VARIATION IN THE SIZE OF RAY PITS OF CONIFERS.*

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Since Haeckel proposed the word Ecology in 1886, there has been an ever growing interest in the influence which environmental factors may have in determining the form and structure of plants. "Anatomy, particularly stimulated by Haberlandt, has recently been greatly enriched by numerous researches dealing with the question of the harmony between structure and environment."[1] Trees of the same species, but grown under different conditions, will show differences in the structure of their woody tissues that materially affect the durability, strength, and other properties of the wood. In a general way, many of such structural differences have been related to the conditions under which the tree was grown.

To some extent, at least, the physical factors may influence the structure of wood. Cieslar[2] found that certain conifers would form "Rotholz," a tissue of great strength under compression, due to the mechanical influence of a one-sided crown or the weight of a branch. But since one of the main purposes of the woody elements of a tree is to conduct and store the products of assimilation, and to convey the watery solutions, gathered by the roots, to the leaves and other parts where they may be needed, it may be inferred that factors more directly related to the vital processes of the tree will also be more directly related to structural variations.

Of the tissues which go to make up the woody part of the stem of coniferous trees, the medullary ray is one of the most complex, in both its structural and functional aspects. While they make up only 4-8 % of the volume of the wood, their height and width is so small that often over 2,500 rays may be counted in one sq. cm. on the tangential surface (Fig. 1). The average volume of a typical coniferous ray shown in this plate is but one twentieth that of a fine silk thread. None the less, the ray of Picea and Larix, the genera selected for comparison in this paper, is composed of at least two kinds of tissue with an accompanying difference in function (Fig. 2). At the margins are the ray tracheids (r.t.), which communicate with the adjacent wood tracheids by means of bordered pits. "Their purpose is to facilitate the transfer of water radially between the tracheids."[3] Distinguished from the

*Contribution from the Botanical Laboratory of the Ohio State University, No. 90.

1. Warming. 1909. Ecology of Plants, p. 3.
2. Centralblatt f. d. gesamte Forstwesen. Apr., 1896.
3. Strasburger. 1908. Bonn Text-Book, p. 140.

ray tracheids are the ray parenchyma cells with semi-bordered pits (s. b. p.) upon their lateral walls and simple pits upon their end walls (e. w.). These cells make up the storage tissue of the ray, in which the products of assimilation are conducted and stored. Still more complex in structure and function are the rays which

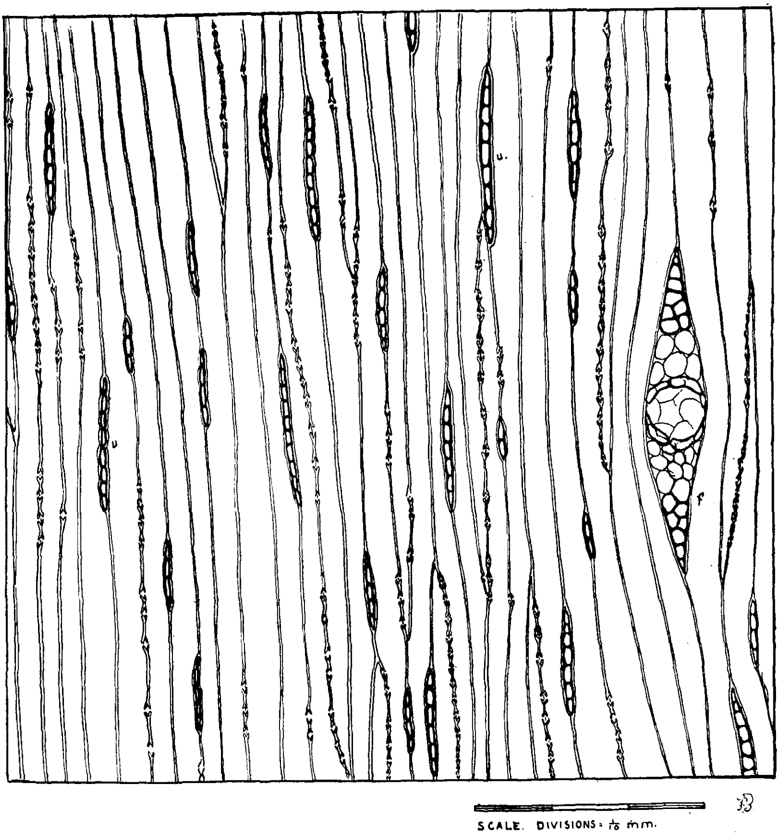

Fig. 1.

Fig. 1. Tangential view Pinus monticola, showing arrangement of the rays with reference to the tracheids.
f. fusiform ray with resin duct. u. uniseriate rays.

have, in addition to the above tissues, a third tissue designed for the secretion, conduction, and storage of resin. A very intimate connection of the rays with the vital activities of the wood may be inferred from the fact that the rays continue living for fifteen years or more, or probably as long as the wood performs

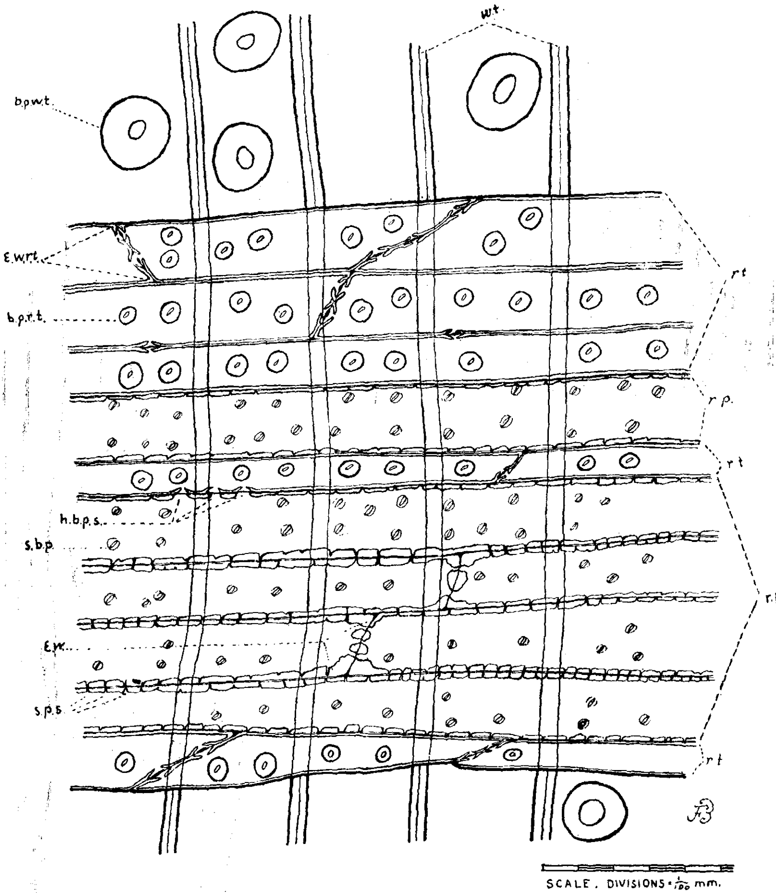

Fig. 2.

Fig. 2. Radial view of Picea canadensis, showing uniseriate medullary ray in section.

r. t. ray tracheids.
r. p. ray parenchyma.
w. t. wood tracheid.
e. w. r. t. end wall of ray tracheid, showing bordered pits in section.
e. w. end wall of ray parenchyma cells with simple pits in section.
s. p. s. simple pits in section.
h. b. p. s. half bordered pits in section.
b. p. w. t. bordered pit of wood tracheid.
b. p. r. t. bordered pit of ray tracheid.
s. b. p. semi-bordered pit of ray parenchyma.

its physiological functions, and are so disposed that, so far as it has been possible to observe, *they come in contact with each individual tracheid of the wood.* It is not uncommon to find tracheids which show four or five points of contact with the ray system. The ray system, is, in turn, through the direct contact of each of its component rays with the cambium and the phloem, in communication with the leaves and all other living structures throughout the tree.

The ray pits formed at the point of contact of the storage cells with the wood tracheids exhibit a number of variations which seem to be related to the life conditions of the species. Unlike the tracheid pits, they differ widely in shape, size, and number for the different genera and species of conifers, affording both generic and specific points of distinction of high taxonomic value. In Larix and Picea, however, these constant characters are similar, especially in P. sitchensis and L. occidentalis, where the ray characters are insufficient to separate the two genera. For this reason, together with the fact that the two genera have widely different habits of nutrition, the two genera have been selected for comparison, since a more direct comparison of the variable characters is possible with woods similar in structure than where the problem would be complicated by structural differences.

In leaf habit, differences are at once apparent that are associated with differences in the storage of reserve and in other processes of nutrition of a fundamental character. The leaves of Larix remain through but one season; being a deciduous conifer, the entire foliage must be regenerated each year. In Picea, the leaves remain for 4-7 years, or the spruce is only ¼ to 1/7 deciduous, and needs to regenerate ¼ or less of its foliage each year. Larix, as with other deciduous trees,[4] is totally dependent upon reserve food for the regeneration of its leaves. Such reserve is stored in the ray system and a heavy demand will therefore be made upon the rays early in the season. Picea, on the other hand, could probably meet this need partly, if not wholly, by the newly formed products of assimilation, since it has been found that first, second, and third year leaves of conifers begin to form starch by the middle of March, even when the temperature often falls below 0° C.[5] Picea, then, should make a relatively slight demand, early in the season, upon the stored reserve.

To determine the relative difference in the amount of starch stored by Larix and Picea, trees of Larix decidua and Picea excelsa ten inches in diameter and growing on the Ohio State University Campus, were felled during winter and the volume of starch

4. Lutz. 1897. Büsgen's Bau und Leben unserer Waldbäume, p. 196.

5. Mer. 1885. Ueber eine Methode zur Beobachtung der Assimilation. Landwirtschaftl. Jahrb.

contained in the storage tissue of the rays estimated from planimeter measurements of projected drawings. In all cases Picea showed little or no starch in its woody tissues, while Larix contained starch in all of its corresponding living parts. The highest relative amount of starch was found in the dwarf branches where

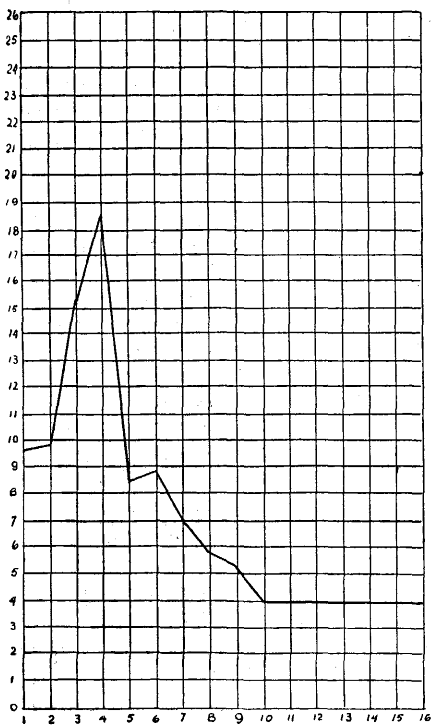

Fig. 3.

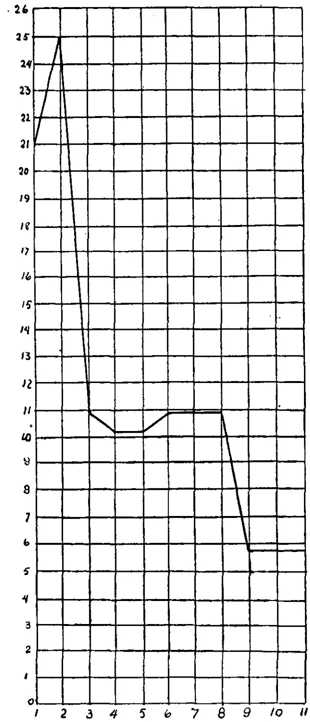

Fig. 4.

Fig. 3. Curve showing variation in size of ray pits of Larix occidentalis, through one annual ring of 16 tracheids, commencing with earliest formed tracheid of spring wood and ending with last formed tracheid of summer wood. Vertical scale, diameters squared.

Fig. 4. Curve showing variation in size of ray pits of Larix laricina, through one annual ring of 11 tracheids, on same scale as Fig. 3.

the rays were stored to their full capacity, but varying amounts of starch were found in all other portions where the wood was living. Rays of the sapwood zone, which was fifteen rings in width in the lower portion of the trunk, contained starch throughout the width of the zone. In some portions, 2% of the volume of sapwood was starch, though the rays in this portion of the tree were not, as a rule, filled to this extent; but, in general, it may be stated that the rays of Larix are, during winter, stored with starch through fifteen years of growth.

Such reserves have been found to be used for two main purposes, the production of leaves and of seed. In rare instances, a

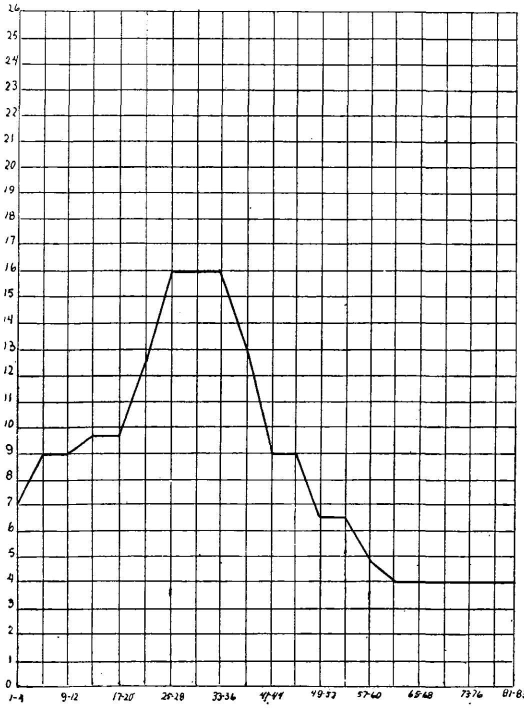

Fig. 5.

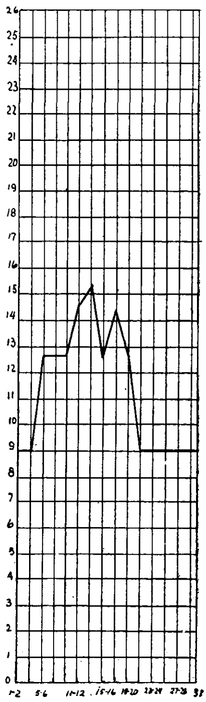

Fig. 6.

Fig. 5. Curve showing variation in size of ray pits of Picea sitchensis, through one annual ring of 83 tracheids, plotted on same scale as Larix, except that the horizontal scale of Larix is four times as great because of the fewer number of tracheids.

Fig. 6. Curve showing variation in size of ray pits of Picea canadensis, through one annual ring of 31 tracheids, on same scale as Fig. 5.

portion may be diverted to the growth of wood, but this is not usual. Use of the reserves for seed production will occur, as a rule, at periods of from two to several years; hence annual rigns will occur not subject to any modifications from this source. On the other hand, that used for the regeneration of leaves will be used yearly, and every annual ring will be subject to structural modifications by this factor.

It has been shown that the reserves stored in the rays are forced into the tracheids and are conveyed to the developing new shoots at the beginning of the growing season.[6] The yearly occurrence of this temporary current would be likely to influence the development of the semi-bordered pits through which it passes, providing such pits had not fully completed their development. Since a period of about 90 days is consumed in the development of an annual ring in Picea and Larix,[7] the ray pits of any given ring will be of successively greater age with the youngest at the commencement of the ring, in the earliest spring wood, and differing in age at the extremes by 90 days; hence certain of them, it may be assumed, would still be plastic when this current is formed. By way of confirmation, twigs of L. decidua were sectioned May 20, when leaves had apparently attained their full size. It was found that the sixth tracheid was then being formed, which would bear out the predicted sequence of the maturity of the ray pits, and be in proper position with respect to the greatly diminished current indicated by the fall of the curve. (Figs. 3 and 4).

The curves referred to were obtained from measurements taken of the diameter of the ray pits, commencing with the first spring tracheid and ending with the last summer wood tracheid. Such pits will, then, be arranged in series according to age. For sake of comparison, these measurements are squared, since the efficiency of circular osmotic membranes, other things being constant, should be proportional to such values. The accompanying curves plotted from the results so obtained, show graphically the existence of exactly such a variation in size as would be expected had the above outlined modifying influence of the assimilation current been manifest. As anticipated, both species of Larix show an early and strongly pronounced increase in the size of their ray pits corresponding to the probable time, intensity, and duration of the demand made upon the stored reserve, for the regeneration of leaves. Also, the curves of Picea show the expected absence of the early high point. The problem is here complicated by the presence of currents of newly formed assimilation products commencing in March and increasing with the advance of the season; but, in a general way, the shape of the curve is in accord with the probable influence exerted by the later leaf habit of the genus and the absence of growth conditions that would make the early and brief demand upon the stored reserve noted in Larix. The data thus collected has also demonstrated the intimate connection of the ray with the vital processes of growth and nutrition and the reaction of such processes upon the structure of the ray.

6. Fischer, Alfred. 1890. Pringsheim's Jahrbücher, XXII, p. 73.
Strasburger. 1891. Uber den Bau und die Verrichtung der Leitungsbahnen in den Pflanzen, pp. 98, 297.

7. Hartig, Robert. 1885. Holz der deutschen Nadelwaldbäume.

TABLE I.

Number of tracheid	Number of pits	Average Diameter in microns	Average Diameter squared
1	3	4.6	21.
2	6	5.	25.
3	7	3.3	10.9
4	1	3.2	10.2
5	3	3.2	10.2
6	6	3.3	10.9
7	6	3.3	10.9
8	3	3.3	10.9
9	5	2.4	5.8
10	2	2.4	5.8
11	3	2.4	5.8

Measurement of the ray pits of Larix laricina through one annual ring.

TABLE II.

Number of tracheid	Number of pits	Average Diameter in microns	Average Diameter squared
1	10	3.1	9.6
2	10	3.1	9.6
3	10	3.9	15.2
4	10	4.3	18.5
5	10	2.9	8.4
6	10	3.0	9.0
7	10	2.6	7.0
8	10	2.4	5.8
9	10	2.3	5.3
10	3	2.	4.
11	5	2.	4.
12	4	2.	4.
13	2	2.	4.
14	1	2.	4.
15	1		4.
16			4.

Measurement of ray pits of Larix occidentalis through one annual ring of 16 tracheids; 10-16, late wood; 15-16, so compressed that measurements were approximated.

TABLE III.

Number of tracheid	Number of pits	Average Diameter in microns	Average Diameter squared
1-4	7	2.6	6.8
5-8	12	3.	9.
9-12	13	3.	9.
13-16	11	3.1	9.6
17-20	12	3.1	9.6
21-24	12	3.5	12.3
25-28	12	4.	16.
29-32	12	4.	16.
33-36	10	4.	16.
37-40	12	3.3	10.9
41-44	5	3.	9.
45-48	4	3.	9.
49-52	4	2.5	6.3
53-56	4	2.5	6.3
57-60	4	2.2	4.8
61-64	4	2.	4.
65-68	4	2.	4.
69-72	4	2.	4.
73-76	4	2.	4.
77-80	4	2.	4.
81-83	4	2.	4.

Measurement of ray pits of Picea sitchensis, through one annual ring of 83 tracheids.

TABLE IV.

Number of tracheid	Number of pits	Average Diameter in microns	Average Diameter squared
1-2	5	3.	9.
3-4	5	3.	9.
5-6	6	3.5	12.5
7-8	7	3.5	12.5
9-10	8	3.5	12.5
11-12	7	3.8	14.4
13-14	6	3.9	15.2
15-16	5	3.5	12.3
17-18	7	3.8	14.4
19-20	5	3.5	12.5
21-22	2	3.	9.
23-24	5	3.	9.
25-26	4	3.	9.
27-28	5	3.	9.
29-30	4	3.	9.
31	2	3.	9.

Measurement of ray pits of one annual ring of Picea canadensis with 31 tracheids.