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THE FORMATION AND PATHOLOGICAL ANATOMY OF FROST RINGS IN CONIFERS INJURED BY LATE FROSTS.

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INTRODUCTION.

Various writers have shown that an abnormal or pathologic parenchyma tissue may occur as an interruption of the normal course of the wood elements in the growth rings of coniferous trees, resulting from a variety of widely different causes, which may either directly or indirectly influence the growth of the cambium. Among these causes may be enumerated mechanical injuries of any kind; attacks by various cryptogamic and phanerogamic parasites which stimulate the woody tissue to an abnormal development; abnormal physiological conditions of growth and nutrition which per se produce a like effect; premature defoliation; and injuries resulting from such meteorological causes as lightning, frost, and drought. The last-mentioned three forms of injury have rather distinctive anatomical characteristics which are scarcely recognized in this country and additional knowledge of these is highly desirable.

Owing to its close resemblance to the disturbances in the wood caused by certain forms of lightning injury which he was studying, the writer was impelled to investigate also the pathological anatomy of late-frost injury. The present bulletin is therefore designed as a contribution to our knowledge of the pathological anatomy of late-frost injury in the conifers.

The material used as a basis of this study was collected by the writer in connection with his field work in various parts of northern Idaho, northeastern Washington, and northwestern Montana and was supplemented by material collected later in the District of Columbia and in Missouri. The photomicrographs were made by the writer from his own sectional preparations.

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REVIEW OF THE LITERATURE.

Despite the great mass of literature on the subject of frost injury, there are but few descriptions of the pathological effect of the injury on the structure of the wood. In fact, the effect on forest growth of temperatures below the freezing point, or frost, is seldom considered, except in so far as it causes injuries the external manifestations of which are readily apparent.

The so-called frost rings, or "moon rings," as they sometimes are called when extending only a part of the way around the stem, occurring in young trees as a result of the action of frost, have been mentioned by various European writers, but it is only rarely that their structure and origin have been studied from the standpoint of their pathological anatomy, and illustrations of this abnormality are rare.

Mayr (*5*, p. 36)[1] states that the stimulating action of a mild late frost on the annual ring already in a state of cambial activity exerts itself in such a way that in place of the elongated tracheids a short-celled parenchyma arises. According to Mayr (*5*, p. 37), this abnormal wood may occur either on only one side of the stem or extend entirely around it, depending upon the way in which the cold air strikes the plant. In either case internal healing ensues, proceeding from the parenchyma cells of the wood, which fill up possible cavities with wound parenchyma, while a new cambium is developed in the bark from the bast parenchyma remaining alive. In addition, Mayr states that if the frost has killed the bast together with the cambial layer, then the entire plant part dies.

Hartig (*2*) investigated the action of a May frost on the shoots of young trees of *Pinus sylvestris*. He describes in detail the formation of zones of parenchyma tissue, which constitute the so-called frost ring, in the growth ring developing during the year of the injury. He likewise describes the peculiar permanent distortion of the injured young shoots, a circumstance occasioned by their loss of turgor and consequent drooping after the freezing, followed by an effort to redirect their shoots upward. In many cases, however, the whorls of shoots were killed outright.

Hartig also investigated the formation of similar frost rings in young trees of *Picea excelsa*, *Larix europaea*, and *Chamaecyparis lawsoniana*, but he illustrates their formation only in *Pinus sylvestris* and *Picea excelsa*. He states that frost-ring formation was so frequent in a spruce 2 meters high that he counted 10 frost rings in a section about 15 years old, so that 25 rings were to be counted in a casual macroscopic examination. The frost-ring formation extended down into the stem parts, which were 10 to 12 years old. In the larch the frost rings occurred only in its youth, as in the spruce, and were found only in the youngest to the 4-year-old axes; in the Lawson cypress, however, frost rings still occurred in the older axial parts, and such ring formation was noted also in the interior of the phloem. Hartig gives the same account later in his textbook of plant diseases (*3*).

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[1] Serial numbers (italic) in parentheses refer to "Literature cited" at the end of this bulletin.

Petersen (*9*) describes and illustrates the zone of parenchyma tissue or frost ring which resulted in a double-ring formation in beech trees which had suffered from frost on May 17 and 18 in Holland.

Tubeuf (*14*, pl. 31, fig. 1), in an article upon the pathological anatomy of spruce trees that were dying back from the top in consequence of drought injury, evidently for the sake of comparison, illustrates a portion of a frost ring in a small tree of *Picea excelsa*. However, he makes no allusion in the text to frost injury, which would seem to be due to his apparent failure to publish the concluding part of the article.

Sorauer, who was able to add the action of frost to the causes which bring about the formation of false annual rings (*12*, p. 320), later gives the details of an extensive study to determine the effects of early and late frosts on the mature and immature wood of a large number of fruit and forest trees (*13*). He found that eruptions in the vascular cylinder are generally manifested either in radial clefts within the medullary rays or in tangential cracks within the cambial region. In addition, many cavities appear in the pith and the bark parenchyma. The separated tissue within the cambium region gradually heals over, after presenting the appearance of a ring growth of two years. Sorauer discusses the formation of double rings from the activity of frost and gives the same account of this in the last edition of his manual of plant diseases (*12*) as well as a detailed account of the injurious action of frost injury in general upon plant tissue. Here (p. 577) he describes the brown circular zones, or "frost lines," frequently occurring in fruit trees after spring frosts and composed of collapsed, misshapen cells. The occurrence of this phenomenon was also investigated experimentally in artificial freezing experiments.

Graebner (*1*), who investigated the action of late frosts on oak, beech, spruce, and fir, makes no mention of frost-ring formation as such, but does mention a wound-parenchyma formation that can be followed back into the 2-year-old and 3-year-old wood.

Neger (*7*) investigated a tip blight of *Picea excelsa* with which two ascomycetous fungi were associated; however, they were found only on shoots that had been injured by frost. Sections of the stems, taken both through the dead tips and through the still living stems, showed a more or less broad zone of parenchyma wood or frost ring occurring in the beginning of the 1913 growth ring. Since this parenchyma zone followed immediately upon the summer wood of the 1912 growth ring and was not preceded by normal spring-wood tracheids, it was assumed that a late frost was not involved, but rather an early frost occurring in the fall of 1912. While the frost of 1912 did not come particularly early, relatively low temperatures occurred in comparison with other years, following upon a cold wet summer, which greatly retarded the maturation of the axial growth of that year. This injury therefore was considered to be more nearly due to the action of the winter frost upon immature wood. Tubeuf (*15*) had previously briefly described and illustrated a tip blight of *Picea excelsa* due to the same causes, but he does not go into the pathological anatomy of the injured shoots. According to Neger, the frost injury had the effect of suspending or at least reducing the bark pressure, with the result that a zone of parenchyma wood was developed as the first growth in the following spring instead of the normal tracheidal wood, in so far as the stem had remained living and continued its annual ring formation. In his textbook, which appeared later, Neger (*8*) briefly describes frost rings and reproduces an illustration of one caused by this winter frost.

Somerville (*11*) describes an abnormal zone of parenchyma tissue that is very closely related to frost rings, if not actually identical with them. This abnormal zone occurred in the early-spring wood of a large percentage of young conifers whose wood he had occasion to examine. All of the species examined, including *Larix leptolepis*, *Pseudotsuga douglasii* (=*P. taxifolia*), *Tsuga albertiana* (=*T. mertensiana*), *Cedrus deodara*, *Thuja plicata*, and *Picea sitchensis*, exhibited more or less of the injury.

Somerville describes the abnormal wood formation only for *Larix leptolepis*. He says that the abnormal wood formed in the early part of 1912 is easily distinguished by the naked eye. On a cross section it appears as a narrow brown ring, while on a radial section it forms a thin brown streak. A microscopic examination shows that the medullary rays are seen to pursue a most irregular course and to consist of much elongated and swollen cells. The rays frequently are discontinuous with those of the previous ring. The intervening cells, many of which have walls much thickened, instead of getting smaller as one proceeds outward, have a tendency to become larger. A radial section along the junction of the normal summer wood and the abnormal spring wood of 1912 shows that the abnormal zone of tissue is largely composed of irregularly shaped parenchymatous cells with simple pits and rectangular transverse walls. It will thus be seen that the foregoing description of Somerville's abnormal wood formation agrees closely with Neger's description of frost rings, especially since they occur following immediately upon the summer wood of the preceding growth ring.

Somerville, however, states that the cause would appear to be the excessive heat and drought of the summer and fall of 1911, which seriously affected the growth of many trees, notably the Japanese larch. He says:

> This climatic condition evidently so upset the normal function of the cambium that when the wood of 1912 came to be formed it was found to deviate greatly from the usual type.

However, from a consideration of Somerville's description and illustrations of the injury, together with the fact that it occurred also in the spring wood of other years, the writer is inclined to regard this injury as the result of frost rather than of drought. This view appears to gain credence when it is considered that, inasmuch as the drought occurred during the summer of 1911, it would seem likely that the injury to the cambium must have occurred in ample time to have registered in the latter part of the 1911 ring, whereas it did not register until the beginning of the growth ring of the following year.

Mix (*6*) describes and illustrates the formation of a zone of parenchyma wood in apple trees varying in age from 2 to 8 years, following an injury to the cambium due to freezing while in the dormant condition. Macroscopically the injury appeared as a brown line between two annual rings. A microscopic examination showed that the wood first formed in the spring following the injury was a comparatively narrow zone of parenchyma wood, that the normal xylem was soon laid down outside of this zone, and that the remainder of the growth ring was normal. The medullary rays, which had become enlarged and spread out tangentially, could be traced into this parenchyma zone. Mention is made of a yellowish brown amorphous substance occurring in the intercellular spaces. While Mix was unable to definitely determine the exact nature of this substance, the writer, from his investigation of this group of substances (*10*), would regard the brown color as a sign of humification and the brown substance itself as a huminlike compound originating as a decomposition product of the cell contents of the cells killed by frost. The type of frost injury which Mix described is closely related to that described by Neger (*7*) in *Picea excelsa.*

GENERAL SYMPTOMS AND MACROSCOPIC APPEARANCE.

During the field season of 1921 the writer repeatedly observed in frost localities on cut-over lands in Washington, Idaho, and Montana areas of coniferous reproduction on which a large percentage of the young trees showed the effect of repeated late frosts, both externally and internally.

In unusually severe cases the young growth had been killed back until the trees had developed an abnormally compact bushy form.[2] Such a growth form, which was by no means common in such native trees as *Thuja plicata*, *Tsuga heterophylla*, *Pseudotsuga taxifolia*, *Larix occidentalis*, *Picea engelmanni*, *Abies lasiocarpa*, and *Tsuga mertensiana*, was rarely observed in *Pinus contorta*, *P. ponderosa*, and *P. albicaulis.*[3] It was extremely common, however, in *Abies grandis* (Pl. I, *A*). The greater tendency of young trees of *Abies grandis* to assume this compact bushy form after injury by late frost is due to the great readiness with which this species develops compensatory shoots. Since the recovery of any given species from frost injury depends largely upon its ability to retain dormant buds which give rise to such compensatory shoots, it should rank very high in both *Abies grandis* and *A. concolor*.

In the cases of less severe injury the trees did not develop any particularly compact bushy form and often did not appear unusual in any way, yet the same frost rings occurred in the wood, although less frequently and perhaps only in the wood increment of but a single year. Where such frost rings occurred, however, it could be detected upon close examination in practically all cases investigated by the writer that the original terminal shoot of the stem in question had been killed back by frost after the initiation of its growth, and that in some cases the same had happened one or more times to the volunteer shoots. In this connection the writer wishes to state that he has never observed in any of the coniferous species studied

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[2] The writer wishes to make it clear that he does not consider all cases of the brooming of young conifers to be due to late-frost injury, since this abnormal form of growth may be induced by parasitic fungi alone. In the latter case, however, the formation of frost rings does not occur within the zones of annual increment.

[3] Host names for American species follow the usage in the publications of George B. Sudworth, of the United States Forest Service.

by him any pronounced permanent distortion of the living shoots which would indicate injury by late frost, except in the case of *Pinus densiflora* Sieb. and Zucc., a Japanese species which will be considered later.

In every case where the terminal growth had been killed, a narrow brownish zone of abnormal tissue, or frost ring, could be traced from the base of the dead shoot down the stem for a distance of several inches, or often for several feet in the case of saplings. This zone of abnormal tissue, which has the appearance of a brownish stripe in sections of the stem, usually occurred in the immediate beginning of the growth ring or else a short distance beyond the outer limit of the growth ring of the preceding year. In the latter case it gave the appearance of a double ring formation, especially when the growth rings were rather narrow. As a rule, the action of late frost manifests itself in a closed ring, although occasionally the zone of injury appears only on one side of the stem. In no case of late-frost injury observed by the writer was any external sign of mechanical injury to the bark visible.

Measurements of the linear extent of the frost rings were made in only a few instances where larger trees were involved, since this point was not deemed of any particular importance. In general, it may be said that in the smaller trees they usually extend down to or nearly to the ground line. In the larger trees, however, they terminate rather abruptly as the older and therefore better protected portion of the stem is reached. While the writer has observed the occurrence of frost rings in the outer growth rings of saplings of *Larix occidentalis* and *Pseudotsuga taxifolia* 2 inches in diameter, he has not observed their occurrence in coniferous stems of larger size at the time of the injury. Frost-ring formation, however, often occurs in larger stems of fruit trees that are subject to various forms of frost injury. The latter in general, however, perhaps due in part to the cultural practices employed, are more susceptible to frost injury than the coniferous trees. Detailed stem-analysis data are recorded for four saplings of *Larix occidentalis* from an area in which frost rings were found to be especially numerous, as mentioned below.

STEM ANALYSIS OF LARIX OCCIDENTALIS SAPLINGS WITH FROST RINGS, CUT AT IONE, WASH., AUGUST 24, 1920.

Tree No. 1.—The tip of the original leader formed in 1918 had been killed and was dead down to an elevation of 223 centimeters above the ground, at which point a 2-year-old volunteer had developed subsequent to the injury, giving the sapling a total height of 278 centimeters. A conspicuous brownish zone of parenchyma wood, located in the 1919 growth ring and developed very soon after the initiation of the growth of that year (Pl. II, *C*), could be traced down the stem to an elevation of 65 centimeters above the ground, at which point it was no longer apparent under a hand lens. A section of the wood at this point showed under the microscope practically no distortion of the wood elements.

Tree No. 2.—Another sapling, with a height of 365 centimeters and with no evidence of any external injury or dead terminal shoot, showed upon dissection a similar brownish zone of parenchyma formed shortly after the beginning of the 1919 growth ring. This line of parenchyma could be traced from the apex of the 1918 growth, at an elevation of 300 centimeters, down the stem to an elevation of 175 centimeters, below which point it was no longer in evidence.

Tree No. 3.—In this case the original leader had been killed, and a volunteer leader 2 years old had been put out at a height of 158 centimeters, just below the dead tip of the 1918 growth. A brownish zone of parenchyma, formed shortly after the beginning of the 1919 growth ring, was traceable down the stem directly from the base of the volunteer leader, at an elevation of 158 centimeters to an elevation of 30 centimeters above the ground. In these first three trees there was no evidence of any frost injury in the growth rings of any year other than those enumerated.

Tree No. 4.—The original leader of this sapling had been killed, and a 2-year-old volunteer had been established at a height of 237 centimeters just below the dead tip of the 1918 growth, giving the tree a height of 300 centimeters. A conspicuous brownish zone of parenchyma, developed shortly after the beginning of the 1919 growth ring, could be traced from the apex of the growth of this year, at the base of the dead 1918 tip, at an elevation of 237 centimeters, down the stem to an elevation of 75 centimeters. At this point a faint zone of parenchyma also showed in the beginning of the 1918 growth ring and could be traced up the stem to an elevation of 200 centimeters, a point just below the apex of the 1918 growth, where the stem had a diameter of but 2 millimeters. Beyond this point the injury was not evident with a hand lens, but only in sections examined under the microscope. By means of a microscopic examination this zone of parenchyma formation could be traced up to an elevation of 211 centimeters, at which point the stem, consisting of only the 1918 growth, was but 1 millimeter in diameter, or practically to the apex of the growth ring of that year.

Through the kindness of J. A. Larsen, director of the Priest River Experiment Station in Idaho, the writer was enabled to examine and procure material for the study of a number of nonindigenous conifers that showed the effects of repeated late-frost injury. The trees had been grown to the transplant stage in California and planted some years previously on an open bench at the experiment station. The stock in question comprised young trees of *Pinus lambertiana*, *Pseudotsuga taxifolia*, *Chamaecyparis lawsoniana*, and *Sequoia washingtoniana*, all of which except *Pseudotsuga taxifolia* are nonindigenous to Idaho. All of these trees, especially the two species mentioned last, exhibited an abnormally compact and bushy form and owing to the repeated injury contained frost rings in practically every growth ring. At the time of the examination all of the two species last mentioned, as well as a large number of the first two species, were dead, due probably to the combined action of the repeated late-frost injury and recent drought injury.

The young shoots, however, are by no means always killed back by late frost. Not infrequently the shoots injured by frost may remain alive throughout and still record the injury within their tissues in the usual manner. In this form of late-frost injury the terminal shoots as well as the corresponding lateral shoots sometimes exhibit more or less of a characteristic permanent distortion, which is accompanied by a frost-ring formation in the wood. While not observed in any of the western frost-injured conifers which the writer studied, this type of injury has been described by Hartig (*2*) for *Pinus sylvestris* and has been observed by the writer in a row of young trees of *Pinus densiflora*, a Japanese species of dwarf bushy pine grown in a nursery on the Mall, in Washington, D. C. For the correlation of this form of injury with late frost and the observations on the behavior of the trees immediately after the freezing the writer is indebted to R. H. Colley and G. F. Gravatt, of the Office of Investigations in Forest Pathology.

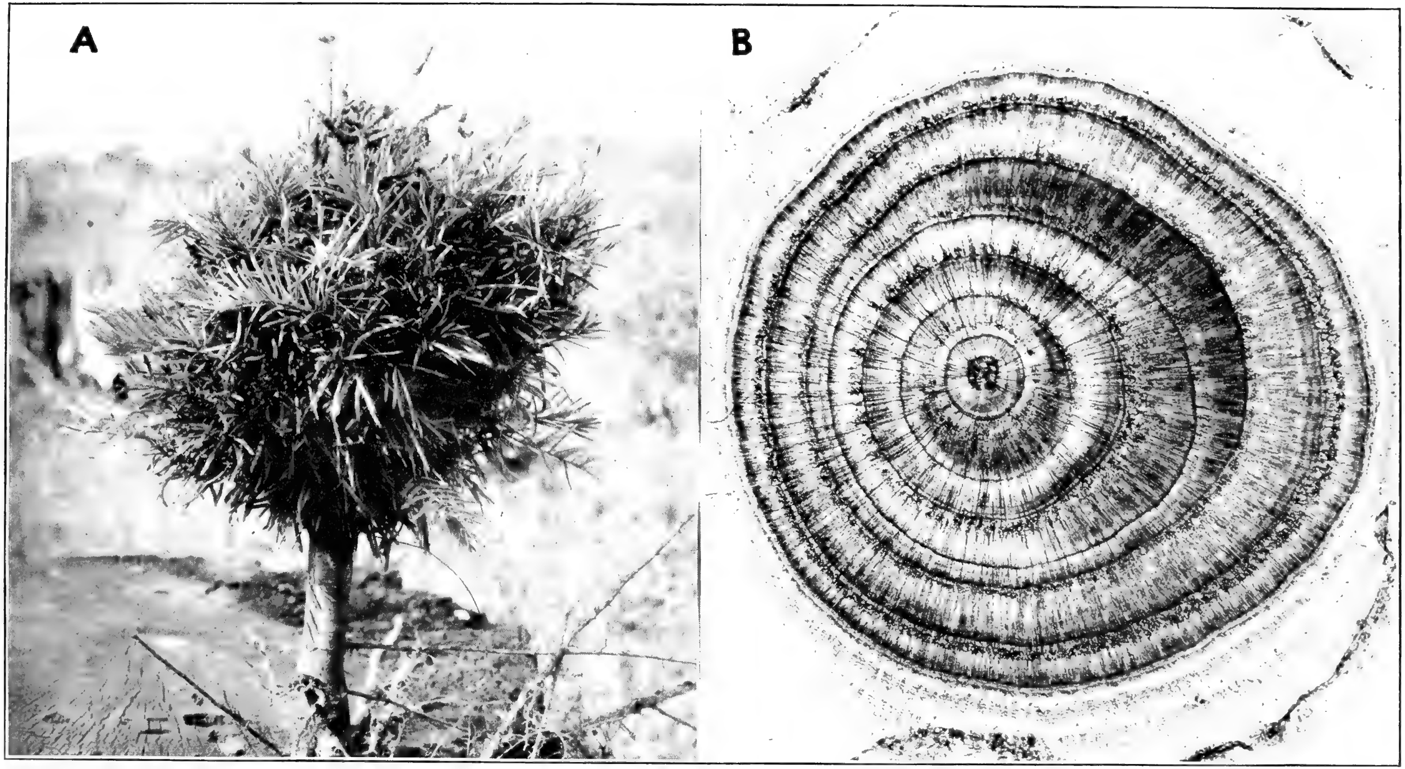
From March 27 to 29, 1921, there occurred a general cold wave, coming after a period of abnormally warm weather, which was very destructive to the active vegetation over a large part of the country east of the Mississippi River. On the day following this freeze, March 30, it was observed that large numbers of the 1921 shoots along this entire row of *Pinus densiflora* trees, which was the outermost row on one side of the nursery, had wilted and drooped, due to loss of turgor. On a row of trees of *Taxus baccata* near by in the same nursery it was observed that a large number of the new shoots, which averaged half an inch in length, were killed outright.

On September 30 the writer had the opportunity to observe these trees. The entire row of *Pinus densiflora* trees showed numerous cases of permanent deformation of the terminal and many of the lateral shoots of the last whorl, but all had remained living and had regained to a large extent their normal erect position, although not without leaving more or less of an S-shaped kink in their stems (Pl. III). In all cases which the writer examined, such shoots exhibited a frost ring in the beginning of the 1921 growth ring, which could be traced readily down the stem for several inches from the base of the last whorl, although it was scarcely to be distinguished, even with a hand lens, from the outer limit of the 1920 growth ring, owing to its close coincidence (Pl. IV, *A*). The frost ring likewise was traceable macroscopically on sections cut with a keen microtome knife, though better microscopically, for a distance of several centimeters above the bases of the deformed terminal and lateral shoots of the last whorl, where it appeared in the first wood elements bordering upon the pith and in the outer cells of the pith. It was lacking in those few lateral branches of the last whorl that sometimes escaped injury by reason of their lack of development at the time of the freeze. In the far less numerous cases of frost injury in *Taxus baccata*, however, there was no evidence of any deformation of the young shoots, such as occurred in *Pinus densiflora*, but the young terminal shoots were killed outright and replaced by one or more volunteer shoots. In all such cases, where the terminal shoot had been killed by late frost, a frost ring could be traced down the stem for several inches below the base of the dead terminal shoot in the beginning of the 1921 growth ring.

A row of trees of *Pinus montana* var. *uncinata*, a more hardy appearing species planted next to the row of *Pinus densiflora*, showed no single external symptoms of frost injury, and none of the shoots which the writer cut into showed any frost rings. On the other hand, with the exception of the two species mentioned, there was no evidence of any deformation or killing of the shoots by frost on any of the other conifers, of which a large variety were in the nursery.

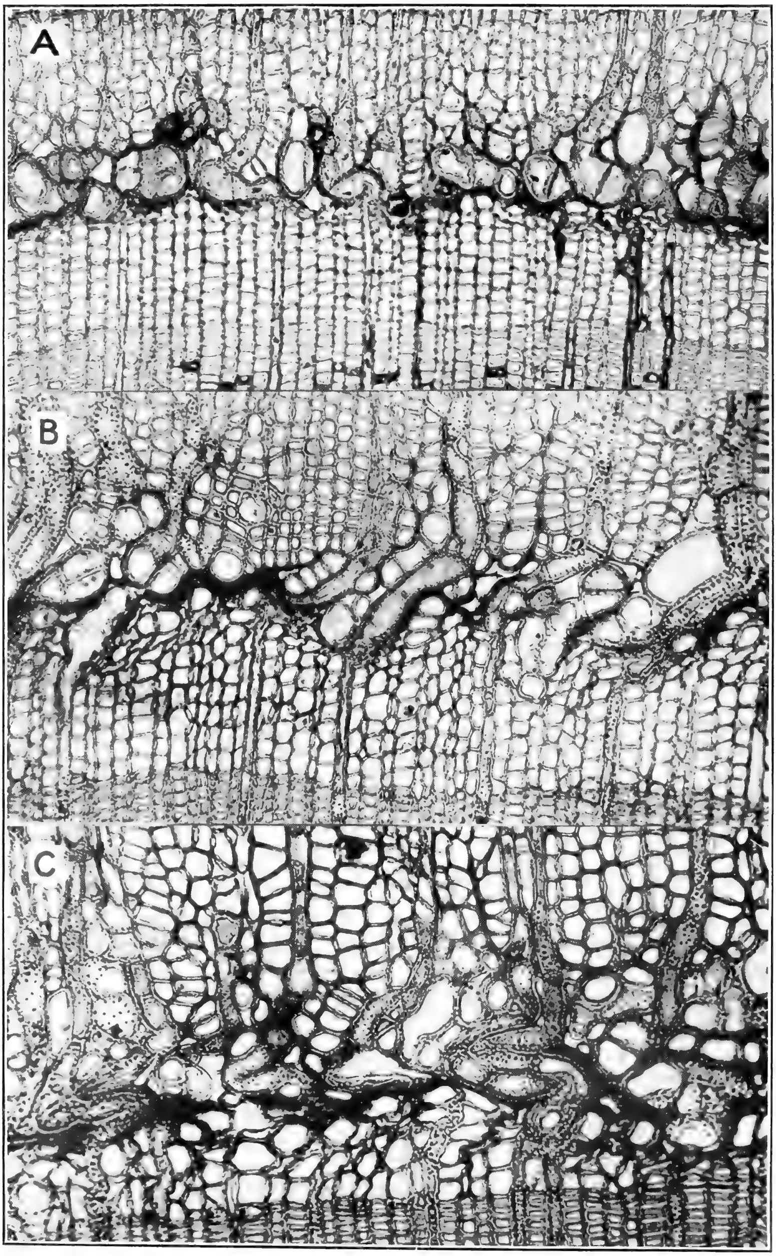
ANATOMICAL STRUCTURE OF THE FROST RINGS.

As is well known, when living plant tissue is frozen the water is withdrawn from the cells, solidifying to ice in the intercellular spaces or other tissue gaps. Upon the initiation of the freezing the water from the still living cambial wood passes out between the wood and the bark and forms an ice mantle there. The extraordinarily tender nature of the youngest cambial cells favors the separation of the tissue, and a loosening of the phloem is facilitated either by the stronger shrinkage of the frozen wood or by the expansion of the cortex due to the stress exerted by the ice formation beneath it. The lower the temperature falls the thicker the ice mantle becomes, and it compresses the tender cambial cells until their outlines are more or less indistinguishable, as is to be seen in Plate IV, *A*, *B*, and *C*.



FROST INJURY TO ABIES GRANDIS AND TSUGA HETEROPHYLLA.

A.—Young tree of *Abies grandis* repeatedly injured by late frosts, showing the abnormally compact and bushy form of growth as a result of the ready development of numerous compensatory shoots. This tree exhibited frost rings in practically every growth ring. (One-fifth natural size.) *B*.—Transverse section of a branch of a similar tree of *Tsuga heterophylla*, showing frost-ring formation, either partially or entirely around the stem, in every growth ring after the first one. (×10.)

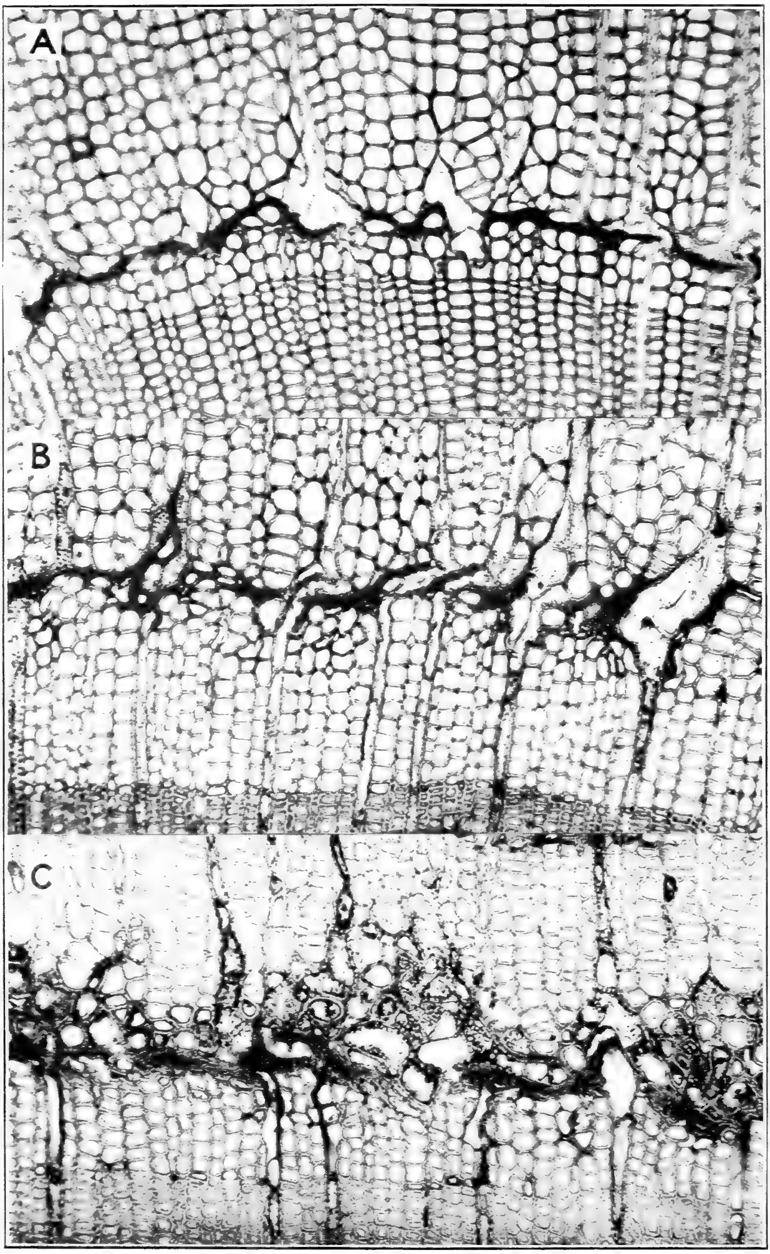


FROST INJURY TO THUJA PLICATA, PSEUDOTSUGA TAXIFOLIA, AND LARIX OCCIDENTALIS.

A.—Transverse section through frost ring in *Thuja plicata*, showing a pronounced distortion of the medullary rays. (×135.) *B*.—Transverse section through frost ring in *Pseudotsuga taxifolia*, showing the crumpling of the wood cells that were but slightly lignified at the time of freezing. (×135.) *C*.—Transverse section through frost ring in *Larix occidentalis* sapling (tree No. 1), at 146 centimeters above the ground, showing an extreme case of lateral displacement of the medullary rays. (×135.)

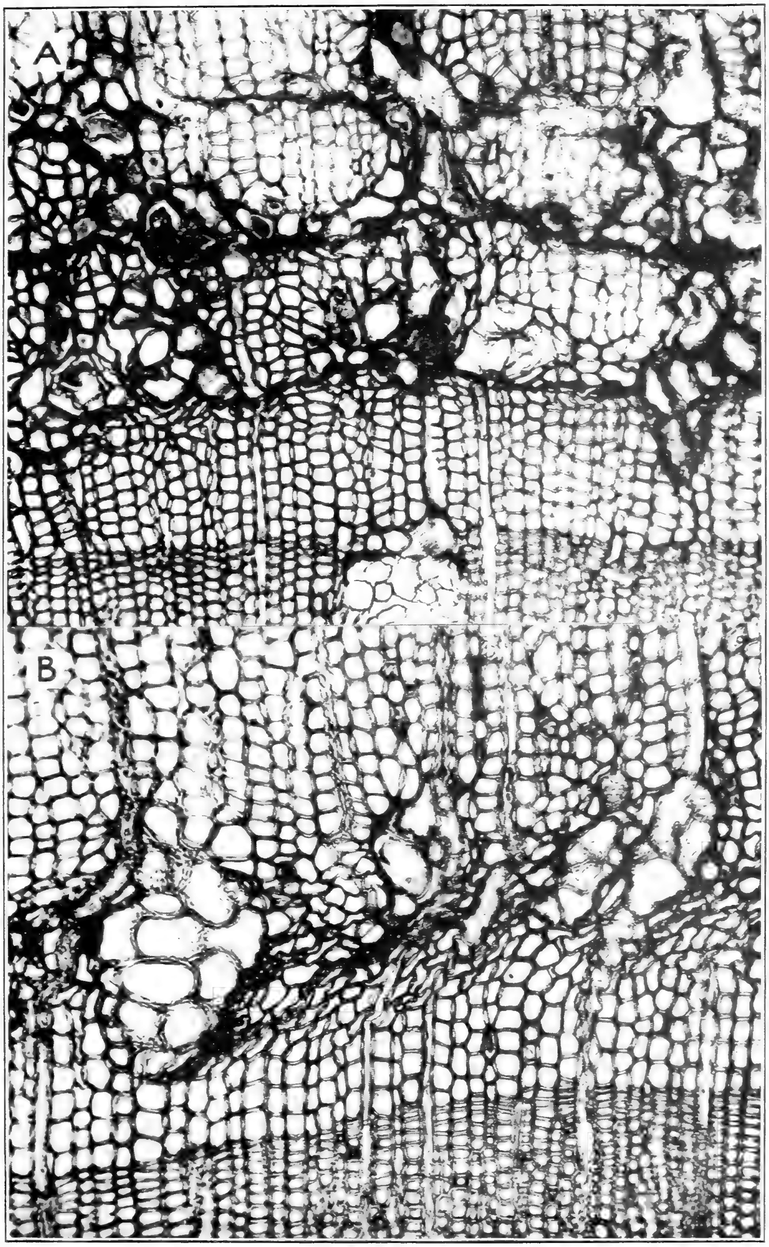
FROST INJURY TO PINUS DENSIFLORA.

Effect upon *Pinus densiflora* of a late March frost occurring after the development of many of the 1921 shoots had been initiated, showing the characteristic permanent distortion of the terminal shoot and three of the five lateral shoots. Photographed September 30. (Two-thirds natural size.)



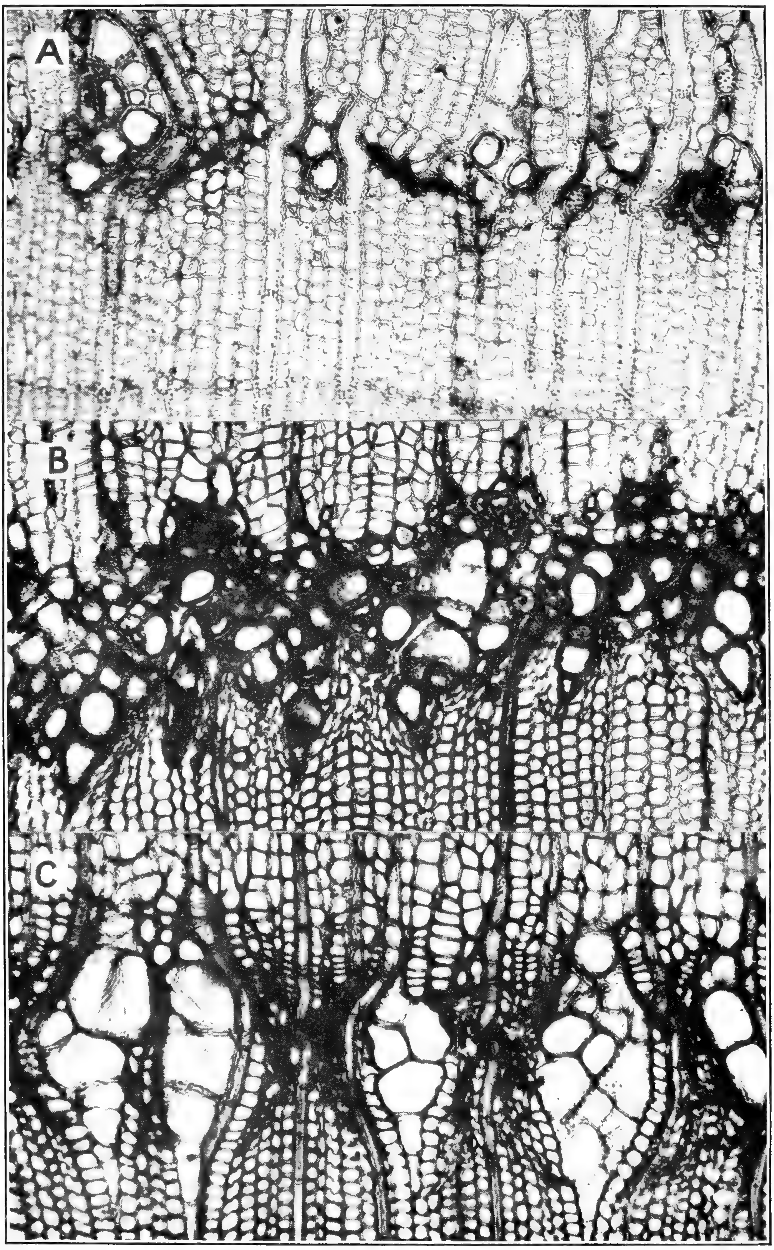
FROST RINGS OF PINUS DENSIFLORA, ABIES GRANDIS, AND TSUGA HETEROPHYLLA.

A.—Transverse section of stem of *Pinus densiflora* taken 10 centimeters below the 1921 whorl of branches, showing a slight frost ring formation in the 1921 growth. (×135.) *B*.—Transverse section of *Abies grandis*, showing a more pronounced frost-ring formation, with the characteristic lateral displacement of the medullary rays and their proliferation. (×135.) *C*.—Transverse section through a frost-ring formation in *Tsuga heterophylla*, showing the formation of a broad zone of parenchyma wood (×135.)



FROST INJURY TO PINUS MONTICOLA AND PINUS ALBICAULIS.

A.—Transverse section through a stem of *Pinus monticola*, showing the termination of the preceding annual ring (at the outer margin of the resin canal at bottom of picture) and three frost rings occurring in the early portion of the succeeding growth ring. (×135.) *B*.—Transverse section through a frost ring in *Pinus albicaulis*, showing the crumpling of the wood cells that were but slightly lignified at the time of freezing and the formation of a radial cleft (at the left) which has become filled by large-celled parenchyma. (×135.)



FROST INJURY TO TSUGA MERTENSIANA, CHAMAECYPARIS LAWSONIANA, AND SEQUOIA WASHINGTONIANA.

A.—Transverse section through frost ring in *Tsuga mertensiana*, showing the outer face of a preceding growth ring at bottom and a large number of well-lignified tracheids developed before the freezing; also a radial cleft (at upper left-hand corner) filled up with large-celled parenchyma. (×135.) *B*.—Transverse section through a frost ring occupying a median position in a growth ring of *Chamaecyparis lawsoniana*, showing an unusually broad zone of dark-brown parenchyma and radial clefts also filled up with large-celled parenchyma. (×135.) *C*.—Frost ring occurring at the outer limit of a summer-wood formation in *Sequoia washingtoniana*, showing a series of radial clefts subsequently filled up with large-celled parenchyma. (×135.)

The already thick-walled but still unlignified cells collapse also, their walls presenting a crumpled appearance (Pl. II, *B;* Pl. V, *B*).

After the thawing, the cell tissue that has been compressed does not expand to its previous form and size, but remains permanently distorted. In the cases of the more severe injury there begins at the periphery of the wood formed before the injury a more or less broad zone of large-celled parenchyma, which is distinguished by its greatly thickened simple-pitted walls and by the dark-brown color of the walls and the cell contents. This zone of parenchyma tissue quickly passes over into tracheidal tissue, which at first is usually somewhat larger celled than that developed before the frost injury, but which quickly becomes typical. In this manner the frost injury results in the formation of a false ring, especially if it occurs after the development of several spring-wood tracheids (Pl. IV, *B;* Pl. V, *A;* Pl. VI, *A* and *B*).

As may be seen from the accompanying reproductions of photomicrographs, the frost rings exhibit great dissimilarity in structure, according to the degree of intensity of the frost action and the susceptibility of the wood tissue at the time of its occurrence.

The medullary rays, which extend through the frost ring and stretch in accordance with the stress exerted upon them, naturally suffer most from the displacement of the tissue. Their deformation varies according to the severity of the injury, but in general is very characteristic. On the inner side of the frost ring the rays widen out abruptly, often becoming 2-seriate or 3-seriate instead of uniseriate (Pl. IV, *B*; Pl. II, *B*). The rays apparently are stimulated to lateral broadening by the diminution of the pressure normally exerted by the adjoining wood elements, caused by the crushing together of the young wood elements. This broadening ensues immediately in the region of the frozen young wood and reaches its greatest extent within the region which, in the frozen condition, was filled by ice. In addition to broadening out laterally, the rays usually are also more or less sharply displaced, often undergoing a knee-shaped bending (Pl. II, *A* and *C*). Within any one stem the medullary rays are usually, although by no means always, displaced uniformly either to the one side or to the other. As the wood ring enlarges after the thawing, the medullary rays are brought into an oblique position and later grow out again in their original direction, continuing in equal number in the newly formed wood and causing the wood tissue to appear as though a fault had occurred in it. The lateral displacement of the medullary rays apparently depends upon the circumstance that their stretching during the ice formation remains preserved after the thawing. This lateral expansion and displacement of the medullary rays is by far the most conspicuous and characteristic feature of late-frost injury and is a constant feature of all injuries to wood by late frost. In at least the more severe cases of injury the frost ring is further accentuated by a more or less broad zone of brownish parenchyma tissue.

There also may arise after the thawing a series of radial gaps or clefts, occurring with variable frequency and conspicuousness within the tracheidal tissue, where it had been stretched apart previously by the excessive tangential contraction. With subsequent growth, these tissue gaps become filled with large-celled parenchyma derived from the new cambial formation (Pl. V, *B*; Pl. VI, *B* and *C*.) An unusually striking example of this radial cleft formation occurred in the frost rings observed in stems of *Sequoia washingtoniana*, where clefts were present not only in the early formed portion of the growth ring but also at the outer limit of the summer-wood formation (Pl. VI, *C*). In the latter case the frost rings appeared to lie between the summer wood of one growth ring and the spring wood of the next, so that there was no sharp demarcation between the two annual rings except where the frost ring did not extend completely around the stem. Still other stems from the same material, which had been injured by frost near the close of the growing season and had died without subsequent growth, exhibited the same radial clefts at the periphery of the xylem, but in this case the clefts were still open and free from any occlusion by parenchyma cells. Such tissue disturbances result in a very pronounced false ring formation.

A large part of the phenomena which come to light in frost injuries to young stems, however they may vary, can be traced to simple mechanical processes. Sorauer (*12*) has proved experimentally that processes of loosening are initiated in the cell membranes by the action of frost; and this explains the formation of this parenchyma zone instead of the normal wood elements as the result of a weakening of the compressing influence exerted by the bark girdle on the youngest tissue, that is, the cambium. According to Sorauer, the frost, without necessarily forming ice crystals in the intercellular spaces, contracts the tissue in direct proportion to the thinness of the walls of the tissue. The bark suffers considerably more than the wood, which, reached later, cools down less easily and contracts less. The tangential contraction is greater than the radial. As Sorauer states, this difference acts like a one-sided strain and exerts itself in the direction of the circumference of the trunk, to which the different layers of the bark will respond to a different degree when the bark as a whole is very young. Consequently, with the action of the frost there must take place everywhere within a woody axis a preponderance of tangential strain over radial contraction, and under certain circumstances this must increase to a radial splitting of the tissue. With an equal degree of contraction at all points in the bark, the cells lying nearest the periphery and most elongated in the direction of the circumference of the trunk will be the most displaced. As Sorauer also states, if one considers that the outer cells of the primary bark, because of the greater coarseness of their walls, are not as elastic as the underlying thinner walled ones, it is clear that when the strain ceases in them the permanent stretching, caused by the incomplete elasticity, will be the greatest there. After the action of the frost, which continues but a short time in late frosts, has stopped, the tissue that has become stretched is not sufficiently elastic to contract again to its original volume, and the cells retain their distended and distorted form. In this way each frost action leaves behind an excessive lengthening of the peripheral tissue layers in proportion to the adjacent layers which lie more toward the inside. The bark body as a whole is therefore larger and either does not have room enough on the wood cylinder, so that in places it is raised up from it, or it at least decreases its constricting influence on the cambial elements of the wood cylinder. The cambial zone responds to this with the formation of parenchyma wood, as may be seen in every wound in which the bark is raised. If the bark girdle closes together again into a connected layer the cambial cylinder by growth in thickness must again resist the constricting effect of the bark and on this account again forms normal wood elements.

In sections containing frost rings that when viewed macroscopically appear to be only one-sided, it can be recognized in a microscopic examination that, as a rule, a lesser disturbance has occurred on the other side of the stem (Pl. II, *B*). However, a disturbance of the wood tissue by no means always extends entirely around the stem, the same often being purely local and consisting of numerous isolated groups of parenchyma elements. The frost rings occasioned by late frost vary greatly in their position within the growth ring, but usually occur early in the spring wood, either in the immediate beginning or after the formation of a few normal tracheids. On the other hand, they may not be formed until late in the growth ring when the frost must necessarily occur during the summer. Frost rings in the latter position are comparatively rare, however.

More than one frost ring may occur within the wood of any one growth ring, depending upon whether or not the frost occurs more than once after the spring growth has been initiated. Two frost rings within one annual ring are fairly common, and the writer has observed the occurrence of three frost rings in the spring-wood zone of an annual ring in *Pinus monticola* (Pl. V, *A*) and in *Picea engelmanni*.

Frost-ring formation may occur in the wood from the action of either late or early frosts during the course of the growing season or from the freezing of the cambium during the winter when the tree is dormant. The frost rings, therefore, may register at any point within the growth ring, the relative position of the frost ring within the growth ring signifying the time at which the injury occurred.

According to Hartig (*2*, p. 4), frost rings arise through late-frost injury only when the cambial activity has already commenced and at least some few cells have been cut off toward the interior, if, therefore, the annual ring formation has been initiated. It has been the writer's experience with late-frost injury that, while the number of spring-wood tracheids that intervene between the outer limit of the summer wood of the preceding annual ring and the frost ring is usually fairly uniform on any radius, the frost rings sometimes appear to abut directly on the summer wood of the preceding growth ring, although groups of normal spring-wood tracheids usually intervene in places. The formation of at least some normal spring-wood elements would therefore appear to be a diagnostic feature of late-frost injury.

In the case of late frost occurring unusually late in the season, the frost rings may register in the median or outer portion of the growth ring (Pl. VI, *B*). In the case of early frosts occurring late in the season, at a time when the annual accretion of wood has not matured, or in the case of frost injury occurring during the dormant period of the year, the resulting frost ring registers in the immediate beginning of the next growth ring, often tending to obscure the normally sharp demarcation between the two rings (Pl. VI, *C*).

In general, it appears that frost injury occurring shortly after the initiation of active growth causes a greater distortion of the wood elements than that occurring when the growth ring is practically mature or when the tree is dormant.

Frost rings are often confusing to those who have occasion to engage in age determinations or stem analyses of trees. The frost-ring formation, however, usually occurs within such close limits of the beginning of the annual ring formation that, macroscopically at least, the parenchyma zone appears to coincide more or less closely with the outer limit of the preceding growth ring. Frost-ring formation should prove confusing in age counts only when it occurs late in the season after a considerable portion of the growth ring has been formed. Moreover, since only the younger stems appear to be susceptible to frost-ring formation, it is believed that in conifers at least, false ring formation from this source need be expected chiefly only in the first several growth rings formed in the life of the tree.

As may be expected from their structure, frost rings constitute a plane of weakness in the wood, since there is no strong bond between the wood formed before the injury and the parenchyma wood formed immediately after it. In chopping off a face on stems containing one or more frost rings in order to follow their linear extent, the wood frequently splits peripherally along the plane of these zones of abnormal wood. In future years it seems likely, as Somerville (*11*) states for the abnormality which he describes, that they may lead to the formation of ring shakes within the trees.

The writer's investigation of the pathological anatomy of late-frost injury confirms those of Mayr, Hartig, and Sorauer in all particulars except the occurrence of the chains of pathologic resin canals, which Mayr (*4*) suggests may be caused by frost and which Hartig (*2*) found sometimes associated with the frost rings.

Mayr (*4*, p. 29), in a discussion of the chains of abnormal or pathologic resin canals sometimes found in the wood of *Abies firma* and Tsuga, suggests that they may be caused by late frost, which, he states, is of fairly common occurrence. However, he observed that such chains of resin canals may also be found in the hard summer-wood zone of the annual ring, where late frost is excluded as a cause. Although not considered by Mayr, a number of other types of injury could easily have been responsible for this pathologic resin-canal formation.

Hartig (*2*, p. 7) states that he has repeatedly found that the wound parenchyma developing in the frost ring contained resin canals, so that a more or less complete ring of them was recognizable in the frost zone. Despite the writer's particular consideration of this point and his extensive investigations on pathologic resin-canal formation in general, which will appear shortly, he has never observed the formation of chains of pathologic resin canals as the result of frost injury. While zones of pathologic resin canals do occasionally coincide with the frost rings in a stem, the writer has always traced their origin to some mechanical wound. It is by no means impossible, however, for such zones of pathologic resin canals to arise schizogenously within the broad aggregates of parenchyma wood comprising the frost ring.

Hartig (*2*, p. 7) likewise mentions the occurrence of chains of abnormal resin canals, which he regards as due to the action of late frost, throughout the entire circumference of the phloem of stems of *Chamaecyparis lawsoniana* 2 centimeters thick, at a slight distance from the cambial layer. He states that these arise by the medullary rays stretching and becoming broadened laterally through cell division and that between each two rays the delicate-walled tissue composed of sieve tubes and parenchyma was crowded apart. He assumes that here also the tissue gaps are not closed after the thawing of the ice, and finds that the surrounding living cells become enlarged more or less into these gaps and become converted into resin-secreting cells, pouring large quantities of resin into them. As a result of this formation a festoon of large resin beads appears from the bark on the ends of cut-off shoots. The writer, however, did not observe any formation of chains of pathologic resin canals in the phloem of the frost-injured material of *Chamaecyparis lawsoniana* studied by him.

SUMMARY.

The pathological anatomy of late-frost injury has been studied in detail by the writer in *Pinus albicaulis*, *P. contorta*, *P. densiflora*, *P. lambertiana*, *P. monticola*, *P. ponderosa*, *Picea engelmanni*, *Larix occidentalis*, *Pseudotsuga taxifolia*, *Abies grandis*, *A. lasiocarpa*, *Tsuga heterophylla*, *T. mertensiana*, *Thuja plicata*, *Chamaecyparis lawsoniana*, *Sequoia washingtoniana*, and *Taxus baccata;* also in apple and pear trees.

The young shoots injured by late frost may either wilt through loss of turgor and after again directing their points upward usually become permanently distorted, or, as generally happens, they may be killed outright and replaced by one or more volunteer shoots. The structural disturbance initiated by the action of late-frost injury is not confined to the shoots then developing, but extends down the stem for distances varying from several inches to several feet below the base of the injured shoots, or as far as the cambium has been injured by the freezing without entailing the death of the stem. The healing proceeds internally and results in the formation of a brownish zone of parenchyma wood, or frost ring, within the growth ring, developing at the time of the injury.

Late-frost injury results in very characteristic disturbances in the tissue of the growth ring forming at the time of the injury. The abnormal tissue of the frost ring varies greatly, according to the severity of the injury, and may be characterized by various combinations of such features as the crumpling of the wood cells that were but slightly lignified at the time of the injury, a marked broadening or proliferation of the medullary rays, a strong lateral displacement of the medullary rays together with a marked broadening or proliferation, the presence of radial clefts subsequently filled up by large-celled parenchyma, and more or less broad zones of wound parenchyma. The displacement of the medullary rays is occasioned by their stretching and lack of elasticity; the radial clefts, to the preponderance of the tangential contraction over the radial contraction; and the interpolated zone of parenchyma wood, to a transitory weakening of the compressing influence exerted by the bark girdle on the cambium, due to the disrupting action caused by the freezing.

Frost-ring formation may occur in the wood from the action of either late or early frost during the course of the growing season or from the freezing of the cambium during the winter when the tree is dormant. The frost rings, therefore, may register at any point within the growth ring, the relative position of the frost ring within the growth ring signifying the time at which the injury occurred.

Frost rings arise through late frost only when the cambial activity has already commenced and some new xylem cells have been differentiated. As a rule, there is a definite zone of spring-wood tracheids intervening between the outer limit of the summer wood of the preceding annual ring and the frost ring. In the case of early frosts the frost ring may either register late in the summer wood of the growth ring or not until the immediate beginning of the ensuing growth ring. Frost injury occurring during the dormant period likewise is recorded as a frost ring in the immediate beginning of the ensuing growth ring.

Young trees injured by repeated frosts often develop an abnormally compact and bushy form, especially in *Abies grandis* and other species, which readily form compensatory shoots. Frost injury that results in the killing of the young shoots often detracts greatly from the straight axial growth of the trees and, where frequently repeated, may render the tree absolutely valueless for commercial purposes. In addition, late-frost injury may render young conifers more susceptible to weakly parasitic fungi than they would be otherwise.

Late-frost injury, when occurring late in the season after any considerable portion of the growth ring has been formed, results in a false or double ring formation, which is often confusing in age determinations. Frost-ring formation from late-frost injury has not been observed by the writer in coniferous stems larger than 2 inches in diameter, although it often occurs in larger stems of fruit trees that are subject to various forms of frost injury.

As may be expected from their structure, frost rings constitute a plane of weakness in the wood, which may not only predispose to the formation of circular shake in the standing tree, but may require the manufactured wood to be discriminated against for use in small pieces where great strength is required.

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