorter than those under nearby smooth bark and those of control trees. Elongation of mother cells during differentiation does not play a role in bringing about longer cells in vascular tissue under smooth bark.

Shortened fusiform initials under cork bark result from a 2.7 increase in rate of anticlinal division. Concommitant with an accelerated rate of multiplicative division is a nearly three fold increase in rate of fusiform initial loss so that the net change in number of fusiform initials is similar under smooth and cork bark. Abnormal pressure and fungal secretions are among the possible effectors of an increased rate of anticlinal division in the cambium in cork bark areas.

Fusiform initials are lost from the cambium by a method

common to other conifers. Subdivision of a fusiform initial is followed by differentiation of most or all of the segments. Subdivided fusiform initials fail to produce xylem derivatives. Segments not differentiated become ray initials. Based on secondary phloem record, this is the primary method of ray initial formation in control and canker bearing trees. Only 8% of all ray initials were cut off ends and sides of fusiform initials.

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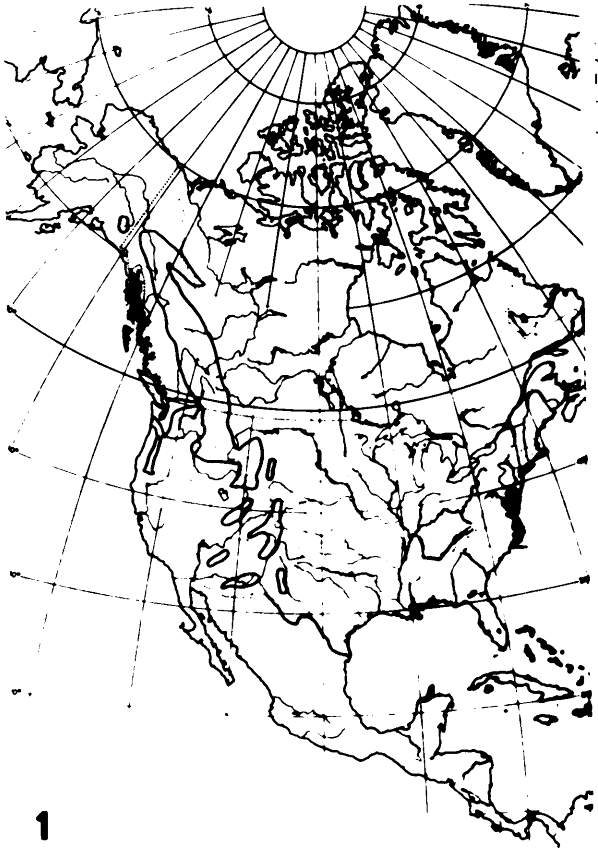
APPENDICES

Figure 1. Distribution map of alpine fir.

Figure 2. Map showing the two alpine fir collection sites.



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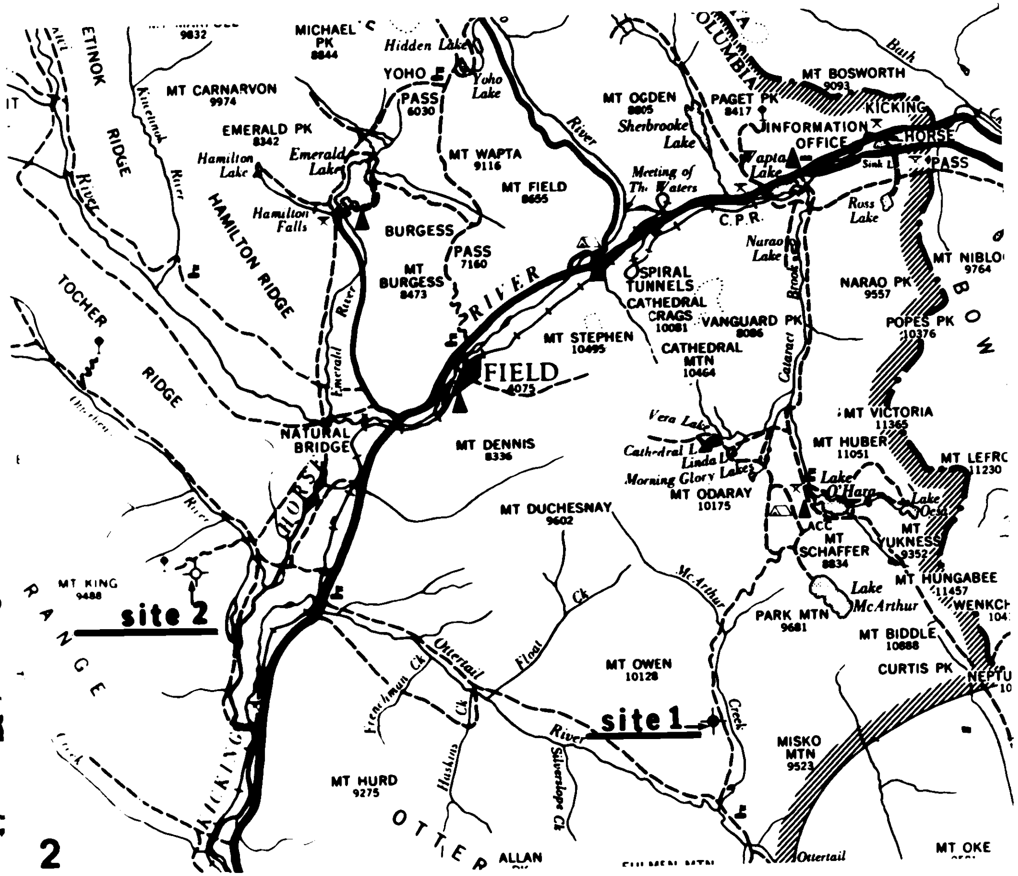

MICHAEL'S PK 8844
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YOHO PASS 6030
Yoho Lake
MT CARNARVON 9974
EMERALD PK 8342
Emerald Lake
Hamilton Lake
Hamilton Falls
BURGESS PASS 7160
MT BURGESS 8473
MT WAPTA 9116
MT FIELD 8655
MT OGDEN 8805
Sherbrooke Lake
Meeting of The Waters
PAGET PK 8417
INFORMATION OFFICE
Wapta Lake
MT BOSWORTH 9093
KICKING HORSE PASS
C.P.R.
Ross Lake
Narao Lake
NARAO PK 9557
SPIRAL TUNNELS
CATHEDRAL CRAGS 10081
VANGUARD PK 8086
CATHEDRAL MTN 10464
MT STEPHEN 10495
FIELD 4075
TOCHER RIDGE
HAMILTON RIDGE
NATURAL BRIDGE
MT DENNIS 8336
Vera Lake
Cathedral L.
Linda L.
Morning Glory Lakes
MT ODARAY 10175
MT VICTORIA 11365
MT HUBER 11051
MT LEFROY 11230
Lake O'Hara
Lake Oesa
MT YUKNESS 9352
MT HUNGABEE 11457
MT SCHAFFER 8834
Lake McArthur
PARK MTN 9681
MT BIDDLE 10888
CURTIS PK
MT DUCHESNAY 9602
MT KING 9488
site 2
RANGE
MT OWEN 10128
site 1
Ottertail River
Float Ck
McArthur Creek
Frenchman Ck
MISKO MTN 9523
MT HURD 9275
OTTER
ALLAN
MT OKE
POPES PK 10376
MT NIBLOCK 9764
BOW

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Figure 3. Smooth bark control tree showing two sampling wounds.

Figure 4. Cork bark fir (A. lasiocarpa var. arizonica) bole.

Figure 5. Alpine fir bole covered with cork bark.

Figure 6. Bark thickness of cork bark area (center) and smooth bark area 12 inches below (left).

Figure 7. Smooth bark control (background) and cork bark bearing tree (foreground).

Figure 8. Two cork bark cankers on an alpine fir bole.

Figure 9. Irregular distribution pattern of cork bark areas.

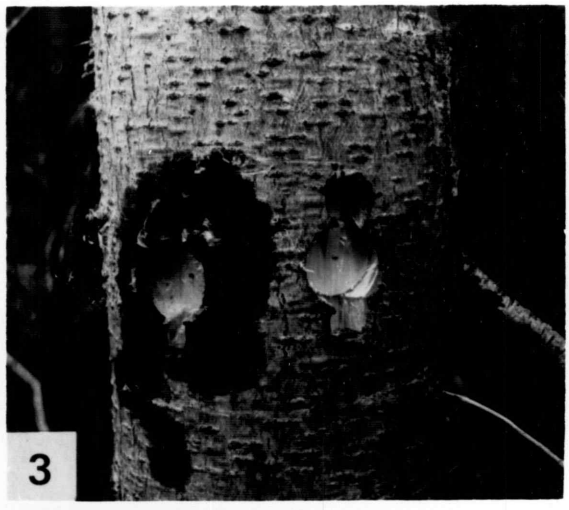
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Figure 10. Cross section of cork bark rhytidome composed of many cork increments (ic). 80X.

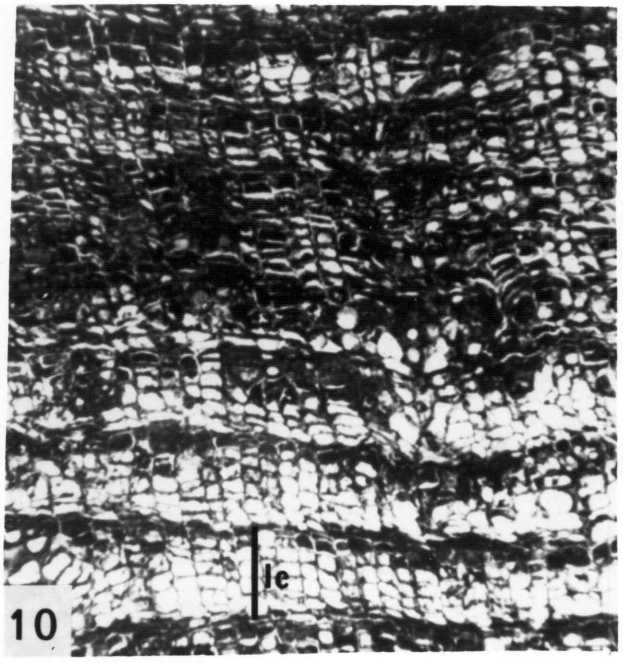
Figure 11. Cross section of cork bark rhytidome composed of increments of dead cork cells (lc, dc) and dead secondary phloem (sp). 150X.

Figure 12. Cross section of control tree periderm; ph, phellem; p, phellogen. 100X.

Figure 13. Cross section of A. lasiocarpa var. arizonica periderm; ph, phellem; p, phellogen. 150X.

Figure 14. Cross section of part of control tree periderm; ph, phellem; p, phellogen; pd, phelloderm. 800X.

Figure 15. Cross section of cork bark phellem containing fungal hyphae (fh). 350X.



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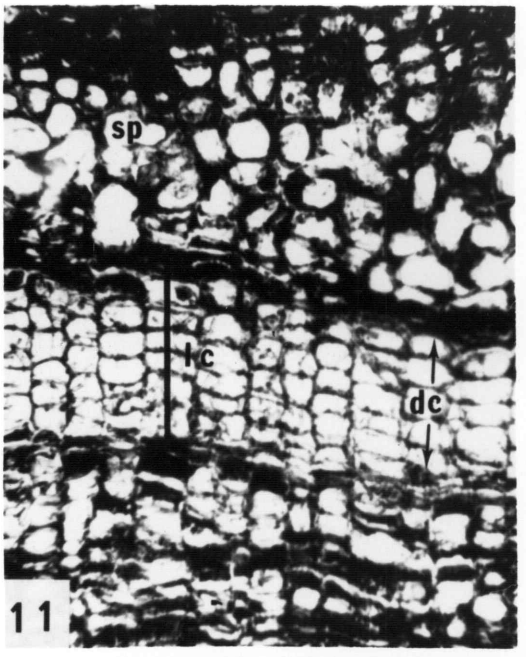

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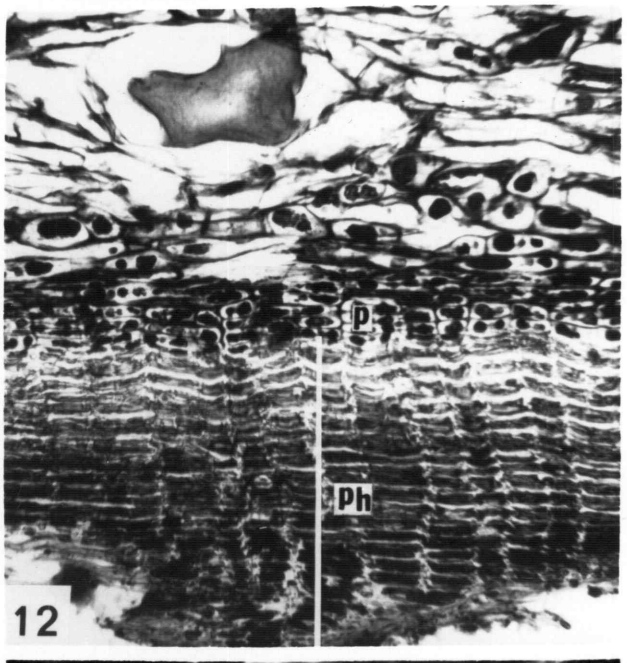

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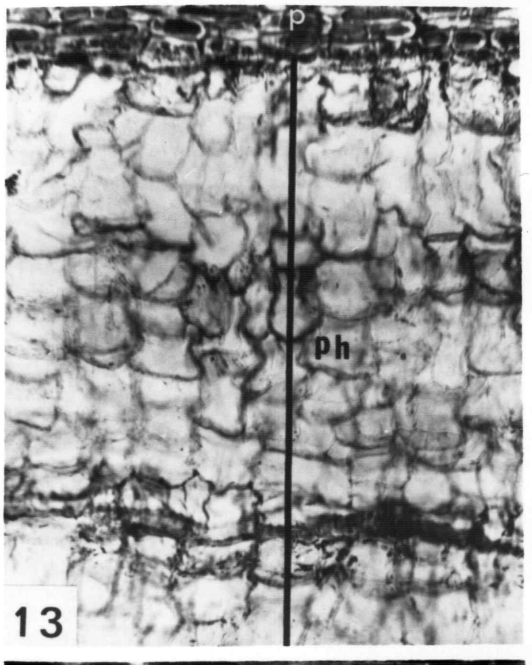

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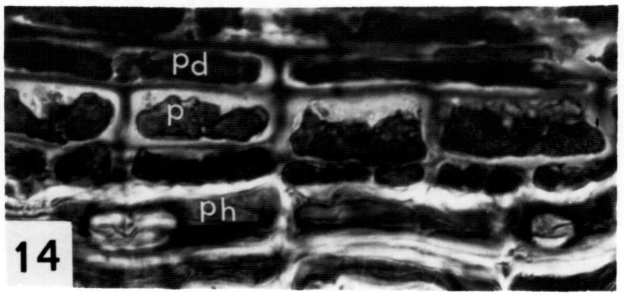

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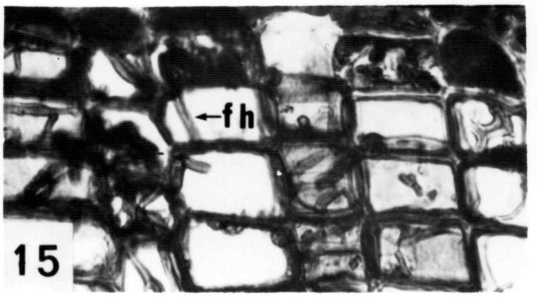

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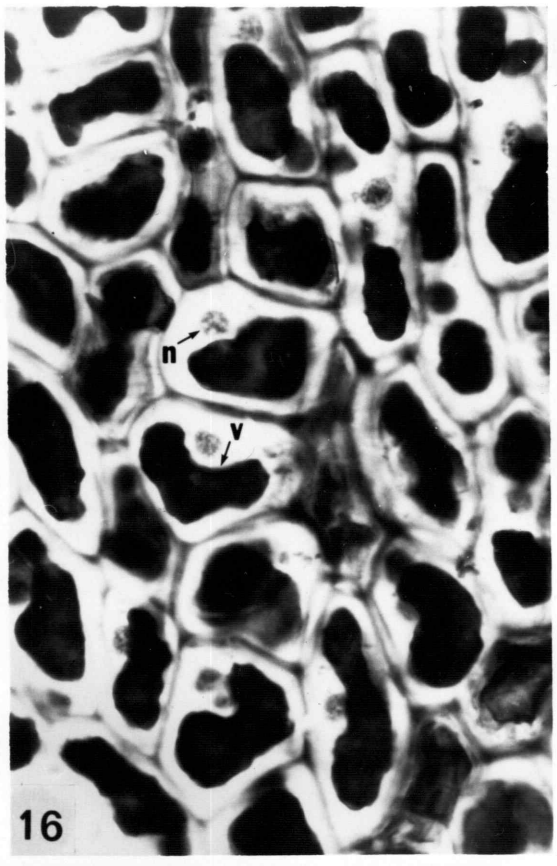
Figure 16. Tangential section of control tree phellogen showing each component cell with a nucleus (n) and vacuole (v). 400X.

Figure 17. Tangential section of cork bark phellogen showing starch grains (sg) in component cells. 400X.

Figure 18. Tangential section of control tree phellem. 400X.

Figure 19. Tangential section of cork bark tree phellem showing fungal hyphae (fh). 400X.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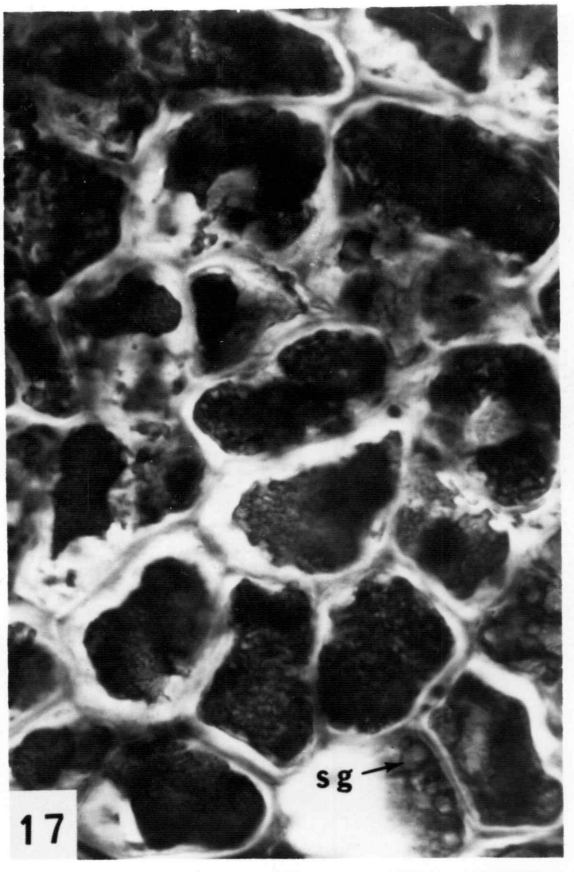
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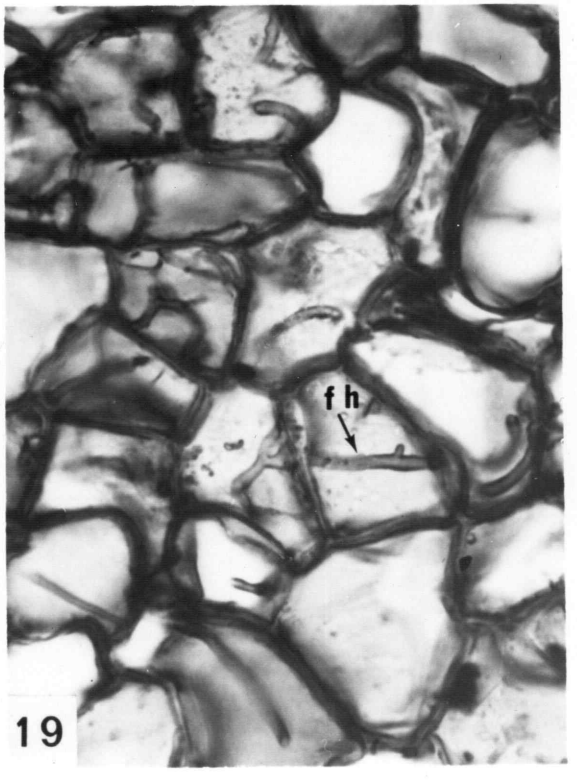
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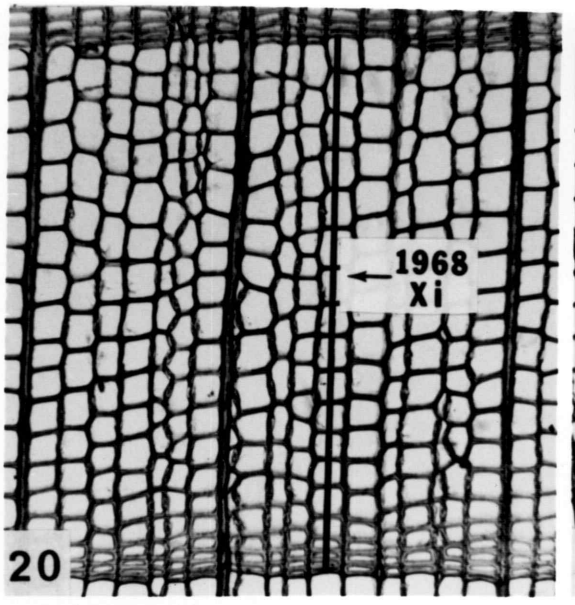
Figure 20. Cross section of 1968 xylem increment in control tree number 1. 120X.

Figure 21. Cross section of 1968 xylem increment under cork bark of tree number 9. 120X.

Figure 22. Cross section of alpine fir secondary xylem with traumatic resin canals (trc). 120X.

Figure 23. Secondary xylem cross section showing irregular outline of increment beneath cracks in cork bark. 100X.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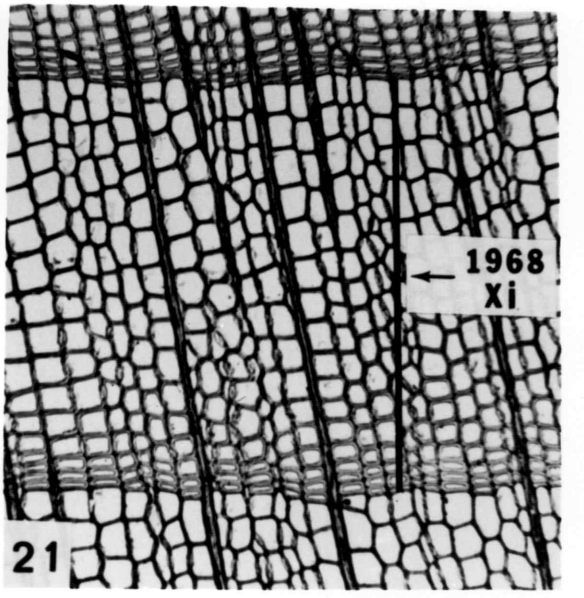
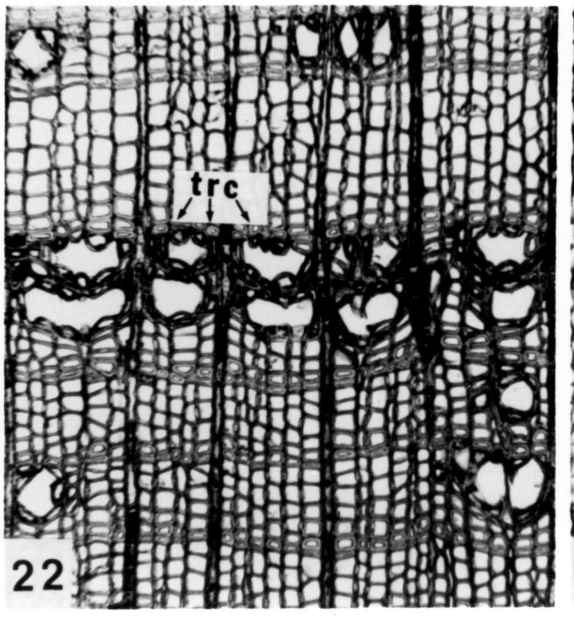

1968
Xi
21


trc
22

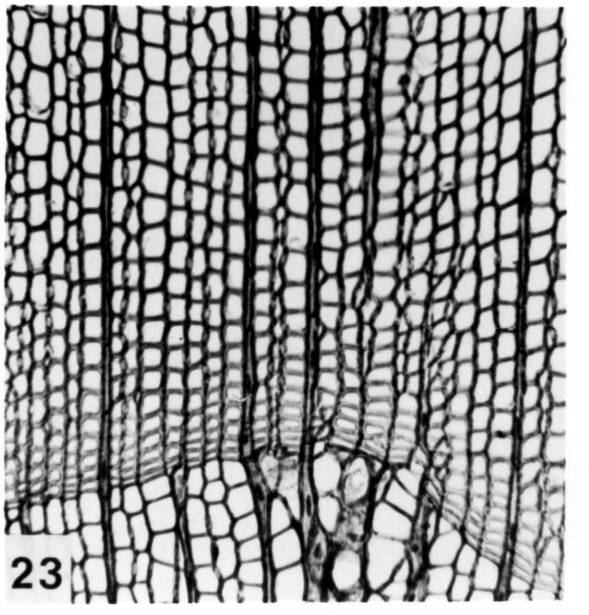

23

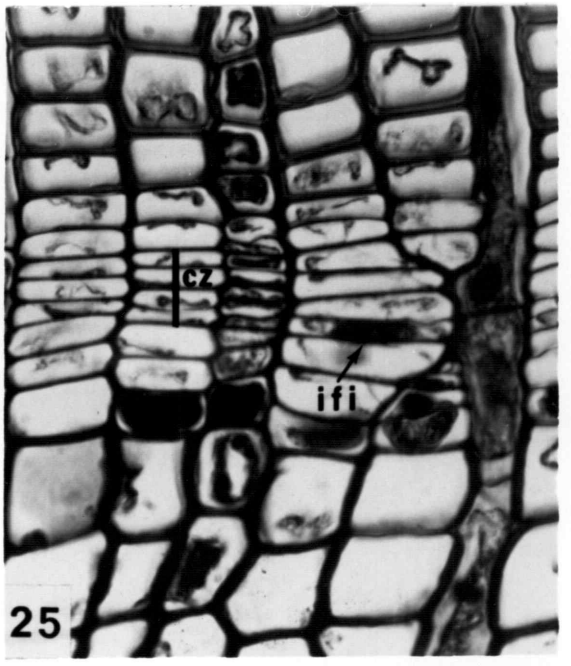
Figure 24. Cross section of control tree cambial zone (cz) with record of a recent anticlinal division (adr). 400X.

Figure 25. Cross section of canker cambial zone (cz) showing the record of fusiform initial loss and intrusion of the fusiform initial from an adjacent tier (ifi). 400X.

Figure 26. Cross section of 1968 phloem increment in control tree number 3 showing parenchyma strands (ps). 400X.

Figure 27. Cross section of 1968 phloem increment under cork bark of tree number 7 showing parenchyma strands (ps.). 400X.

24



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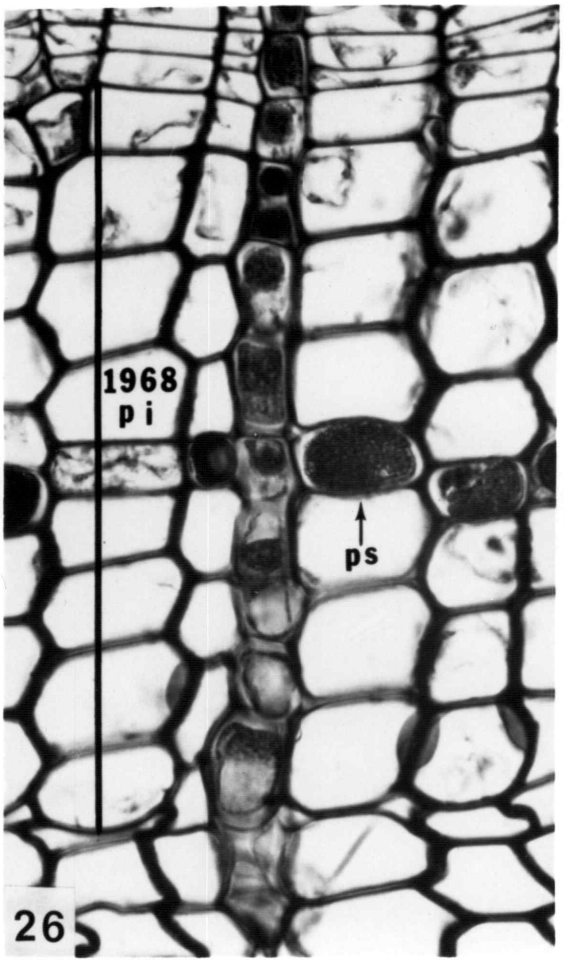
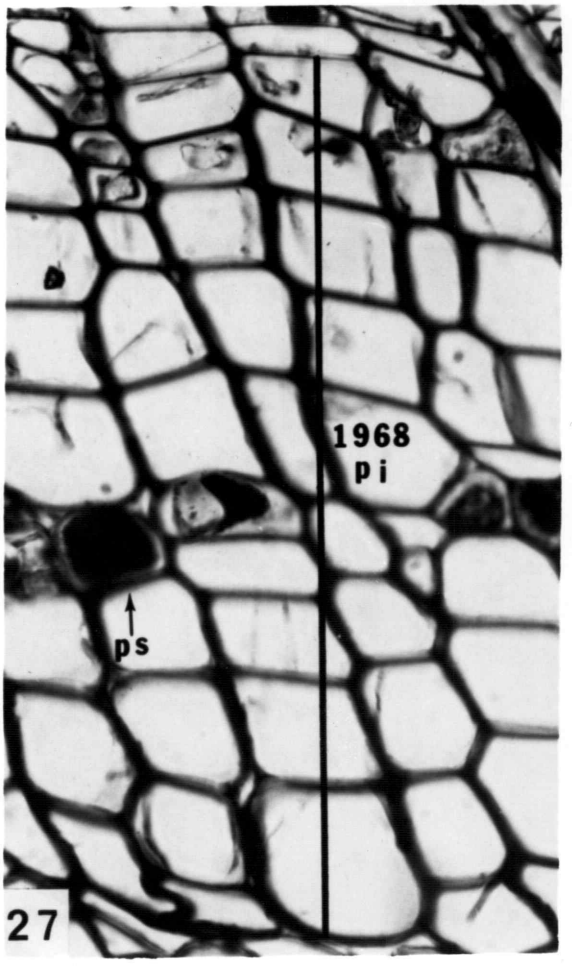


26



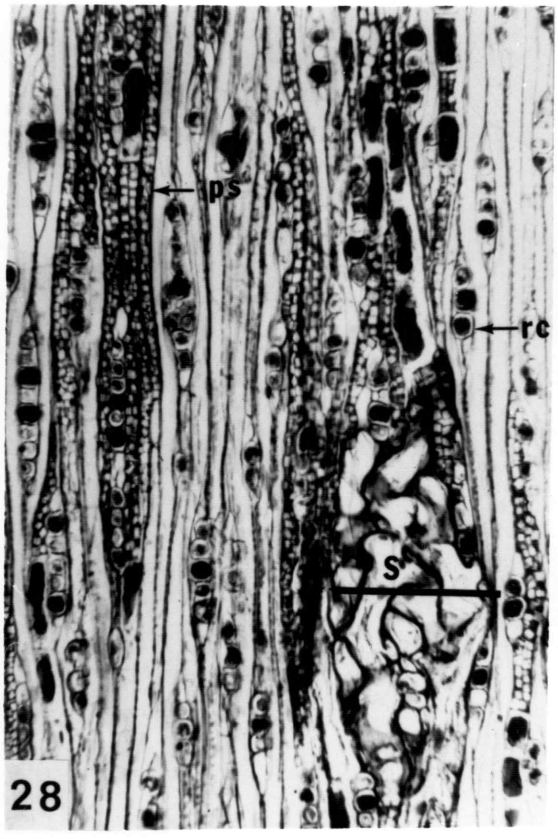
27

Figure 28. Tangential section of nonfunctional phloem with sclereids (s), small resin cells in rays (rc) and crystal containing parenchyma strands (ps). 100X.

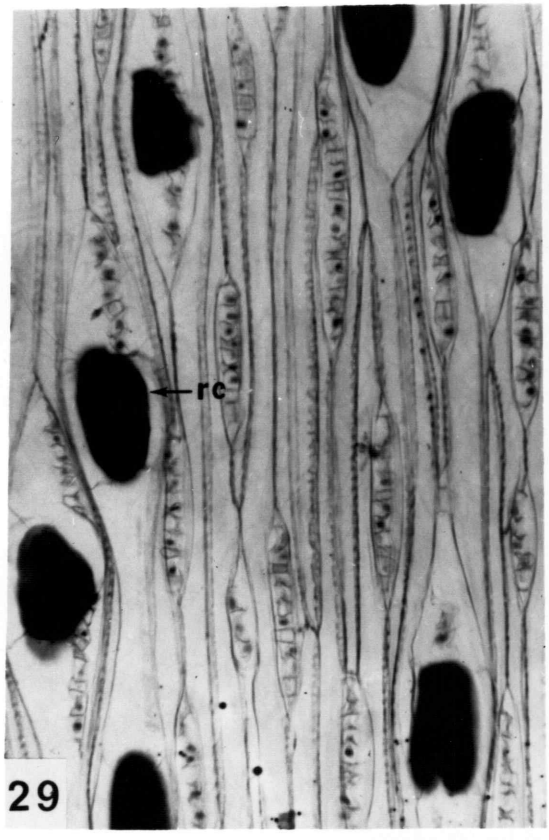
Figure 29. Tangential section of older nonfunctional phloem with enlarged resin cells (rc). 120X.

Figure 30. Cross section of cambial zone and adjacent vascular tissues of canker tree sclereids (s). 100X.

Figure 31. Cross section of cambial zone (cz) and adjacent vascular tissues of control tree with phloem ray (pr) and parenchyma strands (ps). 300X.



28



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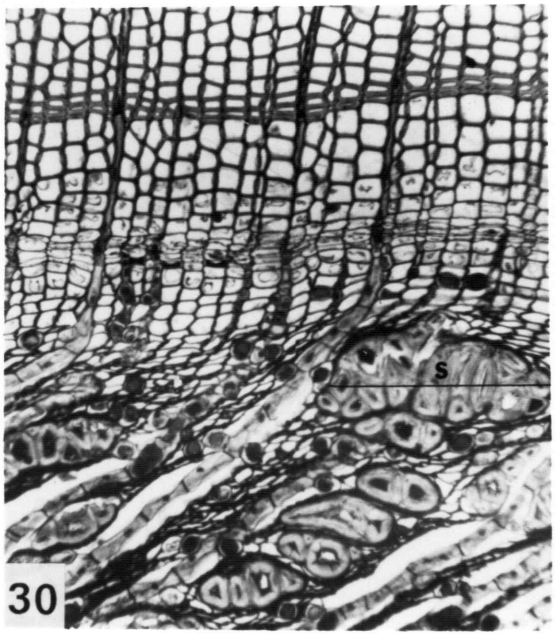

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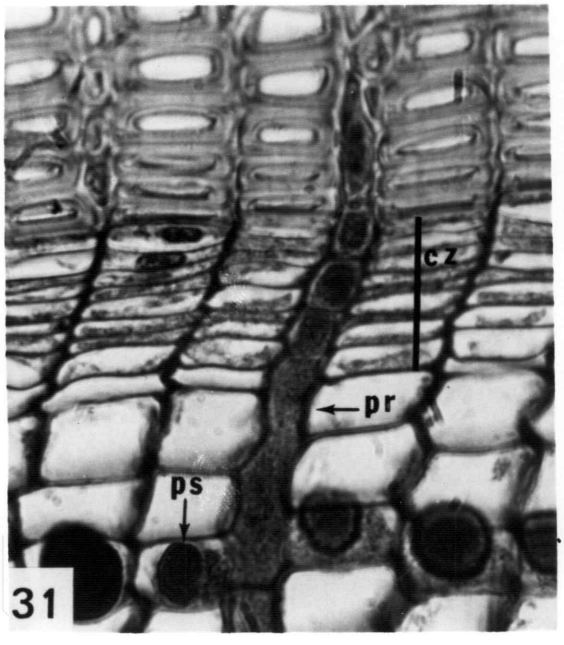


31

Figure 32. Percentage of fusiform initials undergoing anticlinal division during the 1968 growing season in control trees (C), cankers (CA) and smooth bark areas below cankers (BCA).

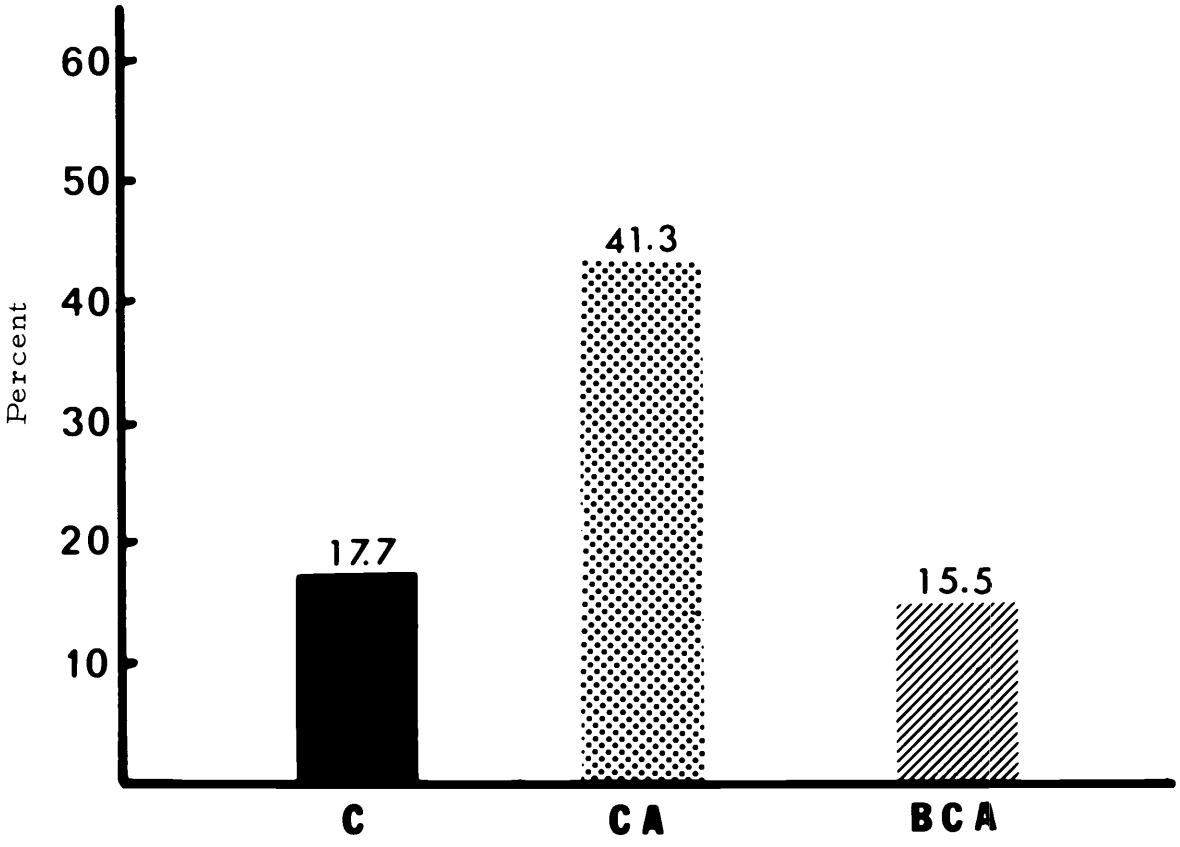
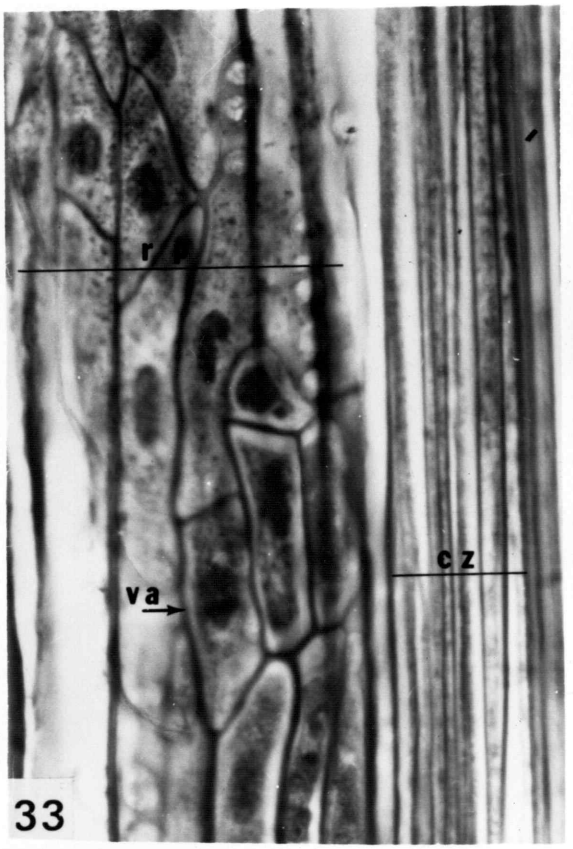

Percent
60
50
40
30
20
10
17.7
41.3
15.5
C
CA
BCA

Figure 33. Radial section of control tree cambial zone (cz) and adjacent secondary phloem with a radial plate (rp) of vertical albuminous cells (va). 400X.

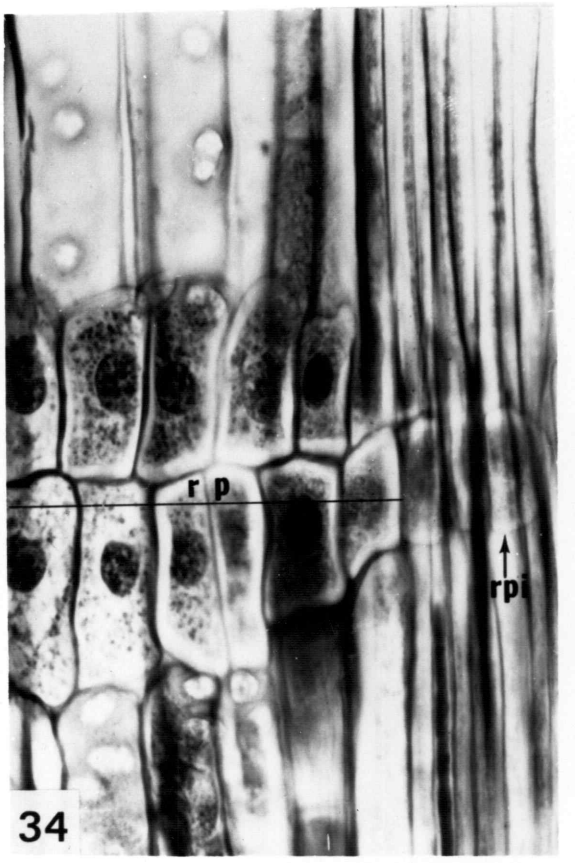
Figure 34. Radial section of control tree cambial zone with last two remaining segments of fusiform initial (radial plate initial, rpi) producing a radial plate (rp) in adjacent phloem. 400X.

Figure 35. Control tree cambial zone and adjacent secondary phloem with radial plate (rp) and sieve cells with sieve area (sa). 400X.

Figure 36. Tangential section of cambial zone with fusiform initials (fi) and ray initials (ri). 400X.



33



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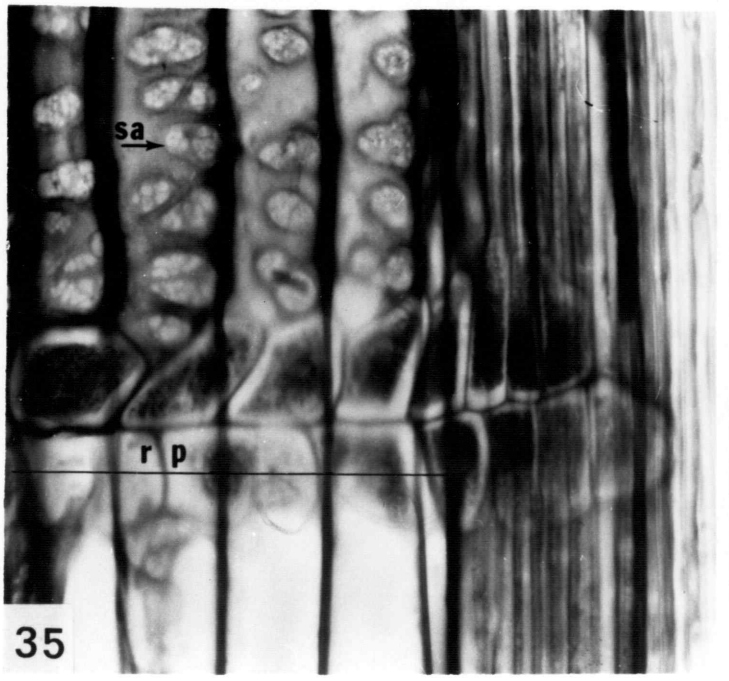

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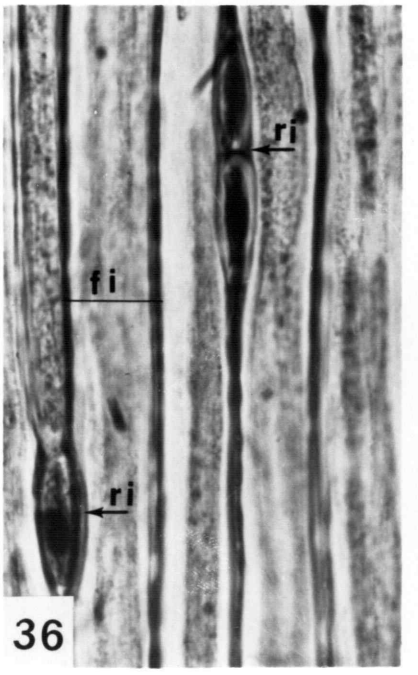


36

Figure 37. Tangential section of secondary phloem in control tree produced near end of 1968 growing season; va, vertical albuminous cells. Figures refer to height of designated rays in number of cells. 200X.

Figure 38. Cambial zone adjacent to secondary phloem shown in Figure 37; rpi, "radial plate initial" or declining fusiform initial. Figures refer to height of designated ray initials in number of cells. Question mark designates location occupied prior to differentiation by initial that produced albuminous cells shown in Figure 37. 200X.

Figure 39. Photomicrograph showing secondary xylem temporally related to secondary phloem shown in Figure 37. Figures refer to height of designated rays in number of cells. Question mark indicates absence of xylem derivatives of declining fusiform initial shown in Figure 38. 200X.

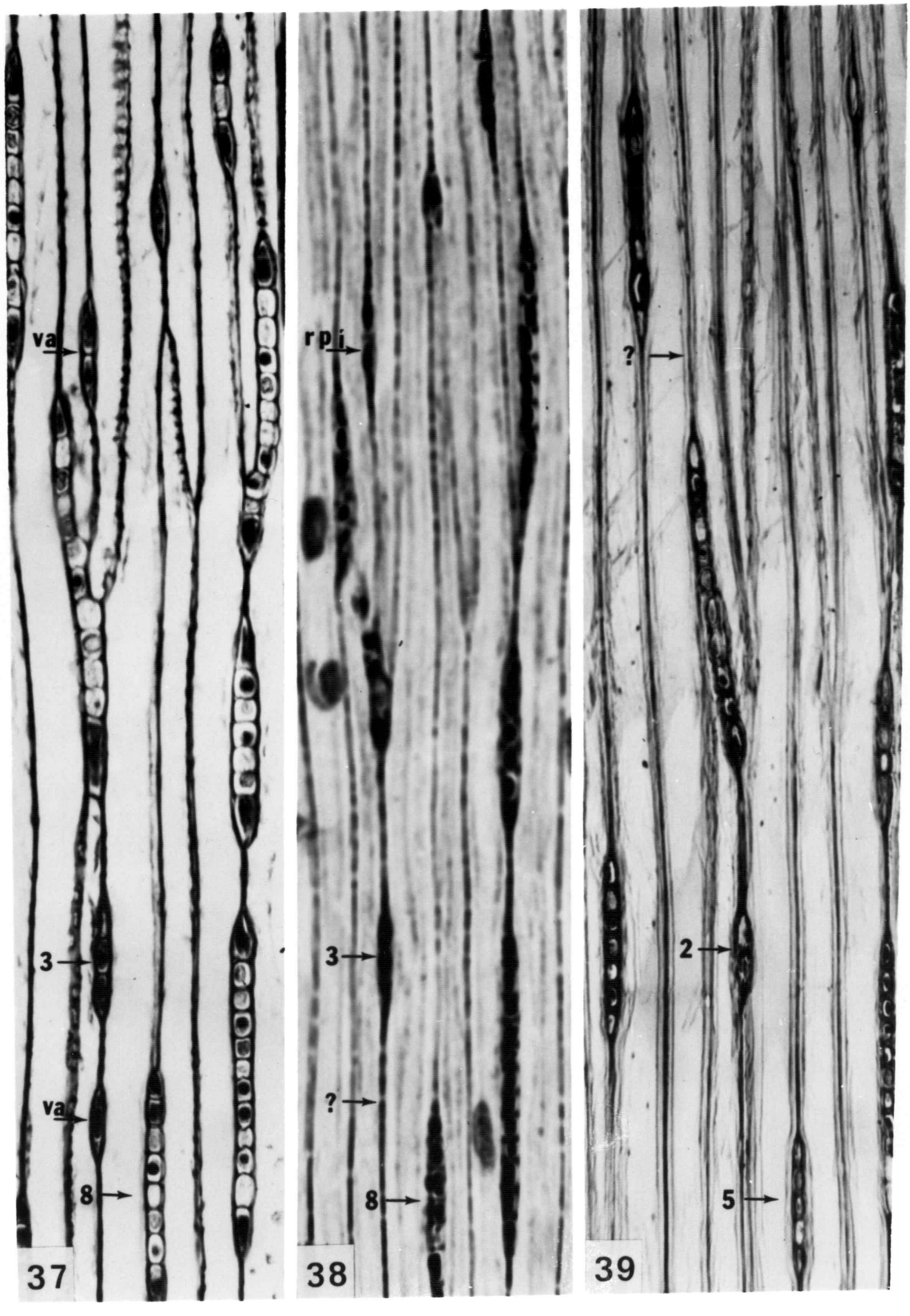
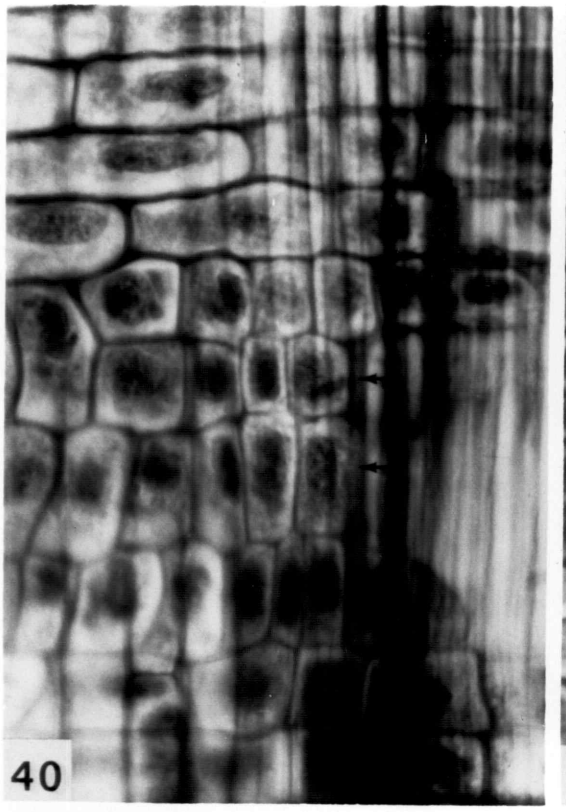

va
3
va
8
37
rpi
3
?
8
38
?
2
5
39

Figure 40-43. Radial section of vascular ray and ray initials. Arrows designate ray initials not producing xylem derivatives. 400X.



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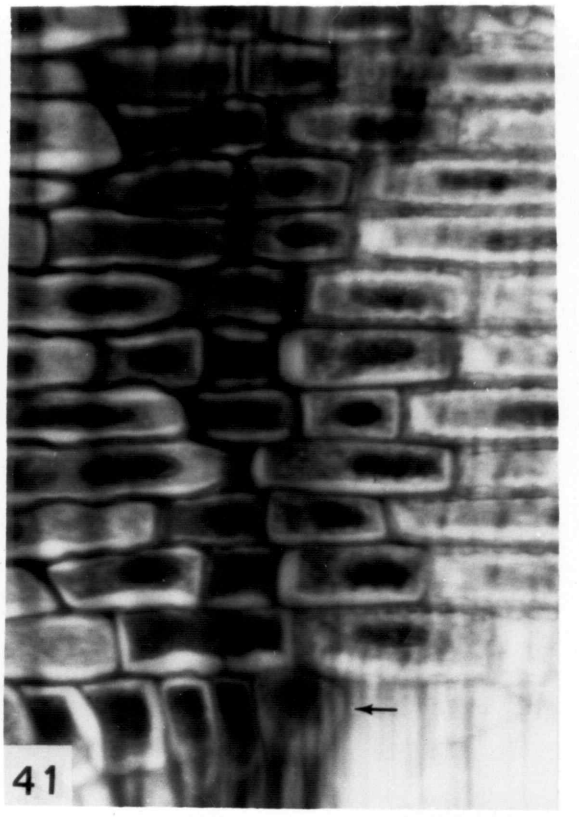

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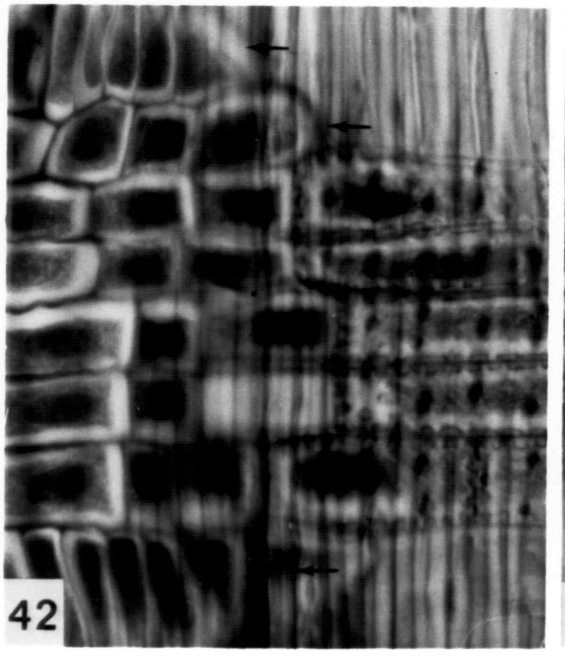
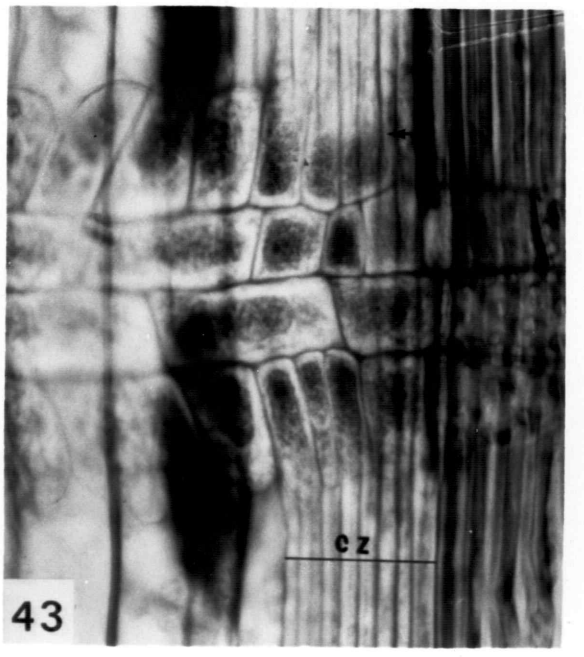


42

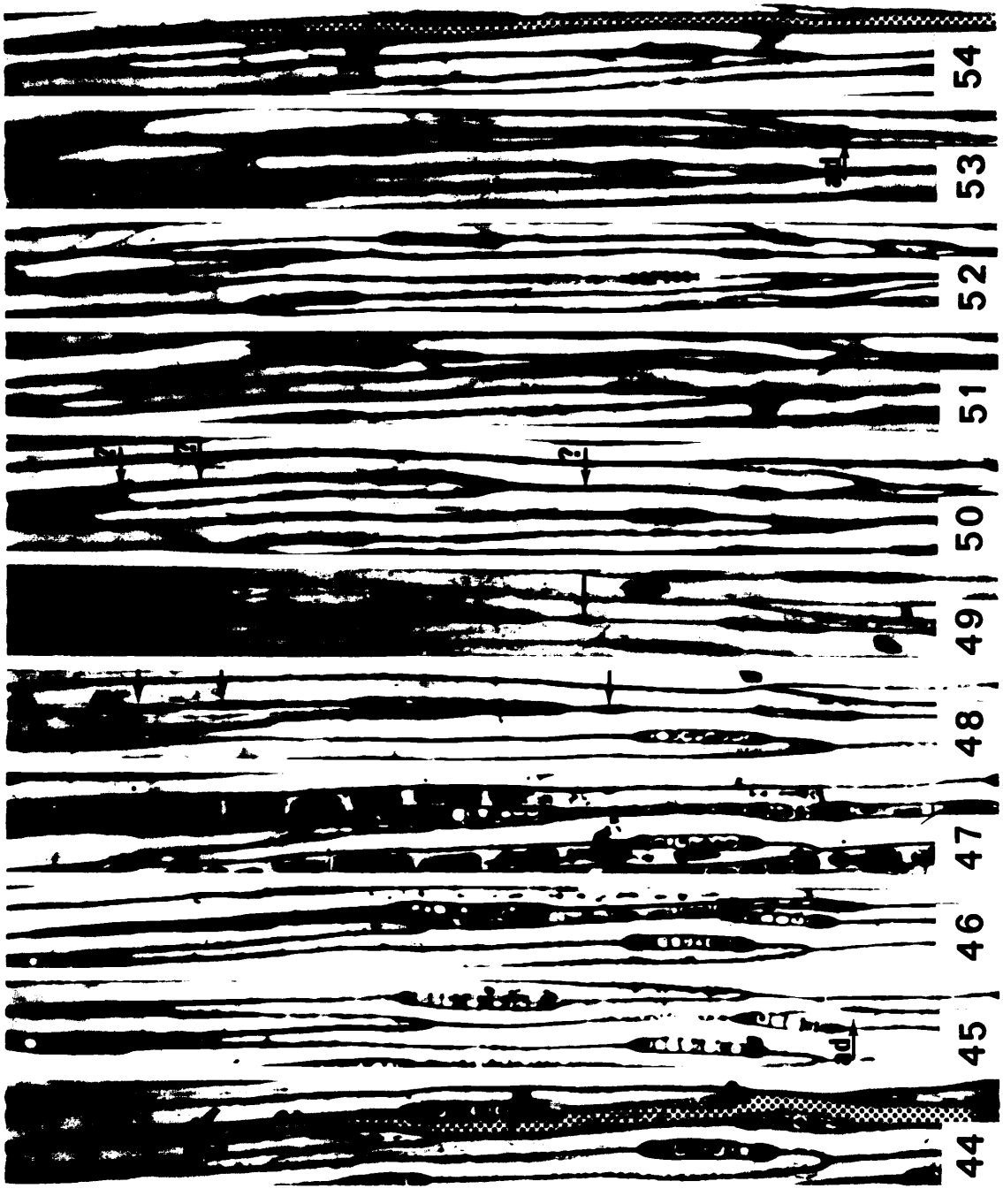


43

Figures 44-48. Serial tangential sections through control tree secondary phloem illustrating preliminary steps in ray initial formation. Arrows designate vertical albuminous cells produced by declining fusiform initial; ad, anticlinal division. 100X.

Figure 49. Photomicrograph of tangential section through cambial zone producing cells shown in Figures 44-48 and 50-54. Arrows designate surviving segments of declining fusiform initials which may become ray initials. 100X.

Figures 50-54. Every fifth serial tangential section through xylem temporally related to phloem is shown in Figures 44-48. Fusiform initials fail to produce xylem derivatives as indicated by the question marks; ad, anticlinal division. 100X.


44
45
46
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49
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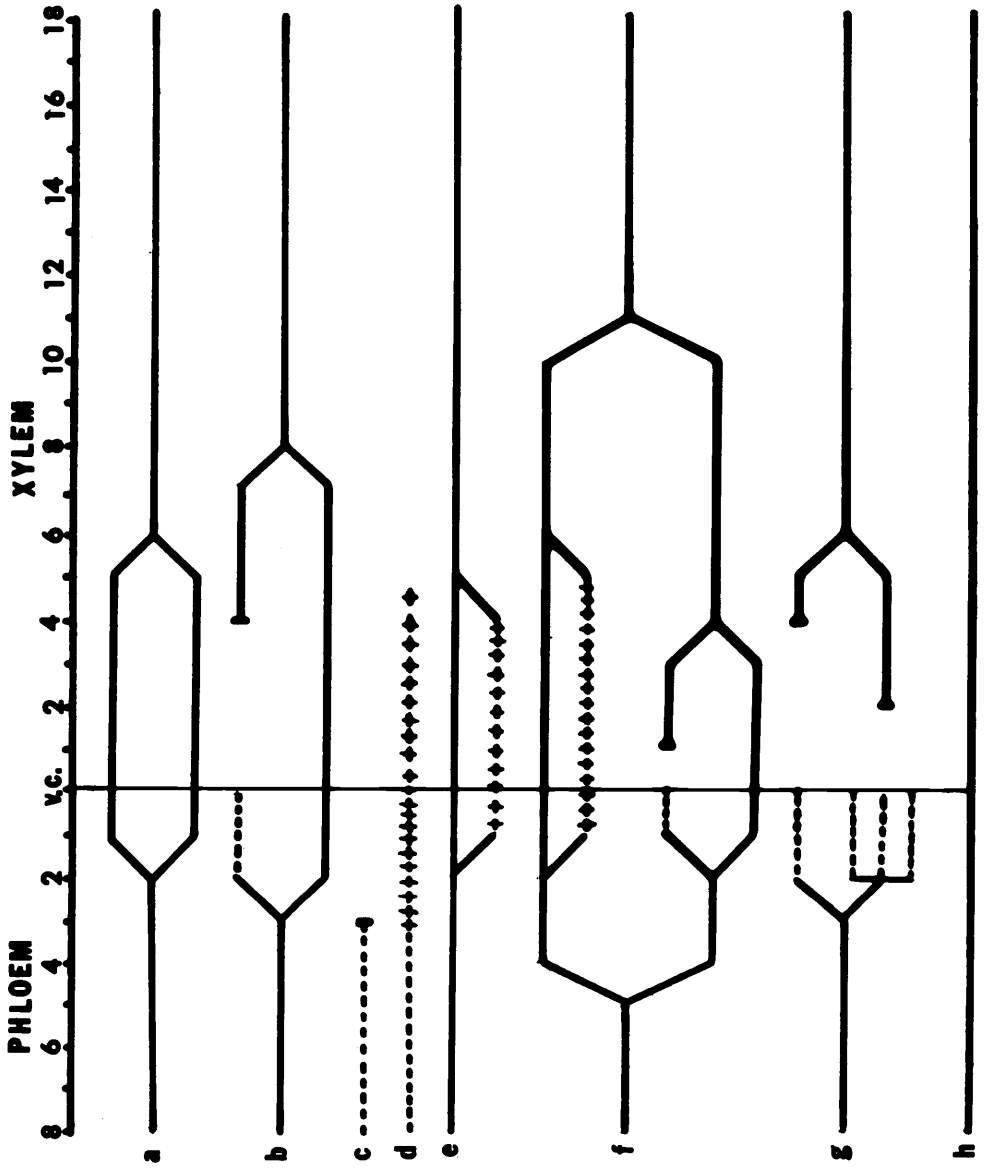
52
53
54

Figure 55. Diagramatic presentation of selected patterns of fusiform initial activity which occurred in control and diseased trees during the 1968 growing season. Vertical line represents vascular cambium (vc) at end of growing season. Figures across horizontal axis represent distance from vascular cambium in number of cells. Other details in text.


PHLOEM
8 6 4 2
vc.
2 4 6 8 10 12 14 16 18
XYLEM
a
b
c
d
e
f
g
h