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Title THE EFFECTS OF BALSAM WOOLLY APHID INFESTATIONS ON WOOD ANATOMY OF TRUE FIRS

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(Major professor)

Three species of true firs in the Pacific Northwest--Abies grandis, grand fir; A. amabilis, Pacific silver fir; and A. lasiocarpa, subalpine fir--are severely damaged or killed by an imported insect pest, the balsam woolly aphid (Chermes (Adelges) piceae Ratz.). Infestations of this insect cause abnormalities in the wood and, in some cases, result in death of the tree.

Wood samples were collected from five infested and five noninfested trees of each of the three species. Cross, radial, and tangential sections were taken from the wood samples, and samples were also macerated to separate the cells. Measurements were made of four anatomical characteristics: cell wall thickness, cell width, fibril angle, and tracheid length. Measurements were made of wood that was produced before infestation of the tree, wood of the same tree that was produced after infestation, and wood of noninfested trees.

Wood produced after infestation in all three species is like compression wood in that the percentage of summerwood is greatly increased, tracheids are round in cross section, intercellular spaces are present, microscopic checking occurs in the cell walls, and false rings are present. The number of rays is almost double the number found in noninfested trees, and the diameter of the ray cells appears to be greater. Springwood cell walls of infested trees are sinuous in nature. Traumatic resin canals in tangential bands may be differentiated at any time during the growing season.

Cell walls of the springwood of infested trees were significantly thicker than the springwood cell walls of wood produced before infestation and also of noninfested trees for all three species, but there were no differences with regard to the summerwood.

There were no significant differences in cell width for wood from each species. This was true for both springwood and summerwood.

Fibril angle in the summerwood and transition area in infested trees of each species was two to three times greater than the angle found in wood produced before infestation and in noninfested trees. No differences in the fibril angle in springwood occurred.

Tracheid length in infested wood was considerably reduced following infestation. Tracheids of wood produced before infestation, and in noninfested trees, were approximately one and one-half to two times longer than tracheids of infested trees.

THE EFFECTS OF BALSAM WOOLLY APHID INFESTATIONS ON WOOD ANATOMY OF TRUE FIRS

by

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THE EFFECTS OF BALSAM WOOLLY APHID INFESTATIONS ON WOOD ANATOMY OF TRUE FIRS

During the past half century, trees of several species of North American true firs have been severely damaged and often killed by infestations of an imported insect pest, the balsam woolly aphid, *Chermes* (*Adelges*) *piceae* Ratz. The insect was introduced from Europe into southeastern Canada about 1900 and has since moved to fir stands in Oregon and Washington (1, p. 5; 8, p. 794). Principal hosts of the aphid in the Pacific Northwest are: Pacific silver fir, *Abies amabillis* (Dougl.) Forbes; subalpine fir, *A. lasiocarpa* (Hook.) Nutt.; and grand fir, *A. grandis* (Dougl.) Lind. (3, p. 1).

The aphid damages the host (11, p. 2) by injecting unknown substances into the tree through its piercing, thread-like mouthparts (Figure 1, 3). These substances may affect the newly formed tissues of the twigs, branches, or main stem (9, p. 450). Infestations on the main stem cause the tree to produce abnormally wide rings composed of very dense, reddish wood. The wood is very similar in appearance, and presumably structure, to compression wood found in some coniferous trees. Although the exact nature of this dark, abnormal wood is unknown, reaction of the tree suggests that the water conducting ability is impaired (5, p. 10).

The small aphid is only about 0.8 millimeters long in the adult stage and is covered with a white, waxy, wool-like material from which it received the name balsam woolly aphid (Figure 2). The mouthparts or stylets, which are only about 2.0 millimeters in length, are inserted into the living part of the bark, but are still several millimeters from the cambium region when the main stem is infested. Yet it is possibly this region which is most affected by aphid infestations.

Main stem infestations follow different patterns in various species. Infestations in grand fir and Pacific silver fir begin at the lower portion of the tree and gradually move up the tree. In subalpine fir, infestation begins in the upper portion and moves downward.

This study was established as a 12 month cooperative-aid project between the Pacific Northwest Forest and Range Experiment Station, United States Forest Service, and the Botany and Plant Pathology Department, School of Science, Oregon State University. The Forest Products Department, School of Forestry, also participated in the project in an advisory capacity.

OBJECTIVES AND PURPOSE

The objective of this study was to determine anatomical differences between the wood of infested and non-infested grand, Pacific silver, and subalpine firs by:

1. Measuring four variables: cell wall thickness, cell width, fibril angle, and tracheid length; and

2. Comparing non-measurable cellular and histological features.

The purpose of this project was to lay a foundation for future physiological and chemical studies of aphid-infested wood.

METHODS AND PROCEDURES

Wood characteristics were determined from samples taken from three-inch thick discs cut from infested and noninfested trees at breast height, except for the sections of subalpine fir which were cut at a height of 12 feet since the bole infestation of this species begins near the top of the tree. A total of 30 discs were collected, five from infested trees and five from noninfested trees of each of the species studied. All of the samples were collected in Oregon: grand fir in the Willamette Valley near Monroe; subalpine fir in the Cascade Range near the Santiam Pass summit; and Pacific silver fir in the Coast Range near Grand Ronde. For each pair of samples, an infested and noninfested tree which were near each other were selected.

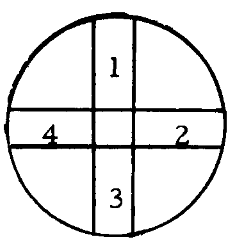
The procedure in preparing the wood samples for study was as follows:

1. Four radial segments were delineated on each disc as shown in text Figure 1.
2. Two of the radial segments were randomly selected, using a random number table, for study and cut from the discs. To prevent fungus growth, the segments were stored in a phenol solution in quart jars.
3. The radial segments (20 per tree species) were further cut into 1/2-inch sample blocks as follows:

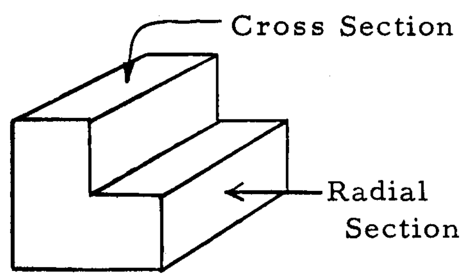
A. Noninfested trees (10 blocks)--One block was cut from the outer rings of each segment.

B. Infested trees (20 blocks)--From each segment, one block was cut from the outer rings that were produced after infestation occurred, and one block was cut from the inner rings that were laid down before the tree became infested.

4. The blocks were trimmed as shown in text Figure 2, to permit both radial and cross sections to be cut with a sliding microtome.



Text Figure 1



Text Figure 2

The blocks were labeled according to species, tree, radial segment number, and which 1/2-inch block was used; i. e. for a block labeled G, I-4, 2-1, the first letter, G, is for the species, _A. grandis_ (_A._ for _A. amabillis_, and L for for _A. lasiocarpa_); the I-4 is the fourth infested tree collected (N for noninfested); and 2-1 is the second radial section and the outside 1/2-inch block.

5. One usable section was cut from each surface of the block, the cross sections at 24 microns and radial sections at 18 microns. The sections were stained with 1% safranin 0, mounted in glycerin, and the edges of the coverslip sealed with H. S. R. synthetic resin mounting medium. Each slide was labeled with the block number followed by X for a cross section or R for a radial section.

6. With the remainder of the block, part of the wood from the two rings farthest from the pith was cut off and macerated by heating in a sodium chlorite-acetic acid solution (2. 3 grams sodium chlorite, and 22 drops glacial acetic acid in 100 ml. of water) in a 25 ml. erlenmeyer flask for two and one-half hours. The tracheids were then washed, separated, stained with dilute safranin 0 and mounted in water on a slide.

Cell wall thickness measurements were made by using a compound microscope equipped with a calibrated ocular micrometer disk. The determinations were made from the cross sections by measuring the combined thickness of two adjacent cell walls and dividing by two. A total of 120 measurements were made per section; 40 from each of the three rings farthest from the pith, 20 in the springwood and 20 in the summerwood. The method of choosing the rows to be measured was the same for every ring. The first row measured was 50 rows from the bottom of the slide and the second row 25 rows above this. In grand fir, ten measurements were made of two radial rows in the springwood and summerwood. Four measurements of five different rows were made from the Pacific silver fir and subalpine fir because of the small amount of summerwood in each ring.

Cell width measurements were made at the same time that the cell wall thickness measurements were made, and of the same cells. The cell width was the width of two adjacent walls plus the cell lumen width of one of the cells. The measurements were made in a radial direction only.

The fibril angle of a cell is the angle between the axis of the vertical tracheid and a line through the elongated aperture of taxodioid pit pairs in the ray crossings. "Fibrils are thread-like components of cell walls requiring special chemical treatment for their demonstration. The fibrils are composed of chain molecules of cellulose extending through regions of parallelism (crystallites) and regions of nonparallelism (amorphous regions)" (2, p. 616). "It is the alignment of the fibrils in the middle layer of the secondary wall that controls the alignment of pit apertures of bordered pits when the apertures are flattened" (2, p. 94).

The fibril angle was measured by using a microscope fitted with a protractor ocular disk. Ten measurements were made of three different regions of each ring: (1) the early summerwood; (2) the transition area (where the cell lumen width is equal to the width of the two adjacent cell walls); and (3) the late summerwood. The three rings farthest from the pith were used so that 90 measurements were made of each slide, 30 in each region.

Tracheid length measurement were made from the macerated material by using a 27X ampliscope which had three lines across the face of the screen. Six slides were made of the tracheids from each wood block and ten measurements were made of each slide for a total of 60 measurements. The tracheids were measured randomly by selecting the first ten complete tracheids which crossed the lines on the face of the screen. Measurements of the tracheids were taken directly from the screen using a flexible rule with calibrations which were equivalent to millimeters. Springwood and summerwood tracheids were not separated, and in general did not appear to be different in length.

RESULTS

Cell Wall Thickness

With one exception, cell wall thickness in the summerwood was not significantly different for the three types of wood for each species. The summerwood cell walls of subalpine fir produced before infestation were significantly thinner than those of both infested and noninfested trees.

For grand fir, the mean wall thickness in the summerwood was 6.76 microns for infested wood, 7.33 microns for wood laid down before infestation, and 7.33 microns for noninfested wood. The mean wall thickness in the summerwood of Pacific silver fir was 5.73 microns for infested wood, 5.24 microns for wood before infestation, and 5.28 microns for noninfested wood. In subalpine fir, the mean wall thickness was 5.88, 4.58, and 5.75 microns for infested wood, wood before infestation, and noninfested wood respectively (Table 1).

An analysis of variance test (4, p. 151-187) was performed on the means and in each case the test showed that at the 1% level of significance the means were equal for grand fir and Pacific silver fir. The means for subalpine fir were significantly different at the 1% level. There was no difference between the infested and noninfested wood, but the cell walls of summerwood produced before infestation

Table 1. Anatomical effects of balsam woolly aphid infestation. Each item is the mean of all measurements taken (Appendix Tables).

	Grand fir			Pacific silver fir			Subalpine fir		
	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested
					(microns)				
Cell wall thickness									
Summerwood	6.76	7.33	7.33	5.73	5.24	5.28	5.88	4.58	5.75
Springwood	2.85	1.76	1.84	3.04	1.87	2.00	3.09	1.69	1.80
Cell width									
Summerwood	19.26	22.31	20.74	17.78	17.22	16.93	17.76	14.37	18.30
Springwood	37.70	47.53	49.86	32.24	32.89	34.47	32.24	33.41	36.18
					(degrees)				
Fibril angle									
Summerwood	25.49	12.31	8.97	24.36	13.29	9.43	27.47	17.49	14.72
Transition area	28.14	14.58	9.18	26.17	14.87	10.65	30.01	18.54	16.51
Springwood	60.22	56.01	61.42	49.46	45.55	42.34	53.28	57.57	56.07
					(millimeters)				
Tracheid length	2.14	3.41	3.77	2.07	3.31	3.57	2.00	2.41	3.14

were significantly thinner.

The situation was somewhat different in the springwood (Table 1). The mean cell wall thickness in the springwood was 2.85 microns for infested wood, 1.76 microns for wood before infestation, and 1.84 microns for noninfested wood in grand fir; 3.04 microns for infested wood, 1.87 microns for wood before infestation, and 2.00 microns for noninfested wood in Pacific silver fir; and 3.09 microns for infested wood, 1.69 microns for wood before infestation, and 1.80 microns for noninfested wood in subalpine fir.

An analysis of variance test showed that for each species the means were not equal at the 1% level. An individual degree of freedom test (4, p. 226-233) indicated that for each species, the mean cell wall thickness in the infested wood was significantly different at the 1% level from the average for the other two means. The cell walls of the springwood of infested trees were markedly thicker in all three species.

Cell Width

Cell width measurements revealed very little difference in the cell widths of the three types of wood of each species. This was true in both the summerwood and the springwood (Table 1).

In the summerwood, the mean cell width was 19.26 microns for infested wood, 22.31 microns for wood before infestation, and 20.74

microns for noninfested wood in grand fir; 17.78 microns for infested wood, 17.22 microns for wood before infestation, and 16.93 microns for noninfested wood in Pacific silver fir; and 17.76 microns for infested wood, 14.37 microns for wood before infestation, and 18.30 microns for noninfested wood in subalpine fir.

In grand fir, an analysis of variance of the means showed that the infested wood mean was different at the 1% level from the average of the means of wood produced before infestation and noninfested wood. There were no significant differences in the means of Pacific silver fir. In subalpine fir, the means were significantly different at the 1% level. In this case, the low value was the mean for wood before infestation, but the infested wood and noninfested wood means were not significantly different from each other.

The mean cell width in the springwood was 37.70 microns for infested wood, 47.53 microns for wood before infestation, and 49.86 microns for noninfested wood in grand fir; 32.24 microns for infested wood, 32.89 microns for wood before infestation, and 34.47 microns for noninfested wood in Pacific silver fir; 32.24 microns for infested wood, 33.41 microns for wood before infestation, and 36.18 microns for noninfested wood in subalpine fir.

An analysis of variance test of the grand fir means showed that there was a significant difference in the means at the 1% level. The infested wood means were significantly lower than the average of the wood before infestation and noninfested wood means as indicated by an individual degree of freedom test. In both Pacific silver fir and subalpine fir the means were not significantly different.

Fibril Angle

A very drastic change in fibril angle occurs in the summerwood and transition area of infested trees of the three species studied. For each species, the fibril angle of infested wood is one and one-half to three times greater than that of noninfested wood, except in the springwood area where the angles were the same (Table 1).

The summerwood of infested trees of grand fir had a mean fibril angle of 25.49 degrees as compared to 12.31 degrees and 9.18 degrees for summerwood produced before infestation, and noninfested wood respectively. An analysis of variance test of the means showed that at the 1% level the means were not equal, and an individual degree of freedom test indicated that at the 1% level the mean value for infested wood was significantly different from the average of the other two means (wood produced before infestation, and noninfested wood).

The results with Pacific silver fir were very similar to those for grand fir. The mean fibril angle in the summerwood of infested trees was 24.36 degrees; whereas, the mean of wood produced before infestation, and noninfested wood was 13.29 degrees and 9.43 degrees respectively. Again an analysis of variance indicated that the means were not equal at the 1% level, and an individual degree of freedom test showed that the mean for infested wood is significantly different from the average of the means of the wood produced before infestation and noninfested wood.

Practically the same results were obtained from the summerwood of subalpine fir. The fibril angle was 27.47 degrees for infested wood, 17.49 degrees for wood produced before infestation, and 14.72 degrees for noninfested wood. An analysis of variance showed that at the 1% level the means were not equal, and an individual degree of freedom test indicated that the mean from infested wood is significantly different from the other two means.

It is interesting to note that the mean fibril angle of the summerwood of noninfested subalpine fir is noticeably higher than corresponding means of grand fir and Pacific silver fir. The fibril angle of this species may normally be greater than for the other two species, but the fact that the sections of subalpine fir were taken 12 feet above the base of the tree may be a factor in the increase in fibril angle. The grand fir and Pacific silver fir sections were taken at breast height. The fibril angle of an annual ring increases with increase in height. Elevation and other environmental conditions may also be influencing factors.

The mean fibril angles in the transition area were very similar to summerwood means except that in each case the former mean was slightly higher (Table 1). The means for the three types of wood, infested wood, wood before infestation, and noninfested wood, were: 28.14 degrees, 14.58 degrees, and 9.18 degrees in grand fir; 26.17 degrees, 14.87 degrees, and 10.65 degrees in Pacific silver fir; and, 30.01 degrees, 18.54 degrees, and 16.51 degrees in subalpine fir. An F-test for the analysis of variance of means showed that for each species the means were significantly different at the 1% level, and an individual degree of freedom test indicated that the mean for infested wood was significantly different at the 1% level from the average of the means of wood produced before infestation and noninfested wood in each species studied. Again one can see that the means for wood produced before infestation and normal wood in subalpine fir are noticeably greater than the values in grand fir and Pacific silver fir. A possible explanation for this was mentioned above.

A different situation was encountered in the springwood of the three species where the means were considerably higher than those for the transition area and summerwood. The means for infested wood, wood before infestation, and noninfested wood were: 60.22 degrees, 56.01 degrees, and 61.42 degrees in grand fir; 49.46 degrees, 45.55 degrees, and 42.34 degrees in Pacific silver fir; and 53.28 degrees, 57.57 degrees, and 56.07 degrees in subalpine fir. An analysis of variance test showed that there was no significant difference in means of the three types of springwood for each species.

Tracheid Length

The most outstanding anatomical change in the wood from balsam woolly aphid infested trees was the production of shorter tracheids following infestation. In grand fir, the mean for the five infested trees was 2.14 mm as compared with 3.41 mm for wood of the same trees that was produced before infestation, and 3.77 mm for noninfested trees. The range for the averages was 1.77 mm to 2.57 mm for the infested wood; 2.90 mm to 3.77 mm for wood produced before infestation; and 3.46 mm to 4.18 mm for noninfested wood.

An F-test for the analysis of variance of the means indicated at the 1% level that the means were different. An individual degree of freedom test showed that the infested wood mean was significantly different from the average of the other two means (wood before infestation, and noninfested wood) at the 1% level.

The average tracheid length for the Pacific silver fir was very much the same as for grand fir. The mean value for the infested wood was 2.07 mm with a range from 1.88 mm to 2.53 mm; the mean value for wood produced before infestation was 3.31 mm with a 3.01 mm to 3.60 mm range; and the mean value of the noninfested wood was 3.57 mm with a range of 3.22 mm to 4.00 mm. In an analysis of variance test of the means, the F-value showed that the difference in the means was highly significant at the 1% level. An individual degree of freedom test showed that the mean of the infested wood was significantly different than the average of the other two means (wood before infestation, and noninfested wood) at the 1% level. This follows very closely the pattern of grand fir, although each mean is slightly less than that of grand fir.

The mean value for infested wood of subalpine fir was 2. 00 mm with a range of 1. 58 mm to 2. 31 mm. For wood before infestation the mean was 2. 41 mm with a range of 2. 29 mm to 2. 64 mm, and for noninfested wood the mean was 3. 14 mm with a range of 2. 68 mm to 3. 58 mm. The mean tracheid length of the wood produced before infestation was much lower than expected if it had followed the pattern of grand fir and Pacific silver fir. The mean was only about 0. 4 mm greater than that of the infested wood, and the ranges of the two types of wood overlapped slightly. Although the two ranges overlap, it should be noted in Appendix Table 4 that the low sample means of the wood produced before infestation are higher than for the infested wood of the same tree. A student's t-test (4, p. 127-133) was run to test the hypothesis that the means were equal and showed that the means were not equal at the 1% level.

The overall mean of the noninfested subalpine fir wood was noticeably lower than in grand fir and Pacific silver fir. One possible explanation for this (as noted earlier) is that the subalpine fir samples were taken from the tree at a height of 12 feet, whereas the grand fir and Pacific silver fir samples were taken at breast height.

OTHER OBSERVATIONS

It was mentioned earlier that the wood of balsam woolly aphid infested trees appeared to be very similar to compression wood which is found in many species of conifers. One of the features of compression wood is the large percentage of summerwood in each ring. In most cases, compression wood occurs only part of the way around the tree. In the aphid infested trees, the percentage of summerwood is also greater than in wood from noninfested trees (approximately 70%-80% as compared to 15%-25%), but occurs around the entire tree. Swelling of the tree in the infested area of the bole also occurred and was due to an increase in growth stimulated by the aphid, although the increase in growth is irregular around the tree, i. e., the rings are wider in certain parts of the tree than others.

Other characteristics of compression wood were also found in the infested wood. In cross section, the tracheids were more or less rounded, instead of being square or rectangular in shape, and because of this a large number of intercellular spaces was present (Figure 4). Two other characteristics similar to compression wood were false rings and the presence of microscopic checking in the secondary cell walls (Figure 9).

One obvious characteristic of infested wood was the increase in the number of rays. A count of the number of rays was made by using the field, which is 1.55 mm in diameter, of a low power microscope. The counts were taken at a distance of three millimeters (two field

Table 2. The effects of balsam woolly aphid infestations on the number of rays produced

	Grand fir	Pacific silver fir	Subalpine fir
	(mean number of rays per 1.55 mm)		
Infested	19.4	16.5	19.6
Wood Before Infestation	9.4	8.8	10.6
Noninfested	10.3	8.3	10.1

diameters) from the top of the cross sections. The number of rays in the field were recorded and only one count per slide was made. The averages for the trees are found in Table 2. In each species, the infested wood had approximately twice as many rays as wood produced before infestation or noninfested wood. Biseriate rays are present in infested wood, and the ray cells in infested wood appear to be greater in diameter than in wood produced before infestation or in noninfested wood (Figures 5, 7, 8, 11, 12).

The springwood cell walls of infested trees were sinuous in nature. This was characteristic of each species (Figures 6, 9).

Traumatic resin canals were present in nearly all the infested wood samples (Figures 5, 6). The resin canals were oriented in tangential bands extending,in some cases, entirely around the tree and occurred in any part of the annual ring. No attempt was made to correlate the seasonal development of these canals with degree of infestation, life cycle of the aphid, or other factors.

SUMMARY

Three species of true firs in the Pacific Northwest--*Abies grandis*, grand fir; *A. amabillis*, Pacific silver fir; and *A. lasiocarpa*, subalpine fir--are severely damaged or killed by an imported insect pest, the balsam woolly aphid (*Chermes* (*Adelges*) *piceae* Ratz). Infestations of this insect cause abnormalities in the wood of infested trees.

Wood samples were collected from five infested and five noninfested trees of each species. Cross, radial and some tangential sections were cut, and some samples were macerated to separate the cells. Measurements were made of four anatomical characteristics; cell wall thickness, cell width, fibril angle, and tracheid length. Measurements were made of wood that was produced before infestation, wood that was produced after infestation, and wood of noninfested trees.

Cell walls of the springwood in infested trees were significantly thicker than the springwood cell walls of the wood produced before infestation and noninfested wood for all three species, but there was no difference in the summerwood.

There were no significant differences in cell width for the three kinds of wood from each species. This was true for both springwood and summerwood.

Fibril angle in the summerwood and transition area in infested wood of each species was two to three times greater than the angle found in wood produced before infestation and in noninfested wood. No differences in the fibril angle in springwood occurred.

Tracheid length in infested trees was considerably reduced following infestation. Tracheids of wood produced before infestation and in noninfested trees were approximately one and one-half to two times longer than tracheids of infested trees.

Some general observations of the infested wood were:

1. The wood is like compression wood in that the percentage of summerwood is greatly increased, the tracheids are round in cross section, intercellular spaces are present, microscopic checking occurs in the cell walls, and false rings are present.
2. The number of rays is almost doubled and the diameter of the ray cells appear to be greater.
3. Sinuous cell walls are present in the springwood.
4. Traumatic resin canals are formed in tangential bands that may be found in any portion of a growth layer.

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APPENDIX

Figure 1. The first instar or crawler stage of balsam woolly aphid (*Chermes piceae* Ratz.). Note stylet which is injected into the living part of the bark (100 X) (U. S. Forest Service Photo).

Figure 2. The first instar stage and eggs of balsam woolly aphid on the bark of grand fir (*Abies grandis*). Note the wool-like material from which the aphid received its name (19 X).

Figure 3. The adult stage of balsam woolly aphid (100 X) (U. S. Forest Service Photo).

Figure 4. Cross section of summerwood produced after infestation (*Abies grandis*). Note the rounded tracheids and large intercellular spaces (400 X).

Figure 5. Cross section of wood produced after infestation (*Abies grandis*). Note the traumatic resin canals in both the springwood and the summerwood, and the large number of rays (100 X).

Figure 6. Radial section of wood produced after infestation (*Abies grandis*) showing a longitudinal traumatic resin canal (100 X).

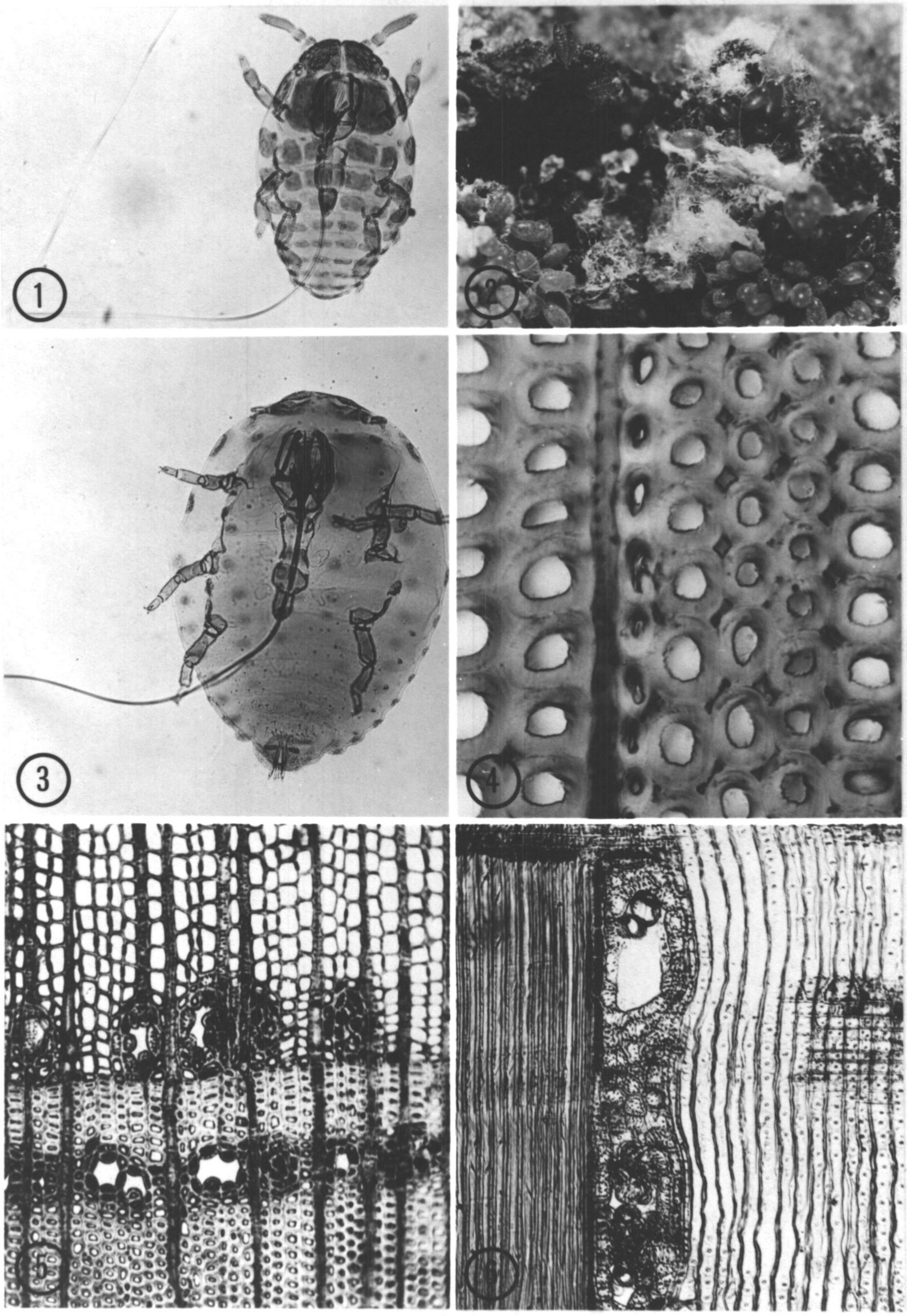
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Figure 7. Cross section of xylen produced following infestation (*A. grandis*). Note the number of rays, the thickness of the springwood cell walls, and the rounded tracheids in the summerwood (100 X).

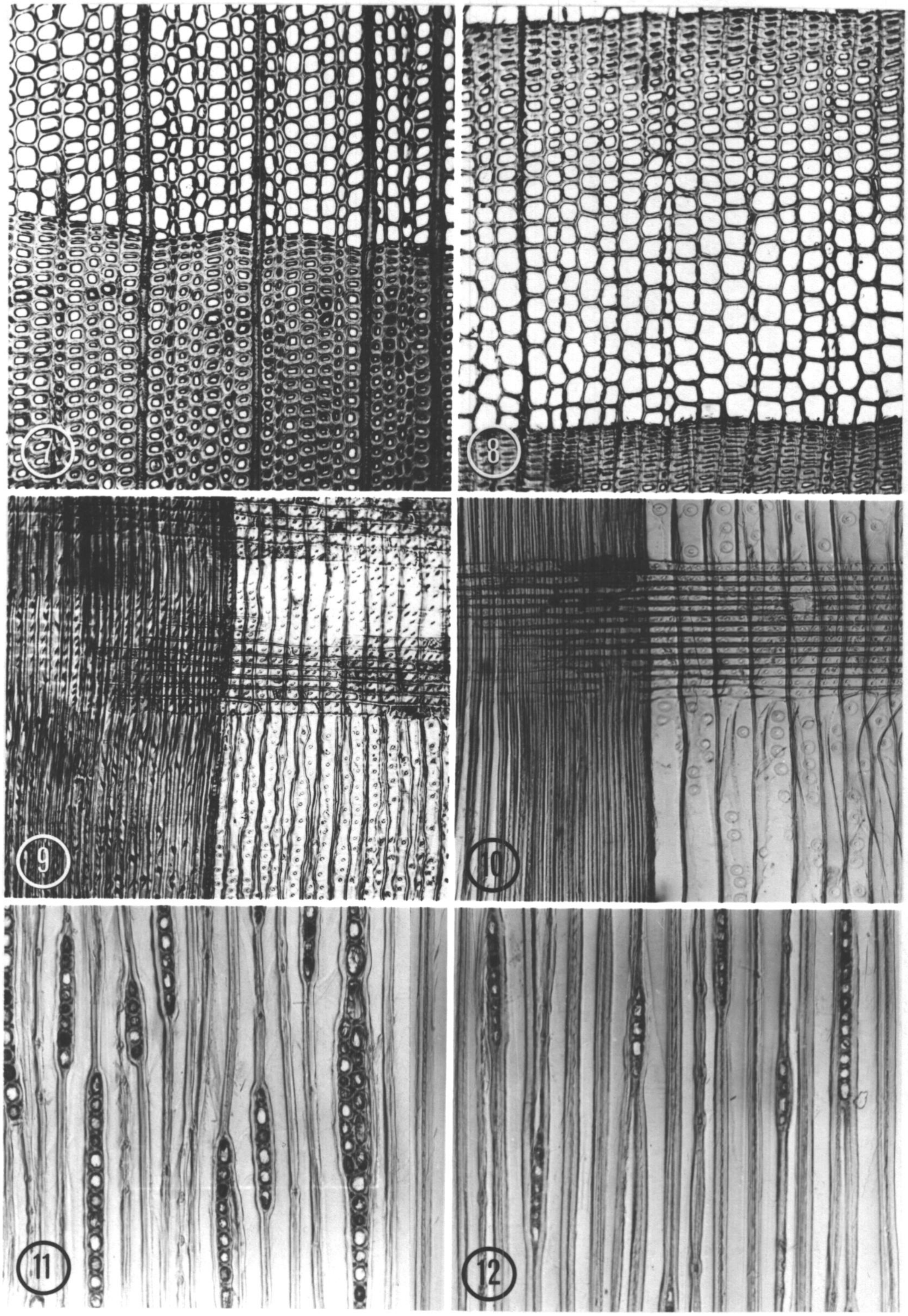
Figure 8. Cross section of xylem produced before infestation (*A. grandis*). Note the number of rays, the thinness of the springwood cell walls, and the rectangular shape of the summerwood cells (100 X).

Figure 9. Radial section of xylem produced following infestation (*A. grandis*). Note the orientation of the pit apertures in the ray crossings, the wavy walls of the springwood tracheids, and the checks in the summerwood tracheids (100 X).

Figure 10.. Radial section of xylem produced before infestation (*A. grandis*). The pit apertures in the summerwood are extremely small and cannot be seen in this photograph (100 X).

Figure 11. Tangential section of xylem produced following infestation (A. *grandis*). Note the biseriate ray, the number of rays, and the diameter of the ray cells (100 X).

Figure 12. Tangential section of xylem produced before infestation (*A. grandis*). Note the number of rays (100 X).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Appendix Table 1a. Effect of balsam woolly aphid infestations on cell wall thickness. Summerwood

Tree No.	Grand fir Infested	Grand fir Before Infestation	Grand fir Non-Infested	Pacific silver fir Infested	Pacific silver fir Before Infestation	Pacific silver fir Non-Infested	Subalpine fir Infested	Subalpine fir Before Infestation	Subalpine fir Non-Infested
					(microns)				
1	7.67	7.18	8.64	5.54	5.54	5.87	5.38	4.24	5.71
	7.34	7.50	7.67	5.38	5.54	5.05	4.89	3.92	6.36
2	5.54	6.52	7.01	4.89	5.05	5.71	5.87	4.57	5.05
	6.69	7.18	7.83	5.38	4.73	5.22	6.20	4.40	4.89
3	6.20	6.69	7.34	6.52	4.40	5.05	5.38	4.40	5.54
	6.69	6.36	7.01	7.01	5.38	4.40	5.22	4.40	5.54
4	7.01	8.64	7.50	5.71	5.22	5.05	5.87	5.22	5.87
	6.36	7.18	7.83	5.54	5.71	6.03	6.85	4.73	6.36
5	6.85	8.15	6.20	5.87	5.05	4.89	6.20	4.57	5.22
	7.18	7.83	6.52	5.71	4.57	5.71	6.85	3.92	5.87
Mean	6.76	7.33	7.33	5.73	5.24	5.28	5.88	4.58	5.75

Appendix Table 1b. Effect of balsam woolly aphid infestations on cell wall thickness. Springwood

	Grand fir			Pacific silver fir			Subalpine fir		
Tree No.	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested
					(microns)				
1	3.42	1.79	1.96	2.94	1.79	1.79	2.94	1.63	1.79
	3.75	1.63	1.96	2.94	1.96	1.79	2.77	1.63	1.79
2	2.44	1.63	1.96	2.44	1.79	2.12	3.42	1.63	1.79
	2.77	1.79	1.79	2.77	1.63	1.96	3.10	1.63	1.79
3	2.77	1.79	1.96	2.94	1.96	2.28	2.61	1.79	1.79
	2.94	1.79	1.79	2.77	2.44	2.28	2.61	1.79	1.79
4	2.28	1.96	1.79	3.26	1.79	1.96	2.77	1.63	1.79
	2.61	1.79	1.63	2.77	1.96	2.28	2.94	1.63	1.79
5	2.61	1.79	1.79	3.75	1.79	1.96	3.10	1.63	1.96
	2.44	1.79	1.79	3.75	1.79	1.79	3.42	1.96	1.79
Mean	2.85	1.76	1.84	3.04	1.87	2.00	3.09	1.69	1.80

Appendix Table 2a. Effect of balsam woolly aphid infestations on cell width. Summerwood

Tree No.	Grand fir Infested	Grand fir Before Infestation	Grand fir Non-Infested	Pacific silver fir Infested	Pacific silver fir Before Infestation	Pacific silver fir Non-Infested	Subalpine fir Infested	Subalpine fir Before Infestation	Subalpine fir Non-Infested
					(microns)				
1	22.82	24.78	21.84	18.58	20.05	16.79	20.54	15.16	20.05
	21.84	25.75	21.52	15.32	18.09	16.46	16.46	14.83	19.23
2	17.44	22.01	19.72	16.30	17.60	17.28	18.09	13.53	16.14
	19.23	22.17	21.52	17.28	15.81	16.95	20.05	12.55	15.97
3	18.42	18.26	19.23	21.35	19.40	17.44	14.02	13.53	19.23
	18.91	18.09	19.07	20.86	17.28	17.28	13.04	12.55	18.26
4	19.40	23.80	20.70	17.93	15.65	16.79	16.95	17.44	17.60
	18.75	20.70	22.49	16.14	16.14	16.63	19.89	16.30	18.58
5	19.07	22.82	20.54	16.79	14.51	16.14	20.21	13.86	18.42
	19.89	24.61	21.19	16.95	17.44	17.44	19.72	14.18	19.89
Mean	19.26	22.31	20.74	17.78	17.22	16.93	17.76	14.37	18.30

Appendix Table 2b. Effect of balsam woolly aphid infestations on cell width. Springwood

	Grand fir			Pacific silver fir			Subalpine fir		
Tree No.	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested
					(microns)				
1	38.47	49.88	47.27	36.51	37.00	36.19	33.90	30.16	37.65
	41.40	46.62	48.57	34.07	33.90	34.39	29.50	32.76	33.90
2	33.42	51.83	43.03	33.90	40.59	38.63	34.56	31.79	30.97
	35.05	33.90	48.41	32.76	37.16	39.12	36.35	34.88	48.09
3	41.24	46.62	49.06	35.53	46.78	36.02	27.38	32.93	36.35
	37.33	42.38	55.75	31.46	32.93	33.74	26.24	30.32	35.21
4	35.86	44.99	56.40	28.36	28.85	33.25	32.27	33.74	40.75
	35.37	50.04	45.31	31.62	30.81	33.09	32.93	32.11	38.79
5	38.47	47.60	51.83	29.01	29.18	30.64	33.09	37.16	37.33
	38.14	47.27	54.44	29.50	29.18	29.67	39.12	38.14	36.51
Mean	37.70	47.53	49.86	32.24	32.89	34.47	32.24	33.41	36.18

Appendix Table 3a. Effects of balsam woolly aphid infestations on Fibril Angle. Summerwood

	Grand fir			Pacific silver fir			Subalpine fir		
Tree No.	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested
					(degrees)				
1	22.3	6.8	7.3	31.0	16.6	11.2	26.4	14.2	12.4
	23.5	11.9	7.0	26.5	14.6	9.4	24.7	15.4	14.0
2	32.2	16.0	4.0	23.5	15.0	8.3	28.0	22.4	17.7
	25.9	14.5	5.0	25.7	9.9	10.0	30.1	21.4	19.7
3	28.7	11.2	10.6	23.6	7.0	6.4	26.6	13.9	16.8
	28.2	8.9	11.9	24.3	14.8	2.7	31.3	12.4	16.4
4	22.1	14.4	7.7	21.5	15.5	9.7	25.4	22.3	13.0
	23.0	11.9	10.8	20.2	14.1	13.0	27.7	20.8	13.8
5	22.5	14.9	13.2	23.8	15.3	10.4	26.8	17.7	14.0
	26.3	12.7	12.1	23.5	10.1	13.2	27.8	14.2	9.4
Mean	25.49	12.31	8.97	24.36	13.29	9.43	27.47	17.49	14.72

Appendix Table 3b. Effect of balsam woolly aphid infestations on Fibril Angle. Transition area

	Grand fir			Pacific silver fir			Subalpine fir		
Tree No.	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested
					(degrees)				
1	27.7	8.1	6.3	28.5	18.1	12.7	30.4	14.0	14.9
	26.6	13.9	6.8	26.7	19.3	10.1	27.3	15.4	14.6
2	34.3	18.1	4.4	24.4	15.6	7.7	32.9	23.6	20.3
	30.3	17.7	4.3	27.4	12.0	11.5	31.9	22.2	21.2
3	29.2	16.8	14.2	26.4	7.2	8.5	28.9	15.1	18.4
	29.7	12.6	14.2	27.3	18.4	3.5	30.1	14.8	17.5
4	24.7	17.8	6.7	25.9	17.5	12.9	28.6	23.2	14.9
	26.5	14.4	10.6	23.5	18.4	14.5	30.2	22.3	15.5
5	24.1	13.6	12.8	26.1	15.1	11.5	29.9	18.8	15.7
	28.2	12.3	11.6	25.4	6.9	13.6	30.0	16.0	12.0
Mean	28.14	14.58	9.18	26.17	14.87	10.65	30.01	18.54	16.51

Appendix Table 3c. Effect of balsam woolly aphid infestations on Fibril Angle. Springwood

	Grand fir			Pacific silver fir			Subalpine fir		
Tree No.	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested
					(degrees)				
1	49.2	42.4	56.3	54.3	46.5	30.3	47.0	50.2	51.3
	52.6	49.7	62.4	52.5	47.3	50.2	48.4	54.8	51.8
2	67.0	62.7	54.2	53.4	53.5	37.7	57.4	59.9	56.7
	61.8	54.1	62.3	59.2	58.2	45.8	49.6	58.1	62.1
3	55.5	50.5	65.9	50.9	28.7	44.5	54.9	55.4	53.6
	58.6	57.8	62.9	43.9	44.8	34.1	40.1	57.9	52.0
4	63.6	62.0	52.6	45.8	42.4	47.1	56.2	60.7	57.2
	62.0	62.8	59.4	42.7	53.8	41.0	55.5	61.8	55.4
5	64.5	61.5	65.0	44.7	46.1	46.1	58.0	59.6	59.5
	67.4	56.6	63.0	47.1	34.3	46.6	55.8	57.3	61.0
Mean	60.22	56.01	61.42	49.46	45.55	42.34	53.28	57.57	56.07

Table 4. Effect of balsam woolly aphid infestations on Tracheid Length.

	Grand fir			Pacific silver fir			Subalpine fir		
Tree No.	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested	Infested	Before Infestation	Non-Infested
					(millimeters)				
1	2.57	3.77	3.71	2.05	3.43	3.67	2.18	2.64	3.56
	2.44	3.56	4.18	1.88	3.30	3.76	2.31	2.53	3.46
2	1.78	3.61	4.12	1.99	3.42	4.00	1.58	2.38	2.98
	1.89	3.31	3.95	1.88	3.60	3.87	1.76	2.29	2.72
3	1.77	3.41	3.60	2.11	3.34	3.51	1.83	2.31	2.80
	1.81	3.29	3.76	1.93	3.30	3.59	1.71	2.33	2.68
4	2.36	3.25	3.64	2.53	3.35	3.54	2.25	2.48	3.46
	2.07	3.62	3.79	2.16	3.08	3.23	2.13	2.38	3.26
5	2.34	3.41	3.46	2.10	3.01	3.35	2.10	2.43	2.94
	2.39	2.90	3.52	2.04	3.30	3.22	2.13	2.34	3.58
Mean	2.14	3.41	3.77	2.07	3.31	3.57	2.00	2.41	3.14