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STUDIES ON POLYSTICTUS CIRCINATUS AND ITS RELATION TO BUTT-ROT OF SPRUCE

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STUDIES ON TOLYSTICTUS CIRCINATUS AND ITS RELATION TO BUTT-ROT OF SPRUCE

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During the writer's study of the butt-rots of spruces in the Province of Quebec, it was found that the most important fungi causing butt-rots are *Poria subacida, Polyporus balsameus, Polyporus Schweinitzii,* and *Polyporus circinatus.* This last was chosen for study because of the irregular occurrence of the species and of its importance locally in causing excessive windfall.

It soon became evident that what had been determined as P. circinatus actually included two distinct fungi. One was characterized by its brighter color and by the fact that it occurred chiefly on the ground; the other was characterized by the darker color of the sporophores and by the fact that it occurred mostly on the trunks of the trees. These differences between the two forms which were so obvious in the field, led to the investigations of the taxonomy. It was found that the two organisms could be separated microscopically by the character of the setae present in the hymenium and this led to their determination as *Polyporus tomentosus* Fr. and *Polyporus circinatus* Fr.

From a review of the literature it appears that there has been considerable confusion as to the identity of these two forms. This confusion has arisen since Fries described the two species, *P. tomentosus* in 1821 and *P. circinatus* in 1848, and it came from the fact that he described *P. tomentosus* as having a homogeneous context, yet according to specimens identified by Fries, both *P. tomentosus* and *P. circinatus* have a duplex context. The only difference, excepting the color and the shape, are the straight setae for the former and the predominantly curved setae for the latter.

Peck (1878) described a new species from New York, which he called *Polyporus dualis*. His species was sessile or short, lateral-stemmed and of rather dark color. Later, Ellis and Everhart (1889) examined specimens from Peck and found the curved setae characteristic of *P. circinatus* Fr. Cooke (1886) and Saccardo (1888) have given *P. dualis* Pk. as a synonym of *Polystictus circinatus* (Fr.) Cke. So it is fairly safe to say that Peck's type specimen is *P. circinatus* Fr.

In 1882, Karsten transferred Polyporus tomentosus to Polystictus. Later (1889) he segregated the new genus Onnia from Polystictus, placing emphasis upon the setal character of the hymenium. He distinguished O. tomentosus from O. circinatus by the homogeneous context of the former. Ellis and Everhart (1889) examined Karsten's specimen later and found straight setae for the plant he designated as Onnia tomentosus. Although Ellis and Everhart's illustration (1889) did not make this point

¹ Thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Harvard University.

Contribution from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, no. 225. clear, Karsten's specimens show that there is a duplex context, hence his *Onnia tomentosus* is the same as *P. tomentosus* Fr. Little is known about his *O. circinatus*.

While Karsten was creating the genus Onnia, Ellis and Everhart (1889) created the genus Mucronoporus based on Polyporus circinatus. They described straight setae for M. tomentosus and curved ones for M. circinatus. Subsequent mycologists have considered these species synonymous with the two Friesian ones.

In 1900, Patouillard made a new genus Xanthochrous based on P. circinatus. He described the setae as being straight. Apparently his X. circinatus is P. tomentosus Fr.

Murrill (1904) refers to Fries' authentic specimens, stating that "the type of *Polyporus tomentosus* at Upsala corresponds in all respects with the plants found in America, having the same kind of spines and a dual context." Since Nannfeldt has reported in a personal letter to Haddow (1941) that there are no type specimens of either of Fries' species at Upsala, it is difficult to understand to which specimen Murrill refers. It is worth observing, however, that he attributed to his Friesian specimen of *P. tomentosus* a double context. Murrill (1916) comprises under the single species *Coltricia tomentosa* both *P. tomentosus* and *P. circinatus* of Fries.

There apparently was much confusion in Lloyd's mind in regard to the status of these two species. In 1908, he described *P. circinatus* Fr. as having straight setae, as in *P. tomentosus* Fr. Later in 1912, he stated that *P. tomentosus* Fr. was unknown from the United States and questioned whether *P. circinatus* Fr. was really distinct from *P. tomentosus* Fr., and finally suggested that "there are three (stipitate) forms of *Polyporus tomentosus* Fr.: first (typical), with thin context, straight setae; second (*circinatus*, American), thick context, straight setae; third (*circinatus*, European and American), curved setae."

Lloyd (1908), on account of the resemblance of P. dualis Pk. to Fries' figure of P. triqueter, suspected it to be P. triqueter of Europe. Bresadola, (1920) following Lloyd's opinion, considered P. dualis Pk. to be a synonym of P. triqueter Fr. Fries described P. triqueter in 1838, while P. circinatus was described only in 1848. He did not mention any relationship between the two species, hence P. triqueter Fr., if different from P. dualis Pk. as seems likely, cannot be used as a synonym for P. circinatus and there is little need to consider it in this discussion.

Neuman (1914) reported P. tomentosus from Wisconsin but gave no description of the microscopic characters. He considered P. dualis as a synonym of P. tomentosus and for that reason the exactitude of his identification may be questioned.

Lloyd (1920) described a new species, *Polyporus peakensis* Lloyd, from a single specimen collected by Hedgcock at Pikes Peak in Colorado. Later, Shope (1931) stated it was conspecific with *P. circinatus* Fr. Sartory and Maire (1922) believed that *P. circinatus* is only a variety of *P. tomentosus*, a point of view shared by Haddow (1941).

Konrad and Maublanc (1926) under Fomes (Xanthochrous) circinatus furnished a picture of curved setae and described it as straight or curved. We previously mentioned the same thing for the wood-loving forms we found in the field. It should be *P. circinatus* Fr. Bourdot and Galzin (1927) made the same observations on what they called *P. circinatus* Fr.

Shope (1931), Overholts (1933) and Lowe (1934) followed Lloyd's opinion and do not recognize P. tomentosus in the American Flora. Furthermore, Overholts states that all American forms should be referred under the name P. circinatus. All three described the typical form as having straight setae because they have been led astray by the statement of Fries that the species was characterized by the homogeneous context of the fruiting bodies. Concerning P. dualis Pk., Shope considered it the same as P. circinatus, while Overholts gave a varietal rank because of the curved setae which in the typical form are straight. Lowe considered it a good species.

Jørstad and Juul (1938) worked out the taxonomy of the species with Norwegian material. They recognized two varieties to *P. tomentosus* Fr.: *P. tomentosus* var. *americanus* and *P. tomentosus* var. *circinatus*. They made the variety *americanus* because of Lloyd's statement (1912) that *P. tomentosus* Fr. does not exist in the American flora, but only a related form. The variety *circinatus* was suggested for *P. circinatus* Fr. because they said there is no definite line of demarcation between Fries' species. They make no mention of Sartory and Maire who made the same variety in 1922.

Haddow, in 1941, based all his discussion on specimens of the Curtis Herbarium identified and labelled by Fries himself. He recognized the duplex context for both *P. tomentosus* and *P. circinatus*; the former had straight setae and the latter curved ones. Haddow did not agree that the curved setae character was sufficient to make a new species as did Fries, thus he called it *P. tomentosus* var. circinatus.

As a resumé, the following table shows the real position of each specimen.

Author	Polyporus tomentosus Fr.	Polyporus circinatus Fr.
Fries (1851) Peck (1878) Cooke (1886) Saccardo (1888) Karsten (1889) Ellis & Everhart (1889) Hennings (1898)	Polystictus tomentosus Polystictus tomentosus Polystictus tomentosus Onnia tomentosus Mucronoporus tomentosus Polystictus tomentosus	P. dualis Polystictus circinatus Polystictus circinatus Onnia circinatus? Mucronoporus circinatus Polystictus circinatus
Patouillard (1900) Murrill (1904) Lloyd (1908) (1912)	Xanthochrous circinatus Coltricia tomentosa Polyporus tomentosus Polyporus circinatus	Coltricia tomentosa Polyporus dualis
Ames (1913) Neuman (1914)	Polystictus tomentosus	Polystictus circinatus Polyporus tomentosus Polyporus dualis

Author	Polyporus tomentosus Fr.	Polyporus circinatus Fr.
Bresadola (1920)		Polyporus dualis
		Polyporus triqueter
Sartory & Maire (1922)	Polyporus tomentosus	P. tomentosus var. circinatus
Konrad & Maublanc (1926)	· · · · · · · · · · · · · · · · · · ·	Fomes (Xanthochrous) circinatus
Bourdot & Galzin (1927)		Polyporus circinatus
	D 1 1	
Killerman (1928)	Polystictus tomentosus	Polystictus circinatus var. triqueter
Shope (1931)	Polyporus circinatus	
	Polyporus dualis	
Overholts (1933)	Polyporus circinatus	Polyporus circinatus var. dualis
Lowe (1934)	Polyporus circinatus	Polyporus dualis
Jørstad & Juul (1938)	Polyporus tomentosus	P. tomentosus var. circinatus
	P. tomentosus var. americanus	•
Haddow (1941)	Polyporus tomentosus	P. tomentosus var. circinatus

It is clear, from what has been written above, that the tangled taxonomy of the two types would not have resulted had it not been for Fries' early statement that *Polyporus tomentosus* possessed a homogeneous context, whereas a study of his specimens by the writer and others, has shown that the context of the sporophore is duplex in both types, the first of which should be recognized as *P. tomentosus* (with straight setae) and the second *P. circinatus* (with curved or straight setae in the same fructification). Assuming for the time being that the two species belong in the genus *Polyporus*, it appears to the writer that Fries was correct in making these separations, since, as it has been stated above, the two species are obviously different when seen together in the field (Plate I, fig. 1, 2). It is for this reason that the writer considers it desirable to follow Fries in recognizing these species as distinct rather than to follow Sartory and Maire, and Haddow in reducing *P. circinatus* to varietal rank under *P. tomentosus*.

The generic position of these two species would be greatly simplified if they were kept in the genus *Polyporus* as has been done by many, although Murrill (1916) and Donk (1933) and others have tended to divide the genus into smaller units and probably rightly so. On the basis of priority, Fries' genus *Polystictus* (1851) must be accepted for this and related species, since *P. tomentosus* was specifically mentioned as an example of the genus and therefore can be taken to represent the type of the genus. For this reason, it seems best to consider that *Polyporus tomentosus* and *Polyporus circinatus* should be known as *Polystictus tomentosus* (Fr.) Fr. and *Polystictus circinatus* (Fr.) Cke.

DISTRIBUTION

Since they have first been described by Fries, *P. tomentosus* and *P. circinatus* have been found abundantly in Asia, Europe and America.

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Because frequently they have been misnamed, the writer has prepared from the literature a list of localities and has tried to indicate the distribution under *P. tomentosus* Fr. and *P. circinatus* Fr. Where there is any question of the accuracy of the determination, the author name is followed by a (?).

Locality	Polystictus tomentosus (Fr.) Fr.	Polystictus circinatus (Fr.) Cke.
Africa	Lloyd(?)' (1920)	
Austria	Lloyd (1908)	
China		Teng (1932)
Canada		
Prince Ed. Is.	Ell. & Evh. (1889)	
Ontario	Lloyd (1908), Faull (1922)	
Manitoba &	Bisby (1938)	
Saskatchewan		
Nova Scotia	McKay(?) (1904, 1908)	Wehmeyer (1940)
New Brunswick	Hay (1903, 1905)	Hay (1903, 1905)
Germány	All. & Schn. (1886), Hen-	Hennings (1898) Murrill
	nings (1898), Murrill (1904)	
Japan		Shirai(?) (1927
Sweden	Fries (1863), Lloyd (1908,	Fries (1863), Lloyd (1908),
	1912), Murrill (1904, 1908)	
United States		
California	Lloyd (1911, 1915)	Murrill (1915)
Colorado	Kauffman (1921), Lloyd (1908	
	1916, 1920), Murrill (1904),	7
	Seaver & Shope (1936),	
	Shope (1931)	
Dist. of Columbia	Lloyd (1922)	
Florida	Lloyd (1920)	
Idaho (northern)	Boyce (1938), Hubert (1929)	Haskell & Wood(?) (1930),
	1931), Martin (1929)	Hubert (1931)
Iowa	Wolf (1931)	
Maine		White(?) (1902), Ricker (?) (1902)
Maryland	Lloyd(?) (1908)	
Massachusetts	Lloyd (1907, 1908, 1911, 1912,	•
	1913, 1914, 1915, 1921).	· · ·
	Murrill (1904)	·
Michigan	Kauffman (1911), Lloyd	
	(1912), Longyear (1904),	
	Overholts (1916), Povah	
	(1935)	
Minnesota	Hubert (1924, 1931), Lloyd	Haskell & Wood (1930)
	(1920, 1922) Martin (?)	
	(1925)	•
Montana	Hubert (1931)	
New Hampshire	Murrill (1904)	Ell: (9) (1000) Ell 9
New Jersey	Murrill (1904)	Ellis(?) (1890), Ell. &
NT N7 1	D 1 0 T 1 (1014	Everh.(?) (1889)
New York	Burnham & Latham (1914	
	1924), Lloyd (1913, 1915, 1916, 1920, 1922), Margarill	
	1916, 1920, 1923), Murrill	E •
	(1904), Peck (1869, 1880	,
	1893, 1899), Saccardo (1888	D <i>1</i>

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Locality	Polystictus tomentosus (Fr.) Fr.	Polystictus circinatus (Fr.) Cke.
North Carolina	Curtis (1867), Lloyd (1914)	Atkinson & Schrenk(?) (1893)
Pennsylvania	Overholts (1933)	
Rhode Island	Bennett (1888)	
Tennessee (east)		Hesler (1929)
Vermont	Llóyd (1908, 1911, 1915), Murrill (1904)	
Washington	Hubert (1931), Lloyd (1916)	
West Virginia	Lloyd (1908, 1920), Mur- rill (1904)	
Wisconsin	Dodge (1914), Neuman (1914), Overholts (1916)	
Wyoming	Seaver & Shope (1935, 1936)	

To complete this list, the writer has plotted on a map the North American localities of the specimens of P. circinatus (Fr.) Cke. kept in the Farlow Herbarium. It seems that this species reaches its southern limit at the 36th parallel of latitude (Plate I, fig. 3). It is probably limited by the temperature and if so it could be expected farther south in the mountains.

HISTORY AS A PARASITE

Many writers have discussed the taxonomy of the two Friesian species since 1878, and still more mycologists have collected them in the forests, but very few, either in the Eastern or Western Hemisphere, have worked out the parasitism of these species.

In the Eastern Hemisphere, Jørstad and Juul (1938), after a discussion of the taxonomy of the species, questioned whether P. tomentosus Fr. has any parasitic tendencies and mentioned the fact that in Sweden it has been found on a root of spruce which did not present any rot. However, the ability of P. circinatus to cause rot is not doubtful and they gave the general characters of the rot as it occurs in Sweden and mentioned the similarity that this particular one has with that caused by Fomes pini.

The first in North America to report this species as a parasite was Dr. Faull (1922) who found that, in Ontario, it was causing a root- and butt-rot in spruce, hemlock and eastern white pine. Giving the description and habits of the sporophores, he identified them as being *P. tomentosus* Fr., but his herbarium specimens for that region show that *P. circinatus* Fr. was also abundant. He mentioned the fact that the infection was very much localized and further added that in the Otter District of Ontario a high percentage of white pine is affected.

Hubert (1931) reported that *P. circinatus* attacked roots and butt sections of western white pines in northern Idaho, but considered it to be a wound fungus and commonly associated with fire scars. He made a comparative study of *P. circinatus* and *Trametes Pini* and clearly described the similarities and differences between the two rots based on the macroscopic and microscopic characters of the two different decays, and the differences in the cultural characters of the two pathogens.

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Christensen (1940) published a brief note on *P. circinatus*, giving the cultural characteristics and a description of the decay and of the sporophores and mentioning the importance of this disease in northern Minnesota as the cause of windthrow and premature death of the trees.

From this brief resumé of the literature it is apparent that although we have a certain body of facts in regard to the type of decay, the microscopical and macroscopical characters of the decayed wood, and of the cultural characters of the fungus, we have very little knowledge concerning the parasitic nature of the fungus, of geographical or other factors influencing infection, and little information about the biology of *Polystictus circinatus*. For these reasons and since the fungus seems to be of local importance because of its effect on the spruce forests of the Province of Quebec, the writer decided to make more intensive studies of the fungus in an endeavor to discover further facts bearing on the biology of the fungus and its relation to the host. At the same time, it was hoped to explain the relation of other butt-rot fungi to their hosts.

STUDIES ON THE HOST-PARASITE RELATIONS

FIELD OBSERVATIONS

In undertaking this study of *Polystictus circinatus*, an intensive survey was made to determine the occurrence of this species in the Province of Quebec, especially along the north shore of the St. Lawrence River and in the Gaspé Peninsula as well as in the Laurentide National Park area.

On the Gaspé Peninsula, and more especially along the northern side, the fungus appears to be of rather frequent occurrence, whereas on the south side it is somewhat scarcer. On the northern side of the Gaspé Peninsula in the vicinity of Mt. Albert, infection² was locally very high, (100%), in the York River area infection amounted to 95%, and at Lake Ste. Anne approximately 50%. On the north shore of the St. Lawrence River, near Lake Walker, the infection in the valley was about 20% and on the mountain slope up to 80–90%. On the other hand, in the Laurentide National Park, no evidence of infection could be discovered, even though that region is intermediate between Ontario, where Faull (1922) states that the fungus is very abundant, and the North Shore of the St. Lawrence.

The high degree of rotting of spruces by *Polystictus circinatus* indicates that this fungus may be of considerable importance in the Province of Quebec, and the gap in the distribution of the species represented by the complete or nearly complete absence of the fungus in the Laurentide National Park indicates that there may possibly be some ecological factor involved which not only would furnish information on the distribution of *P. circinatus* but might also help to explain host-parasite relations in the heavily rotted areas.

² As shown by the obvious symptoms of butt-rot at stump section.

For the understanding of the behavior of the disease, it would be of interest to know if this disease occurs on trees weakened by age, crowding, competition with other species, by storm or insect damages.

Christensen (1940), according to observations made in Minnesota, states that P. circinatus can infect trees as young as fifteen to twenty-five years old. From the writer's observations it can be stated that trees of forty years age presented visible decay at the stump section. Since they must have been infected earlier, it is probable that the age of infection given by Christensen is near the truth. According to the same observations, Christensen stated that "The fungus does not merely accompany stagnation and senescence but, if present at all, is likely to be one of the primary causes of such conditions." The writer agrees with Christensen that it sometimes happens that P. circinatus will kill the tree, but he does not think that it will always bring a premature senescence of the trees. From the data obtained from the Gaspé and North Shore regions, it is shown that the average age for the infected trees in Gaspé is 90 years, while it is 130 years for the North Shore region. The average age for sound trees is respectively 85 and 114 years. Thus, it seems significant that, on the whole, infection by P. circinatus appears to delay senescence.

The effect of crowding does not seem to have much influence on the occurrence of the disease. The disease was found where tree cover was very dense or loose, fruiting bodies having been found in places where the canopy was so dense that herbaceous plants could not grow, as well as in places where the canopy was sufficiently open to permit the growth of these covering plants. Hence, crowding is not a determining factor for the disease. Infection occurred either in pure stands of spruces or in mixed stands of spruce and fir. But in these mixed stands, infection has rarely been found when the percentage of firs was higher than 60%. This might be explained by the fact that the fir grows where soil is richer and where infection of spruce is relatively infrequent. Incidentally, P. circinatus was not found in stands of mixed soft and hardwoods, although P. tomentosus occurred in such stands. Again this may be explained by the fact that infection is less frequent in richer soils. Competition between host species does not seem to favor any tendency for infection. It can be stated, rather, that infection is most commonly found in pure stands where conditions for the growth of the trees are less favorable.

In the Gaspé region and on the north shore of the St. Lawrence River, observations were made on the occurrence of the butt-rot; there was no correlation between spruce sawfly epidemic, which was very severe, and the rotting of spruce by *P. circinatus*. At Mount Albert and at Lake Ste. Anne the black spruce was rotted, whether damaged or undamaged by the spruce sawfly, and the disease was found independently on both of them. Furthermore, in places like Petite Rivière-à-Marte and York River where there was up to 95% and 100% infection by the disease, the damage by the spruce sawfly was nonexistent. Except for the spruce sawfly epidemic

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we have not seen, during our work, any sort of insect attack. It is therefore fairly evident that the rot caused by *P. circinatus* is not related to, or a result of, insect attacks.

Storms which break branches or make scars on the trunks of trees do not appear to have any influence on infection by P. circinatus, since infection takes place through underground parts. Nevertheless, a large number of forest soils in Quebec being thin, the rooting of trees is superficial and hence, under the action of the wind the trees oscillate and some small Yet roots may break off and infection by P. circinatus may take place. careful studies did not furnish evidence of increased infection. In addition, it may be remarked that in no case did entrance of the fungus into the wood take place through other parts than those underground, or which were at least in contact with the duff. Hubert (1931) states that this disease is often associated with fire scars but we believe that those scars had to be in contact with the ground. In places where infection was up to 85% and 100%, we have not seen a single case in which infection occurred at other places than those mentioned above. However, from inoculation experiments carried out in Duchesnay, it has been found that if the mycelium comes in contact with a scar on the trunk, it will invade the wood cells. Thus, it can be suspected that under natural conditions, the spores of the fungus must germinate in the humus.

In our North Shore experiments we have organized some kind of rudimentary meteorological stations in order to determine if temperatures, maximum and minimum, the quantity of rainfall, the relative humidity of the air, and the evaporation rate would be reflected in the number of infected and non-infected stands. The different measurements obtained at the two places had no significance, and none of the meteorological factors could be correlated with infection or non-infection of the stand.

As a rule we can state that the fungus invades very young trees and is seen in old ones, but the occurrence of this disease is not correlated with any crowding, competition or damage of any sort, or with local meteorological factors.

EFFECTS OF TEMPERATURE AND HUMIDITY ON SPOROPHORE PRODUCTION

Bearing in mind that the practical aspect of the subject is the control of the disease, field observations were made to determine the factors bringing about the fructification of the fungus, since the control of a disease is sometimes attempted by the removal of the fruiting bodies.

During the summer of 1941, which the writer spent in Shelter Bay on the North Shore of the St. Lawrence River, it was only on the 15th of August that he found sporophores of *Polystictus circinatus*. As they are produced at about the same time of the year, he has tried to correlate the maximum and minimum temperature and the relative humidity of the air with the appearance of sporophores. For this purpose the following figures of temperature and humidity have been brought together in table I.

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Table I

	Tempe	erature				Tempe	rature	
Date	Max.	Min.	Humidity	Da	ite	Max.	Min.	Humidity
15 July	72.0	51.0	86	4 A	ugust	57.0	49.0	65
16 "	55.0	48.0	55	5	ĩ	59.0	47.0	50
17 "	64.0	53.0	88	6	"	58.0	45.0	58
18 "	64.0	54.0	· 58	7	"	67.0	40.0	57
19 "		46.0	70	8	"	54.0	40.0	79
21 "	72.0	48.0	74	9	"	57.0	39.5	82
22 "	82.0	50.Ò	82	10	"	65.3	45.0	67
23 ''	93.0	61.0	69	11	"		38.6	53
24 "	92.0	64.0	51	12	'	68.0	47.5	74
25 "	61.0	54.0	79	13	"	49.0	38.0	86
26 "	69.0	49.0	60	14	"	58.5	35.5	93
27 ''	70.0	47.0	37	15	"	66.5	32.0	77
28 ''	72.0	· 47.0	33	16	"	64.5	51.5	94
29 ''	71.0	53.0	47	17	"	62.3	43.3	82
30 "	61.0	51.0	43	18	"	60.5	36.5	74
31 ''	58.0	48.0	94	19	"	70.0	31.5	65
1 August	61.2	45.0	68	20	"	60.3	48.3	100
2 "	59.0	53.5	100	21	"	67.0	33.8	76
3"	58.0	48.0	84					

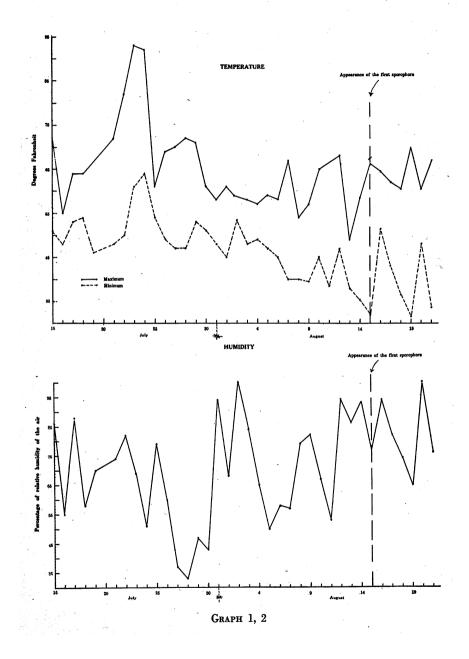
GIVING THE MAXIMUM AND MINIMUM TEMPERATURE AND THE RELATIVE HUMIDITY OF THE AIR IN SHELTER BAY, FROM JULY THE 15TH TO AUGUST THE 21ST 1941

It can be seen from the graphs of maximum and minimum temperatures (Graph 1) that the average of both has a tendency to be lower after the 15th of July. Also, it can be seen that the maximum temperature after the 30th of July averaged 60° F. and fell below 50° F. on the 15th of August. It seems that the 60° F. temperature is the critical one for initiating the fructification of *P. circinatus*. Since the figures given in Table I and in Graph 1 are for air temperature. Although those data have been taken only during one season and at one locality, they seem to indicate fairly well that when the average temperature of the day approaches the minimum temperature for mycelial growth, the vegetative phase is checked and the reproductive stage is initiated a short time before fruiting bodies actually appear.

Reference to Graph 2, presenting the percentage of relative humidity of the air against the time of the year make it evident that after the first day of August and up to the time fruiting bodies appeared, the percentage of relative humidity did not go below 50% and averaged 81.7%, while before that date, from the 15th of July up to August, the relative humidity was as low as 35% and averaged 64.3%. From the 15th of August up to

GRAPH 1. (Above) The relation of maximum and minimum temperatures to the appearance of sporophores.

GRAPH 2. (Below). The relation of atmospheric humidity to the appearance of sporophores.



September, the best time for sporophore production, the relative humidity was never lower than 65%, with an average of 85.7%. We have remarked that the sporophores come on trunks or roots always very close to the soil, a fact that substantiates the evidence tending to show that a relatively high humidity favors not only growth, but at a later date, when vegetative growth has been checked, also favors the production of fruiting bodies. Just how much the percentage of relative humidity becomes a limiting factor cannot be asserted from the data we have, but it is at least certain that an average of around 80% is favorable.

As far as light is concerned, it can be said that the sporophores are more generally found in diffused light. However, in one case, one was found exposed to the afternoon sunlight. From laboratory studies it has been found that the related *P. tomentosus* grows better in diffused than in bright light or in darkness.

Although not conclusive, these data furnish good indications that the appearance of the sporophores of *P. circinatus* is correlated principally with temperature and humidity and that the time of fruiting corresponds with the period when the low temperature checks vegetative growth and stimulates reproductive growth. This period also correlates with the time when the average relative humidity is on the increase and thus is furnished the water necessary to enable the fungus to complete the fruiting stage and to ripen the sporocarps. Exposure to light appears, if it is important at all, to play only a very secondary rôle in initiating the formation of the fruiting body. However, it is possible that once the fructifications are above the surface of the soil, light may have some influence on the formation of the hymenium and on the production of the spores. If this is so, since the fruiting bodies are produced mostly in the deep shade, it is evident that only very low intensities of light are needed to exert an influence on fructification.

Effects on Host

In addition to some ecological data concerning the production of sporophores, field observations have also given some information concerning the effects of this disease on its host as, for instance, the external characters which diseased trees present and the kinds of breaking the rotted, fallen trees will present.

The writer has observed that in early stages of infection the trees do not present externally any signs of disease, but as the infection reaches an advanced stage, the foliage of the trees turns pale yellow-green. Another external character which sometimes accompanies the advanced stage of decay is the exudation of resin at the base of the trees. Although these characters are not specific to the infection by *P. circinatus*, they help to spot the disease in regions where it is known to occur. It has already been stated that field observations indicate that the infection of the host takes place through the lateral roots, as is shown by the fact that when subjected to strong winds the trees blow over very readily and in a characteristic manner. By the comparison of trees infected by P. circinatus and of those attacked by Poria subacida, this point can easily be brought out. In this latter species, it was found that penetration was through the central or tap root and from there the rot progressed into the stump leaving the lateral roots unharmed; as a result the trees broke off about one to two feet above ground level. In P. circinatus, on the other hand, when the lateral roots have been weakened by decay the trees blew over and at the same time the tap roots were pulled from the ground. Further studies substantiate the above evidence. For example, at Shelter Bay in the valley level where both fungi occurred, the trees were blown over in a manner characteristic of trees infected by the two species of fungi. In this connection it should be pointed out that in the valley the soil is sufficiently deep so that the spruces develop both tap and lateral roots. On the mountain slopes however, where the rock is covered only by a layer of humus, and as a result tap roots are not developed. Poria subacida was absent and only P. circinatus was evident. Under such conditions as are present in the mountain habitat, only lateral roots could be infected. Thus there is furnished the added evidence that P. circinatus is confined to the lateral roots, at least during the early stages of growth.

GROWTH STUDIES

During the course of the studies in connection with penetration of the host by the fungus it became evident that it was desirable to make a comparative study of the growth of trees infected by *P. circinatus*³ and non-infected ones, and at the same time to endeavor to discover the relations between the habitat and the infection of the trees as illustrated by their rate of growth. A survey was also made to find out whether or not there was any correlation between the age of the tree and the incidence of buttrot. For this purpose studies were made in five localities, namely: the valley and mountain slope and summit in the vicinity of Lake Walker on the North Shore of the St. Lawrence River, and in the vicinity of York River and Lake Ste. Anne on the Gaspé Peninsula where ecological conditions seemed to be similar.

In these studies sections were made at D.B.H. of trees infected by *P. circinatus* and those not infected. In each type, the age of the tree was determined by a count of the annual rings and the diameter of the tree measured for each ten-year interval. The trees were segregated in age classes: (40-60) (70-90) (100-120) . . . etc. For each year class and for each locality the diameter of the average tree was calculated and from that the area of D.B.H. section was obtained for each ten-year interval.

³ During the discussion on the growth rate of the trees, the terms "trees infected by *P. circinatus*" and "trees non-infected by *P. circinatus*" have been used having in mind the fact that the trees do or do not present visible signs of decay. It cannot be stated that trees which had no decay caused by *P. circinatus* were not in mycorrhizal-association with this fungus, nor can it be said that no other mycorrhizal fungus is present.

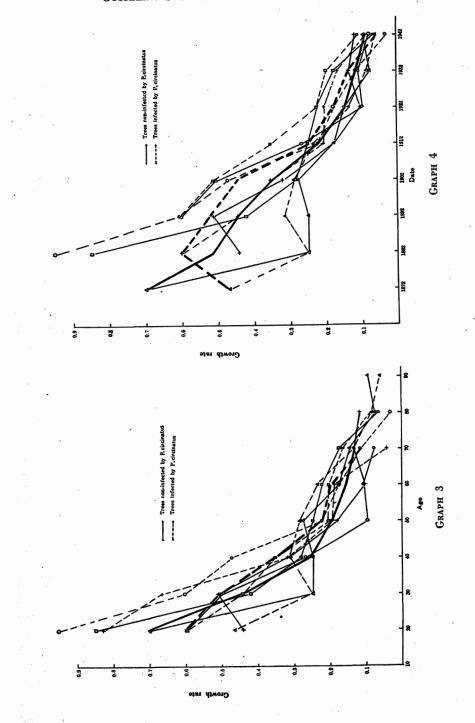
We assumed that the surface of the section of a conifer at breast height increased in proportion to the increase in volume of the tree. The growth rate was obtained by subtracting the logarithm of the surface of the section of two subsequent decades. Appendix I gives the area at D.B.H. section for each ten years and for each classification, Appendix II gives the corresponding growth-rate. In Graph 5, the rate of growth of infected and non-infected trees for the 130-150 year class have been plotted for different sites. From this graph it can be seen that in the York River and the Valley areas where the soils are favorable, the rate of growth of noninfected trees is greater than that of infected trees. Contrarily, on the East Slope and Mountain Top sites where the soil is shallow and leached and hence less favorable, the rate of growth of the infected trees is greater than those that are not infected. The significance of these facts will be discussed shortly. At this point it may be objected that there are not valid grounds for drawing any conclusions since the trees of each class may have encountered different ecological conditions during the different years of their growth. To answer this objection, the average rate of growth of trees for a given site and of infected and non-infected trees, together with the rate of growth of individual trees in each classification, was plotted by age (Graph 3) and by year (Graph 4). A comparison of these two graphs demonstrate that although there are minor differences, there is in general a very close agreement between the results derived by the two methods. Thus, whichever method is employed, the results are approximately the same and equally significant. For convenience and as a resumé of Appendix II, Table II has been prepared to show for each age class and for each region the percentage of number of decades in trees rotted by P. circinatus in which the rate of growth was higher than those not rotted by this particular fungus. Accompanying these percentages are symbols which indicate whether the area at D.B.H. section of the average tree rotted by P. circinatus is greater, equal, or smaller than that of the non-rotted trees.

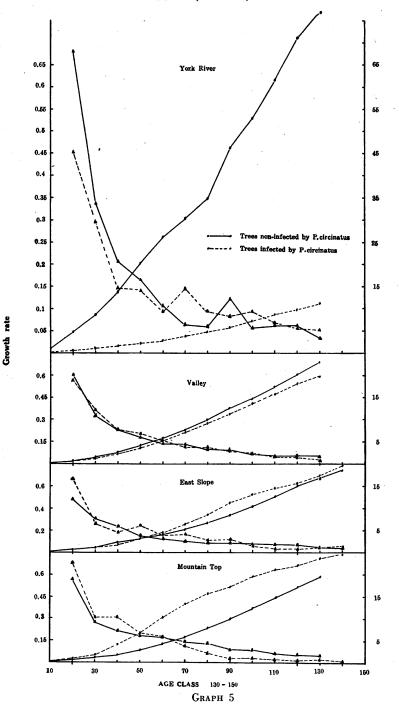
Table II									
Gaspé Peninsula Lake Walker Area									
Age class	L. Ste. Anne	York River	Valley	East Slope	Mountain Top				
40-60	50% []	0%		67% + +					
70–90	100% +			75% + +	29% []				
100 - 120	30% + +	70%	44% +	56% +	64% + +				
130 - 150		42%		54% +					
160 - 180			38%	74% + +					
190–210			33%						
Average	62%	53%	38%	65%	47%				
Area of	rotted trees d	efinitely higher	++, somewh	at higher +	, indifferent []				

somewhat smaller -, definitely smaller -.

GRAPH 3. The average rate of growth (heavy lines) and the growth of individual trees (light lines) of the 130-150 year class plotted by age.

GRAPH 4. The average rate of growth (heavy lines) and the growth of individual 'trees (light lines) of the 130-150 year class plotted by year.





Area at D.B.H. section in square inches

540

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Reference to Appendix I and Table II shows that in the two localities: York River and Valley, the area at D.B.H. section of the average rotted tree by P. circinatus is lower than that of the non-rotted trees except in age classes 70-90 and 100-120, but in all other localities the rotted trees have larger area at D.B.H. section than the non-rotted ones. Thus, it can be concluded that either the infection of the tree by this fungus is beneficial to the host or else that this fungus invades rapidly growing trees. This last hypothesis has to be discarded because the data from York River and Valley regions (Graph 5) show that the reverse is true. Examination of growth rates, Appendix II and Table II more especially, show that in all cases there always has been a period during the life of the tree when the growth-rate of trees infected by P. circinatus was higher than the noninfected ones, except for the age class 40-60 of York River. The percentages given in Table II show how long was this period. To explain why in York River and in the valley of the Lake Walker site, the area at D.B.H. section of trees infected by P. circinatus is smaller, it may be said that in these two regions the conditions for growth of the trees were not as poor as in the other regions, and that the growth of young non-rotted trees was at the beginning very good, while for some unknown reason it was somewhat delayed in the trees rotted by P. circinatus. Thus starting with a larger capital, the area at D.B.H. continued to be larger throughout the life of the tree even though the rate of growth was smaller during a few decades. On the other hand, in the other localities where the conditions of tree growth were poorer, the initial capital of the non-rotted trees was smaller or only slightly greater and was later exceeded by the faster growing but rotted trees.

In general it can be said that when there is little sub-soil, as under the conditions existing in the mountain slope and top, the trees show a larger diameter when rotted than when not rotted; on the contrary, when there is a considerable depth of sub-soil such as exists in the valleys, then the reverse holds true, but in all cases, with one exception, rotted trees always present a higher rate of growth, at least for a time, than do the nonrotted ones.

Soil Constitution

Not having found any correlations between the occurrence of the disease and the state of crowding or competition between species, or the appearance of any insect epidemics, to explain the different relations between fungus and host in the various habitats, we have tried by soil analysis to correlate the occurrence of this disease with some salt deficiency. For this purpose we have used the method given by Hester, Blume and Shelton (1937) for rapid soil analysis. The results are shown in Appendix III which have been made to illustrate the effect of the concentration in the

GRAPH 5. The rate of growth and area at D.B.H. section of infected and non-infected tree at four different sites.

soil of phosphorus, CaO, NH_4 , and potassium on the percentage of rotted trees in the stand. The conclusions are briefly summarized as follows:

1) — Phosphorus: From 0% to 30% infection, increasing concentration of phosphorus is correlated with increasing infection of the stand, but for higher infection than 30% no correlation can be made with the concentration of this element.

2) — Calcium: From 30% to 80% infection, increasing concentration of calcium seems to be correlated with increasing infection of the stand, but outside of these percentages of infection, nothing can be correlated.

3) — Ammonium: From 10% to 80% infection, increasing infection of the stand is fairly well correlated with increasing concentration of ammonium in the soil.

4) — Potassium: Up to 50% infection, decreasing potassium concentration in the soil accompanies increasing infection of the stand.

5) — H-ion concentration: In all the cases seen, infection was never found in stands where the humus had a greater H-ion concentration than pH 3.5. It seems that the average H-ion concentration has a tendency to be lower in stands with a higher percentage of infection, although this does not seem very specific. From culture studies, we know that this fungus can grow in artificial media having a pH between 3.5 and 8.6. The medium with a pH of 6.4 supported the fastest growth, but since there were not any cultures intermediate between pH 4.5 and pH 6.4, it cannot be stated that pH 6.4 is the optimum for growth of the fungus. Nevertheless, the optimum pH appears to be around pH 6.4. The pH of the humus of almost all infected stands are comprised between pH 3.58 and Thus, we can state that generally the mycelium infects trees pH 4.40. when conditions are not the optimum for the growth of the fungus, and accordingly the infection of trees could be interpreted as a reaction of the fungus against adverse conditions.

Thus, in so far as the percentage of rotted trees in the stand is not too high, the increasing degree of infection of the stand can be correlated with increasing concentration in the soil of phosphorus and ammonium, and decreasing concentration of potassium and calcium.

Now, instead of correlating singly the elements with the degree of infection of the stand, we will consider the elements by groups of two: phosphorus and calcium, ammonium and potassium.

1) — Phosphorus and calcium: It can be seen that, when infection is at or below 30%, the phosphorus concentration increases and calcium concentration decreases. From 30% to 50% infection, the phosphorous concentration decreases while calcium concentration increases. This goes on up to 70% infection. From that degree of infection up to 100%, calcium concentration will act in the same manner as phosphorus concentration.

2) — Ammonium and potassium: Ammonium and potassium concentrations always act in opposite ways, except between 0% and 10%, 50%

Gosselin: Studies on Polystictus Circinatus

and 60% infection of the stand. So, it seems that as long as there are opposite (or mirror) correlations between phosphorus and calcium concentrations in the soil, the stand will have only weak infection. But as soon as these two elements correlate in the same sense, the stand is susceptible to a high degree of infection. In general, however, the correlation between ammonium and potassium does not seem so important.

NEEDLE ANALYSIS

According to experiments done at the Black Rock Forest, New York, the salt concentration in the leaves, or needles, is nearly proportional in pure culture to the concentration of these elements in the soil. So, to complete the information given by the soil analysis, we have analyzed needles of spruces from localities in which there were different degrees of rotting. The potassium, ammonium and phosphorus percentage of the dry weight increase in the needles with the increase of infection up to 30% (see Appendix IV). Even if in the soil the potassium concentration is low, the percentage of dry weight of this element in the needles is relatively high. It should be remarked also that the data in the three cases are about similar.

Although there are some indications from the soil analysis that increasing phosphorus and ammonium and decreasing potassium and calcium will favor rotting, those indications are valid only in the cases of low percentages of rotting. There must be some other factors which, in higher percentages, will govern the infection, but unfortunately we have not been able to determine such factors. Even the needle analysis does not give much information for greater rotting than 30%.

EVIDENCE OF SYMBIOTIC RELATIONSHIP

If soil and needle analysis do not give much information as to the factors determining the occurrence of rot, they do furnish good evidence that this parasitic fungus forms a symbiotic association with its host before becoming parasitic. The evidence is furnished by the fact that, as has just been pointed out above, under unfavorable conditions existing on the mountain top, rotted trees show greater growth than the non-rotted trees, whereas in the valleys where the essential nutrient elements have accumulated, the reverse is true and indicates that the symbiotic relationship is only effective when there is some mineral deficiency. The evidence is also furnished by the fact that infection takes place by the lateral roots and that sporophores of *P. circinatus* have been found associated with tree rootlets. The results of needle analysis also tend to show that there is a symbiotic relationship between the host and the fungus.

As stated previously, the introduction of the fungus into the host is made by way of the underground parts of the tree. Thus, the only possible way for the mycelium to penetrate the host will be either by underground scars, by direct penetration through the bark or symbiotic association with the tree. We have dug out about a dozen rotted trees in Ste. Catherine and in Shelter Bay, and there are only a few cases where infection took place through scars on the roots. In all the other cases we could not find any particular place where the mycelium would have penetrated. Rather, we have seen the rot behaving exactly as a river. The main body of the river is the main lateral root and all or many of the secondary roots bring rot to the main lateral roots, and these meet in the trunk. Dr. Faull, in a personal communication, stated that he followed the rot up to the very tip of a root. The writer has made similar observations in Shelter Bay. Hence the mycelium must have penetrated directly through the bark or by symbiotic association. We do not have any evidence that it came through the bark, while we do have some for the symbiotic association hypothesis.

At least twice, sporophores of P. circinatus were found growing out of nests of rootlets. Hatch (1937) reported that sporophores coming out of rootlet-nests are quite frequent in the usual mycorrhizal fungi, and therefore since P. circinatus has twice been found connected with rootlet-nests, the evidence for its mycorrhizal relationships is further strengthened.

As has been previously stated, in the Gaspé and in the Lake Walker area the growth rate of rotted trees was higher than that of healthy ones. It is accepted that trees with mycorrhizae will have a larger rate of growth than those without, at least when the mycorrhizal relationship is efficient. On the other hand, we have seen that in the Valley (North Shore) of the St. Lawrence River and on York River (Gaspé), the diameter was smaller for rotted trees than for healthy ones. This has been correlated with the fact that in these two places the soil is richer in nutrient salts and better. apparently, for tree growth without the aid of P. circinatus as a partner, at least when it does not cause any rot.⁴ We have seen also that the humus of these two places had less phosphorus than the others had. Rosendahl (1941) found that when the phosphorus concentration of soil was low, although mycorrhizal relationship was established, the intake of nitrogen and potassium was less than in similar seedlings grown with an adequate supply of phosphorus. Therefore if symbiotic relationship is to be of greatest benefit to the tree, then a suitable concentration of phosphorus is required.

TABLE III

THE CONCENTRATION OF THE VARIOUS MINERAL ELEMENTS IN THE SOIL IS GIVEN According to the Different Localities Studied

	q	н]	X	Ν	H₄]	P	C	laO
Locality	Inf	Non	Inf 1	Non	Inf 1	Non	\mathbf{Inf}	Non	Inf	Non
Gaspé Peninsula										ſ
Lake Ste. Anne	3.81	3.79	31	35	23	19	5.00	3.63	165	131
York River	3.80	3.74	39	35	26	24	4.75	6.50	97	260
L. Walker area										
Valley	3.74	4.07	20	22	20	22	2.60	12.50	80	40
Mountain Top	4.06	3.75	40	8	13	23	12.50	4.20	80	24
East Slope	3.95	3.95	5	23	15	32	12.50	10.25	40	48

⁴ Refer to footnote page 537.

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As seen from Table III the writer's observations substantiate this conclusion since in the valley of the Lake Walker area and York River area in Gaspé, the concentration of phosphorus was relatively low and this was correlated with a low percentage of length of time beneficial to rotted trees. It can be seen also that at Lake Ste. Anne where the concentration of phosphorus was not optimum, the infection in age class 100–120 was beneficial for only 30% of the time (Table II). The growth rates have been discussed in greater detail in a previous paragraph.

Another good character which seems to indicate the symbiotic relations of P. circinatus with the trees, is the salt content of the needles. Routien and Dawson (1943) suggest "that mycorrhizae increase the salt absorbing capacity of the roots . . . The increased salt uptake may then be reflected in a greater rate of growth." Finn (1942) stated: "It is seen that nitrogen and potassium were taken up in larger quantities by the inoculated seedlings than by the uninoculated ones. Phosphorus was absorbed in a slightly larger quantity by the inoculated seedlings than by the seedlings which were not inoculated." Thus, it is admitted now that plants with mycorrhizae will generally absorb more nitrogen, potassium and phosphorus than those without.

In order to check the mycorrhizal nature of P. circinatus, we have chemically analyzed spruce needles to find the percentage of these three elements in the needles both in rotted and non-rotted trees.

The needle analysis reveals that the phosphorus percentage in relation to the dry weight of the needles is lower for rotted trees than for healthy ones in the general average and in the data from York River, while it is higher at Lake Ste. Anne and at Chandler. Data from Finn (1942) reveal that the phosphorus intake by the mycorrhizal seedlings is higher than for the non-mycorrhizal ones, but the percentage to the dry weight is smaller even though the intake is larger. The difference, as shown by Finn, is 0.020% while the writer found a difference of only 0.011%. On York River this percentage is lower or only 0.007% while at Lake Ste. Anne it is higher or 0.049% and at Chandler 0.054%. This, however, has not definite significance because when there is a greater amount of phosphorus in the needles, there is a correspondingly greater concentration of this element in the soil. Thus, it cannot be unqualifiedly concluded that the infection by P. circinatus was beneficial to the trees although there seems to be evidence tending to indicate that such is the case.

As in the phosphorus relations, the percentage of nitrogen in the needles of rotted trees is higher, in the general average, than in the needles of healthy ones. Although the general average is higher for rotted trees than for healthy ones (Appendix VI), the percentage at Lake Ste. Anne and at York River are lower, respectively of 0.002% and 0.003%, although the soil analysis from these places (Appendix V) shows that soil under rotted stands had a higher concentration of ammonium salts than the healthy ones. Even if the nitrogen percentage of the needles is lower (0.002%) for rotted trees than for healthy ones, this difference is so small that it probably is of little significance. However it is interesting to note that nitrogen concentration in the needles is higher for rotted trees than for healthy ones only when the concentration of nitrogen is lower in the soil. For example, at Lake Ste. Anne and on York River, the rotted stands had higher concentration of ammonium salt than the non-rotted ones and the reverse was true for the percentage of nitrogen in the needles. Exactly the contrary is found at Chandler. Nevertheless there seem to be indications that the infection by *P. circinatus* is sometimes beneficial to the host as a result of increasing the intake of nitrogen.

For the percentage of potassium in the needles, the analysis revealed that, in the general average, this percentage is lower for rotted trees than for non-rotted ones; however in the rotted trees of Lake Ste. Anne and This low percentage in of Chandler this percentage is much higher. rotted trees seems to be prevalent almost exclusively at York River. At that place we have found percentages as low as 0.062, 0.071, 0.085, and 0.094. In none of the other places were percentages found as low as these, and it was remarked that these low percentages came with heavily rotted trees. In Gaspé only 22% of the infected trees were rotted as high as D.B.H. section, but of the trees which have a low percentage of potassium 60% were rotted up to the D.B.H. section. In general the potassium percentage of the needles is low in all rotted trees of York River, 0.236% compared with 0.372% at Chandler and 0.418% at Lake Ste. Anne. This excessively low average might perhaps be explained by the fact that 88% of the most heavily rotted trees were from York River region. It can be seen from soil analysis that, at Lake Ste. Anne, although the concentration of potassium in the soil was smaller for infected stands than for healthy ones, the percentage of this element in the needles was greater. It is logical to suppose that the infection, at least at Lake Ste. Anne, has been beneficial to the trees for larger intake of potassium.

Thus if the data from York River region are excepted, we can state that the infection of the trees with *P. circinatus* has increased the intake of mineral salts. This beneficial effect should not be interpreted too categorically, but rather as a probability. It should be remembered also that the needles analyzed might, in many instances, have come from trees in which the parasitic have exceeded the beneficial effects of the previous symbiotic association. This would have lowered the average percentage for the rotted trees and might explain why, in the York River region where the trees are more heavily rotted than in the other regions, the percentages of all elements are so low.

The field observations, in addition to some facts concerning the behavior of the disease caused by *P. circinatus*, has brought out facts which seem to indicate fairly well that this fungus penetrates into its host by symbiotic association. Each fact in itself is not very conclusive but they all substantiate the same conclusion.

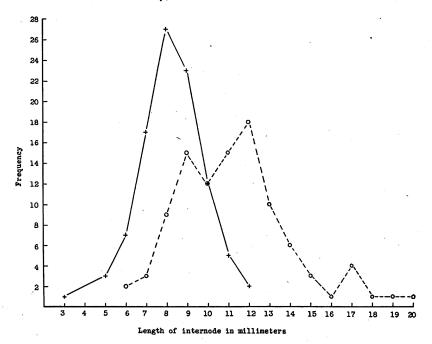
EFFECTS OF SEEDLING INOCULATION WITH P. CIRCINATUS

Having in mind all the evidence from field observations that *P. circinatus* was penetrating into the host through symbiotic association, the writer has tried to establish the mycorrhizal relationship between spruce seedlings and the fungus under laboratory control.

First, we have tried to culture seedlings under aseptic conditions with the Hatch culture chambers, but the experiment did not succeed. Later, loamy-clay soil was obtained from Saskatchewan where no trees are growing, and consequently in which there are no mycorrhizae forming fungi. This was suggested by the experiments done by Hatch (1937). After having sterilized and stratified spruce seeds, they were put in the ice box for two weeks in order to obtain a better germination. The loamy-clay soil was placed in wooden boxes previously sterilized and the seeds were After germination in July, 1942, the seedlings grew in a greensown. house until January, 1943, when they were placed under the snow to allow a dormant period. At the beginning of April, 1943, they were dug out of the snow and put in the cold room (33° F.) for fifteen days to make the transition between the temperatures of the snow cover and the greenhouse less abrupt. After two weeks in the greenhouse, when the buds were bursting, half of the seedlings were inoculated on May 1, 1943, with cultures of P. circinatus, while the other half was reserved to serve as a check, although maintained under the same growing conditions. After three months of growth, namely on August 31, the seedlings from both series were removed and studied to determine what difference existed. It was immediately obvious (Plate II) that the inoculated seedlings had not only made a greater growth but that the needles were of a deeper green color and that the primary roots had produced more secondary roots.

To determine the relative growth of the inoculated seedlings and those not inoculated, they were measured from the primary node to the apex. The results of these measurements are presented in Graph 6 in which the actual figures are represented by crosses for the non-inoculated seedlings and circles for the inoculated ones. These figures are based on the measurements of a hundred seedlings for each series. It is immediately obvious that the non-infected seedlings show a fairly definite curve, whereas the inoculated ones follow essentially the same curve, although there is some deviation from the curve presented by the non-inoculated seedlings. This deviation, it seems, may be explained by the fact that the period of growth after inoculation was so short that complete mycorrhizal relationship had not yet become established. Despite this erratic behavior, however, it is quite obvious that even in so short a time as three months, the fungus did stimulate the growth of the spruce seedlings.

A further examination of the seedlings shows that while the roots of the uninoculated ones are not infrequently longer than the inoculated ones, nevertheless the latter were characterized by the production of a greater number of secondary rootlets which were frequently branched. In the uninoculated plants these secondary rootlets, comparatively speaking, were very rarely branched. Thus, it can be seen that the fungus in this instance has added to the efficiency of the root system for absorption. This becomes all the more evident when it is seen that, despite shorter roots with increased secondary rootlets, the secondary internode of the stem of the inoculated seedlings, on the basis of ten specimens taken at random, totaled to 142.5 mm. whereas in the non-inoculated seedlings that were measured in the same way, the total was 113 mm. Furthermore, the



GRAPH 6. The relative rate of growth of inoculated (0) and non-inoculated (+) seedlings.

inoculated seedlings bore 727 needles and the uninoculated 548 needles, or respectively 51 and 48.5 needles per cm. of internode.

In addition to these obvious differences between the two series, there is the further difference that is furnished by the darker color of the needles of infected seedlings. The needles of non-inoculated seedlings in contrast to those inoculated were mostly yellowish green and in addition show the presence of anthocyanins, an indication, according to Mitchell (1934), that there is a phosphorus deficiency in the soil. Since the inoculated trees did not show this symptom of deficiency, it seems likely that the fungal symbiont helped to make available a larger phosphorus supply. Unfortunately the information is not available to enable us to make any statement as to how the process takes place.

The obvious differences observed in the size of inoculated and uninoculated seedlings, and the greater number of needles per centimeter of internode for the inoculated than for the uninoculated seedlings, led us to examine the microscopical characters of rootlets of the inoculated Rootlets which we considered as having mycorrhizal relationship ones. on account of their larger size were killed and imbedded in paraffin. It can be seen from the sections that the mycorrhizal relationship is of the The Hartig net is two to three cells deep, without apparent regular type. intracellular invasion. The mantle is homogenous (Plate III, fig. 1) and somewhat parenchymatous in structure, about three to four cells deep, with a smooth margin from which arise very few hyphae which penetrate Sections made of rootlets found in a rootlet into the surrounding cells. nest (Plate III, fig. 2) under a sporophore of P. circinatus show essentially the same type of mycorrhizal relationship. The mantle is homogenous, although thicker, parenchymatous in structure, with a smooth The tannin layer is not very apparent, and locally seems to be margin. The Hartig net is not so thick as the type we obtained two cells thick. by inoculation, but essentially the same type of mycorrhizal relationship is evident in the artificially and the naturally invaded rootlets. Thus. although the experiment was not done under aseptic conditions, it seems very probable that the endophyte here concerned is *P. circinatus*.

When all characters are taken into consideration, it seems safe to conclude that the fungus has a beneficial effect on its phanerogamic partner, at least in the early stages. Also these experimental results tend to substantiate the conclusions already drawn from field observations.

The observations that we have made so far, either on growth rates or on soil or needles analysis, seem to indicate that the infection of the trees by *P. circinatus* behaves as if the fungus was mycorrhizal. However, in our northern forests where the pH of the soil is relatively high and where nitrogen is chiefly supplied as ammonium salt, it would seem that the trees must be in mycorrhizal association to live under such conditions. We have seen that trees infected with P. circinatus behave, in comparison with trees not infected by this species, much in the same manner as trees that are in association with known mycorrhizal fungi. This relation between the fungus and the tree exists until some unfavorable factor, as yet unknown, upsets the balance between the symbionts. When this happens. then it would seem that the fungus readily becomes parasitic, and the mycelium, instead of remaining intercellular, as in the Hartig net, penetrates into the cells (Plate III, fig. 3) and travels backward along the rootlets, killing them as it proceeds. This would then explain the reason why the butt-rot seems to have its inception in the lateral roots rather than through wounds or through the tap root. In Polystictus circinatus, then, we have a butt-rot fungus that in the earlier stages of the development of the trees, instead of being a parasite, actually is beneficial until the host reaches a certain age, which might indicate senescence, the age being determined by local ecological conditions.

SUMMARY

The white pocket butt-rot of conifers caused by *Polystictus circinatus* (Fr.) Cke. has been studied because of its local importance in the Province of Quebec and because of its peculiar behavior.

Field observations have been made to correlate the occurrence of this disease with some ecological factors. The disease was localized in such definite loci of infection that it was thought that it was tied up with conditions of temperature, insect epidemics, mechanical damage, or with the chemical nature of the soil. However, none of those factors appeared to be responsible for the occurrence of the disease.

At the same time as the ecological factors were discarded as having no correlation with the disease, the field observations brought up evidence that this disease penetrated into its host by mycorrhizal association. Although none of the facts furnished any conclusive evidence, they all substantiate the same conclusion.

To bring more evidence, the writer has tried to establish mycorrhizal relationship between spruce seedlings and the fungus. The results indicate that the fungus has really formed a mycorrhizal association of the usual type.

If P. circinatus penetrates into its host through symbiotic association, and there is presumptive evidence that such is the case, this fact will open an entire new field in forest pathology. It will associate the two concepts of symbiotism and parasitism which were previously separated by air-tight walls. Those who are specifically interested in symbiotic problems will have to consider the pathological aspect of the question and the forest pathologists will have to be better acquainted with symbiotism in order to deal correctly with certain of their problems. Foresters will no longer be able to consider the butt-rots only as a reducing factor for the volume of the tree but will have to determine under which conditions the damage from parasitism exceeds the beneficial effects of symbiotism on trees, if it is demonstrated later, as it is not at all illogical to suppose, that buttrotting fungi penetrate into the host by mycorrhizal relationship. These fungi in the Province of Quebec are all quite abundant; before trying to eliminate them by short cycle rotations, it will be necessary to know what part they are playing in the biological complex of our forest soil. Future researches will have to determine under which conditions parasitism follows the symbiotic association.

This field is new and wide open. It will certainly be of considerable interest to those who will have the advantage of working on such problems, and it promises to be at the same time of practical interest to foresters.

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ACKNOWLEDGMENTS

The writer wishes to thank Dr. David H. Linder, under whose direction this work was done, for giving his time so spontaneously, for his imaginative suggestions on possible hypotheses, his objective criticism of experiments, and his correction of the manuscript. He also wishes to thank Professor Emeritus J. H. Faull under whom this study was initiated and who furnished the first knowledge on this disease; and to Dr. Gast of the Harvard Forest, who has added to the writer's knowledge of mycorrhizal problems, for constructive criticism of this study, and for information concerning methods for the chemical analysis of spruce needles.

The writer wishes also to thank the officials of the Department of Lands and Forests of Quebec for having made possible this study by the financial help they provided for the academic studies and for the field investigations; among these officials the writer wishes to thank especially M. A. Bédard, Deputy-Minister, M. F. Boutin, Chief of Forestry Service, and Dr. R. Pomerleau, Director of the Bureau of Forest Pathology, under whom the writer has been working during all this study.

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The writer is indebted to Dr. Amiot for the help he so kindly gave during chemical analysis of needles, to M. Y. Garand, Soil Analyst in the Department of Colonization, for advice on soil analysis, and to M. G. Bolduc, Forest Ranger, for his whole-hearted help during field and laboratory work.

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HARVARD UNIVERSITY CAMBRIDGE, MASS.

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Appendix I

AREA OF D.B.H. SECTION FOR EACH AGE CLASS

DATA FROM YORK RIVER, GASPÉ

		DAIA	FROM LOID				
	Class: –60)	(70-	-90)	(100-	-120)	(130	-150)
Numbe	r of trees:						
(1)	(6)	(13)	(19)	(25)	(24)	(2)	(4)
Α	В	Α	В	A	В	А	В
1.34	1.27	1.34	0.61	1.09	0.58	1.03	0.21
5.35	4.13	4.48	2.41	3.06	1.61	4.97	0.58
20.37	8.44	7.96	5.48	5.88	2.77	8.61	1.15
32.15	13.24	11.08	9.45	7.33	4.01	13.87	1.61
40.65	16.73	14.29	14.08	9.80	5.62	20.39	2.24
58.67	23.00	17.90	17.91	11.65	7.34	26.10	2.77
		21.40	22.20	13.87	9.10	30.30	3.90
		22.20	26.36	16.05	11.08	34.80	4.84
		26.36		18.38	13.04	46.20	5.89
				20.89	14.72	53.00	7.33
				25.20	17.91	61.50	8.61
					19.62	71.15	9.81
						77.00	11.08

DATA FROM LAKE STE. ANNE, GASPÉ

Age	Class:				
(40	-60)	(70-	-90)	(100-	-120)
Number	of trees:				
(7)	(3)	(23)	(9)	(4)	(3)
Α	В	Α	В	Α	в
0.54	0.67	0.39	0.26	0.12	0.39
1.76	1.91	1.47	1.21	0.50	1.34
3.26	3.57	2.96	2.96	1.03	2.77
5.09	5.88	5.22	5.62	1.99	5.35
7.18	7.64	7.64	8.44	2.96	8.44
7.80		10.15	12.43	4.72	12.04
		12.84	16.27	6.88	16.27
		13.87	18.63	9.28	21.14
			19.87	12.24	27.80
				14.08	32.80
				19.62	42.10
					44.30

A—Trees not infected (see footnote page 537). B—Trees infected with P. circinatus.

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Appendix I (continued)

		DATA FROM	THE VALI	LEY, LAKE WAI	LKER AR	F. A	
Age	Class:						
(100	-1 20)	(130-	-150)	(160-	180)	(190–	210)
Numbe	er of trees:						
(44)	(5)	(45)	(23)	(7)	(9)	(2)	(3)
А	В	А	в	Α	В	А	в
0.20	0.32	0.18	0.16	0.23	0.04	0.10	0.01
0.67	1.15	0.72	0.58	0.98	0.11	0.29	0.04
1.40	2.68	1.54	1.34	2 . 24	0.26	0.54	0.06
2.50	5.09	2.68	2.32	4.36	0.42	1.15	0.13
3.90	7.80	4.12	3.68	7.18	0.67	1.99	0.26
5.48	10.71	5.75	5.36	11.27	1.03	3.36	0.39
8.12	13.04	7.80	7.03	16.05	1.47	4.36	0.62
10.53	15.82	9.98	9.10	21.14	1.99	6.02	0.82
12.84	20.12	12.64	11.46	26.65	${f 2}$. 59	7.18	1.09
16.73	20.88	14.93	13.66	32.15	3.36	9.10	1.40
	22.73	17.44	15.82	37.13	4.12	11.65	1.76
		20.12	18.15	43.21	5.22	13.87.	2.23
		23.00	19.87	49.72	6.02	16.97	2.59
				55.45	6.88	20.37	3.06
				60.61	7.64	23.81	3.46
				67.38		26.92	3.79
						30.25	4.24
						33.78	4.36
						37.83	4.60

DATA FROM THE EAST SLOPE, LAKE WALKER AREA

•		DATA	FROM TH	IE LAST S	LOPE, LA	KE WALK	ER ARE	4	
Age	Class:								
(40-	-60)	(70	-90)	(100	-120)	(120	-150)	(160	100)
(10	00)	(10	-30)	(100-	-120)	(130-	-100)	(100-	-180)
Numl	ber of t	rees:							
(9)	(1)	(10)	(2)	(11)	(6)	(5)	(1)	(1)	(1)
Α	В	Α	в	Α	В	Α	В	Α	В
0.42	0.77	0.16	0.18	0.20	0.18	0.20	0.13	0.13	0.13
2.41	1.99	$^{\cdot}0.42$	0.46	0.67	0.72	0.62	0.62	0.39	0.50
3.06	4.12	1.03	1.15	1.40	1.48	1.27	1.15	0.77	1.15
5.09	8.12	1.68	1.91	2.15	2.50	2.24	1.76	1.34	2.24
7.18		2.77	3.36	3.26	4.12	3.16	3.16	1.76	3.79
		4.24	4.97	4.60	6.30	4.24	4.48	2.24	5.35
		5.62	7.68	5.48	8.44	5.48	6.59	2.87	7.49
		6.88	10.34	7.96	10.71	6.88	8.61	3.47	9.63
		7.96	15.82	9.98	13.04	8.61	11.46	4.48	12.64
				12.04	15.16	10.53	13.24	5.35	14.50
						12.64	14.50	6.16	16.73
						15.16	15.82	7.03	19.62
						16.97	17.44	8.61	22.19
						18.63	19.62	9.63	24.65
							- /	10.16	26.36
						,		11.46	28.79

A—Trees not infected. B—Trees infected with P. circinatus.

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Appendix I (concluded)

DATA FROM THE MOUNTAIN TOP, LAKE WALKER AREA

Class: -90)	(100	-120)	(130-	-150)
of the trees:				•
(3)	(31)	(1)	(13)	(1)
В	Α	В	Α	В
$\begin{array}{c} 0.20 \\ 0.58 \\ 1.76 \\ 2.67 \\ 4.13 \\ 6.16 \\ 7.64 \\ 10.16 \end{array}$	$\begin{array}{c} 0.16\\ 0.58\\ 1.21\\ 2.32\\ 3.26\\ 4.84\\ 7.03\\ 9.09\\ 11.27\\ 12.74\\ 15.16\\ 15.37\\ \end{array}$	$\begin{array}{c} 0.13\\ 0.39\\ 0.50\\ 2.87\\ 4.48\\ 7.03\\ 10.16\\ 14.29\\ 17.44\\ 20.37\\ 23.81\\ 25.79 \end{array}$	$\begin{array}{c} 0.16\\ 0.58\\ 1.09\\ 1.83\\ 2.87\\ 4.24\\ 5.89\\ 7.96\\ 9.98\\ 12.43\\ 14.72\\ 17.20\\ 19.62\\ \end{array}$	$\begin{array}{c} 0.20\\ 0.98\\ 1.99\\ 4.12\\ 6.59\\ 10.16\\ 13.24\\ 15.82\\ 17.44\\ 19.62\\ 21.14\\ 22.19\\ 23.81\\ 24.65\end{array}$
	-90) of the trees: (3) B 0.20 0.58 1.76 2.67 4.13 6.16 7.64	$\begin{array}{c} -90) & (100\\ \text{of the trees:} \\ (3) & (31)\\ \text{B} & \text{A}\\ \hline 0.20 & 0.16\\ 0.58 & 0.58\\ 1.76 & 1.21\\ 2.67 & 2.32\\ 4.13 & 3.26\\ 6.16 & 4.84\\ 7.64 & 7.03\\ 10.16 & 9.09\\ \hline 11.27\\ 12.74\\ 15.16 \end{array}$	$\begin{array}{c c} -90) & (100-120) \\ \text{of the trees:} \\ \hline (3) & (31) & (1) \\ \hline B & A & B \\ \hline 0.20 & 0.16 & 0.13 \\ 0.58 & 0.58 & 0.39 \\ 1.76 & 1.21 & 0.50 \\ 2.67 & 2.32 & 2.87 \\ 4.13 & 3.26 & 4.48 \\ 6.16 & 4.84 & 7.03 \\ 7.64 & 7.03 & 10.16 \\ 10.16 & 9.09 & 14.29 \\ 11.27 & 17.44 \\ 12.74 & 20.37 \\ 15.16 & 23.81 \\ \end{array}$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$

Appendix II

GROWTH RATE BY AGE CLASSES

DATA FROM YORK RIVER, GASPÉ

0	-60)	(70-	-90)	(100-	-120)	(130-	-150)
Number	r of trees:						
(1)	(1)	(13)	(19)	(25)	(24)	(2)	(4)
Α	В	Α	В	Α	в	Α	В
0.6020	0.5104	0.5246	0.5864	0.4484	0.4436	0.6826	0.4520
0.5806	0.3110	0.2498	0.3574	0.2842	0.2354	0.3388	0.2960
0.1982	0.1956	0.1438	0.2366	0.0956	0.1608	0.2072	0.1468
0.1018	0.1016	0.1104	0.1730	0.1260	0.1460	0.1670	0.1422
0.1594	0.1380	0.0980	0.1044	0.0750	0.1160	0.1072	0.0932
		0.0774	0.0932	0.0756	0.0934	0.0646	0.1484
		0.0158	0.0748	0.0634	0.0858	0.0602	0.0940
		0.0748		0.0590	0.0706	0.1238	0.0848
				0.0554	0.0526	0.0592	0.0956
				0.0818	0.0852	0.0648	0.0694
					0.0396	0.0634	0.0566
	•					0.0342	0.0532
A 70			·	595)			0.0001

A—Trees not infected (See footnote page 537). B—Trees infected with *P. circinatus*.

Age Class:

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Appendix II (continued)

DATA FROM LAKE STE. ANNE, GASPÉ

.

Age Class:

Age Class: (40–60)		(70-	-90)	(100–120)		
Number o		(,,,	50)	(100	120)	
(7)	(3)	(23)	(9)	(4)	(3)	
Α	· B ′	Α	В	Α	В	
0.5142	0.4556	0.5822	0.6716	0.6374	0.5408	
0.2682	0.2718	0.3036	0.3884	0.6168	0.3162	
0.1938	0.2168	0.2464	0.2780	0.2854	0.2858	
0.1492	0.1134	0.1654	0.1770	0.1726	0.1980	
0.0358		0.1238	0.1682	0.2024	0.1542	
		0.1014	0.1168	0.1640	0.1308	
		0.0336	0.0588	0.1298	0.1138	
			0.0180	0.1200	0.1192	
				0.0610	0.0714	
				0.1440	0.1084	
			4		0.0224	

DATA FROM THE VALLEY, LAKE WALKER AREA

	C 1000 1						
(100-	-120)	(130-	-150)	(160-	-180)	(190-	-210)
Number	r of trees:						
(44)	(5)	(45)	(23)	(7)	· (9)	(2)	(3)
Ά	в	Α	В	Α	В	Α	в
0.5166	0.5576	0.6020	0.5706	0.6274	0.4682	0.4748	0.4860
0.3216	0.3672	0.3328	0.3628	0.3604	0.3522	0.2724	0.2182
0.2500	0.2794	0.2398	0.2392	0.2898	0.2128	0.3296	0.3204
0.1938	0.1850	0.1878	0.2002	0.2170	0.2014	0.2384	0.2818
0.1480	0.1378	0.1442	0.1636	0.1956	0.1878	0.2278	0.1742
0.1704	0.0854	0.1324	0.1176	0.1536	0.1544	0.1126	0.2096
0.1128	0.0840	0.1072	0.1118	0.1198	0.1310	0.1406	0.1158
0.0862	0.1044	0.1024	0.1004	0.1006	0.1140	0.0774	0.1262
0.1152	0.0162	0.0726	0.0762	0.0814	0.0888	0.1026	0.1100.
	0.0368	0.0672	0.0638	0.0626	0.1024	0.1076	0.0978
		0.0622	0.0596	0.0658	0.0620	0.0756	0.1044
		0.0580	0.0394	0.0610	0.0580	0.0876	0.0632
	,			0.0474	0.0454	0.0794	0.0730
				0.0386		0.0678	0.0542
				0.0460		0.0536	0.0386
						0.0504	0.0490

A—Trees not infected. B—Trees infected with P. circinatus.

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0.0478

0.0118 0.0492 0.0232

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Appendix II (concluded)

DATA FROM THE EAST SLOPE, LAKE WALKER AREA Age Class: (40-60)(70 - 90)(100–120) (130 - 150)(160 - 180)Number of trees: (9) (1) (10) (11) (2)(6) (5)(1) (1) A в Α В Α в Α в Α

(1)

в

$\begin{array}{c} 0.7574 & 0.4152 \\ 0.1040 & 0.3166 \\ 0.2214 & 0.2940 \\ 0.1492 \end{array}$	$\begin{array}{c} 0.4312 & 0.4082 \\ 0.3892 & 0.3992 \\ 0.2130 & 0.2208 \\ 0.2162 & 0.2454 \\ 0.1848 & 0.1694 \\ 0.1220 & 0.1894 \\ 0.0884 & 0.1292 \end{array}$	$\begin{array}{c} 0.5166 & 0.6020 \\ 0.3216 & 0.3128 \\ 0.1856 & 0.2284 \\ 0.1804 & 0.2182 \\ 0.1592 & 0.1842 \\ 0.0766 & 0.1268 \\ 0.1618 & 0.1034 \end{array}$	$\begin{array}{c} 0.4862 & 0.6666 \\ 0.3098 & 0.2652 \\ 0.2444 & 0.1846 \\ 0.1500 & 0.2544 \\ 0.1280 & 0.1516 \\ 0.1116 & 0.1678 \\ 0.0968 & 0.1160 \end{array}$	$\begin{array}{c} 0.4570 & 0.5682 \\ 0.2980 & 0.3638 \\ 0.2428 & 0.2890 \\ 0.1186 & 0.2290 \\ 0.1044 & 0.1500 \\ 0.1178 & 0.1460 \\ 0.0826 & 0.1092 \end{array}$
			$0.0968 \ 0.1160$	$0.0826 \ 0.1092$
	$0.0630 \ 0.1846$	$0.0984 \ 0.0854$	$0.0970 \ 0.1244$	0.1112 0.1180
		$0.0814 \ 0.0654$	0.0874 0.0628	0.0774 0.0598
			$0.0794 \ 0.0394$	$0.0614 \ 0.0622$
			0.0790 0.0378	$0.0572 \ 0.0690$
			$0.0490 \ 0.0422$	0.0878 0.0536
			$0.0405 \ 0.0512$	$0.0488 \ 0.0456$
				0.0234 0.0292
				$0.0522 \ 0.0282$

DATA FROM THE MOUNTAIN TOP, LAKE WALKER AREA

Age ((70-	Class: -90)	(100-	-120)	(130-	-150)
Number o	f the trees:			(
(20)	(3)	(31)	(1)	(13)	(1)
Α	в	Α	В	Α	В
$\begin{array}{c} 0.5726\\ 0.3422\\ 0.1978\\ 0.2128\\ 0.1608\\ 0.1442\\ 0.1390\\ 0.1392 \end{array}$	$\begin{array}{c} 0.4546\\ 0.4814\\ 0.1826\\ 0.1878\\ 0.1744\\ 0.0934\\ 0.1238\end{array}$	$\begin{array}{c} 0.5706\\ 0.3194\\ 0.2826\\ 0.1476\\ 0.1718\\ 0.1620\\ 0.1118\\ 0.0930\\ 0.0634\\ 0.0654\\ 0.0062 \end{array}$	$\begin{array}{c} 0.4560\\ 0.1110\\ 0.7606\\ 0.1938\\ 0.1960\\ 0.1600\\ 0.1600\\ 0.1480\\ 0.0864\\ 0.0676\\ 0.0678\\ 0.0346\end{array}$	$\begin{array}{c} 0.5706\\ 0.2736\\ 0.2260\\ 0.1940\\ 0.1702\\ 0.1424\\ 0.1310\\ 0.0984\\ 0.0954\\ 0.0732\\ 0.0676\\ 0.0572 \end{array}$	$\begin{array}{c} 0.6800\\ 0.3098\\ 0.3166\\ 0.2034\\ 0.1882\\ 0.1150\\ 0.0772\\ 0.0422\\ 0.0512\\ 0.0326\\ 0.0210\\ 0.0306\\ 0.0150\\ \end{array}$
					0.0100

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A—Trees not infected. B—Trees infected with P. circinatus.

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Appendix III

Concentration in p.p.m. of Phosphorus, Potassium, Calcium and Ammonium and H-ion Concentration of the Humus of Stands of Various Degrees of Rotting

Percentage of rotted trees in the stand

the stand	Phosphorus	Potassium	Calcium	Ammonium	P.H.
0%	5.17 (3.82)*	35 (10)	154 (104)	33 (13)	3.83 (0.29)
5%	6.87(4.06)	47 (5)	110 (78)	23 (2)	3.58 (0.06)
10%	6.25(3.64)	39 (4)	300 (50)	19(5)	4.22(0.5)
15%	5.0	40	165 (69)	20	3.70
20%	8.55(3.33)	35(5)	272 (78)	21 (4)	4.37 (0.03)
30%	10.00(3.54)	33 (6)	53 (38)	24(5)	3.72 (0.09)
50%	5.09(3.45)	34 (14)	222(99)	26(2)	4.20 (0.37)
60%	7.81 (3.98)	40 (8)	111 (67)	27 (10)	3.76 (0.25)
70%	4.38(0.63)	47 (5)	53 (19)	25 (5)	3.92 (0.06)
80%	8.75 (3.57)	42 (24)	300 (41)	30 (7)	4.27 (0.20)
90%	3.82(0.82)	33 (12)	93 (67)	26 (8)	3.76 (0.16)
95%	8.75 (4.61)	40 (10)	165 (85)	27 (3)	3.93(0.25)
100%	2.17(2.05)	32 (13)	300 (50)	23 (7)	5.38 (1.02)

* Standard deviation.

Appendix IV

PERCENTAGE OF THE DRY WEIGHT OF THE NEEDLES OF PHOSPHORUS, POTASSIUM AND NITROGEN

Percentage of rotted trees in the stand

the stand	Phosphorus	Potassium	Nitrogen
0%	0.188% (0.055)*	0.339%(0.70)	0.658% (0.062)
5%	0.146%(0.032)	0.277%(0.053)	0.602% (0.051)
10%	0.143%(0.027)	0.278% (0.060)	0.664% (0.042)
15%	,		
20%	0.157%(0.042)	0.404% (0.082)	0.404% (0.082)
30%	0.194%(0.017)	0.545%(0.091)	0.744%
50%	0.184%(0.028)	0.306%(0.034)	0.631% (0.062)
60%	0.166%(0.030)	0.216%(0.070)	0.620% (0.051)
70%	0.148%	0.198%	0.626%
80%			
90%	0.148%(0.029)	0.232%(0.135)	0.652% (0.093)
95%	0.182%(0.007)	0.264%(0.115)	0.661%(0.061)
100%	0.153% (0.028)	0.294% (0.038)	0.781%

* Standard deviation.

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. 11.2

Appendix V

The pH and the Concentration of K, NH4, P, CaO in the Soil of the Various Localities Studied

	\mathbf{pH}	K	NH₄	Р	CaO
Locality	Inf Non	Inf Non	Inf Non	Inf Non	Inf Non
Gaspé Peninsula					
Gaspé Park	4.95 3.81	41 38	$20 \ 21$	2.75 4.13	290 72
Lake Ste. Anne	$3.81 \ 3.79$	31 35	$23 \ 19$	$5.00 \ 3.63$	$165 \ 131$
Chandler	$4.24 \ 4.01$	$37 \ 32$	$22 \ 28$	5.75 4.13	$260 \ 216$
York River	$3.80 \ 3.74$	$39 \ 35$	$26\ 24$	4.75 6.50	$97 \ 260$
Petit Pabos River	$4.60 \ 4.65$	$43 \ 40$	$19 \ 25$	$5.00 \ 12.50$	$300 \ 250$
West Branch Pabos River	3.81	31	26	3.63	182
Pecan River	4.06 3.90	$34 \ 25$	$25 \ 30$	4.88 3.13	$250 \ 250$
Four Lakes (Marsoui)	3.85	25	25	12.50	40
Petite Rivière-à-Marthe	$4.30 \ 3.85$	$50 \ 35$	$17 \ 17$	5.00 4.38	250 80
North Side Mt. Albert	6.45 3.90	20 50	30 30	0.75 3.75	350 40
Lac des Américains Trail	5.15 4.20	48 40	20 23	1.25 3.75	$350 \ 250$
East Side Mt. Albert	$6.45 \ 3.90$	$20\ 50$	30 30	0.75 3.75	350 40
Lake Walker Area					
Valley	3.74 4.07	20 22	20 22	3.23 12.50	80 40
Mountain Top	4.06 3.75	40 8	13 23	12.50 4.13	80 24
East Slope	3.95 3.93	523	$15 \ 32$	12.50 10.25	40 48
Philibert Slope	3.81	30	18	8.75	56

Appendix VI

Per Cent of Dry Weight of the Mineral Elements in the Needles from the Different Localities Studied

	Phosphorus		Potassium		Nitrogen	
Locality	Inf	Non	\mathbf{Inf}	Non	Inf	Non
Gaspé Park	0.143%		0.271%		0.765%	
Lake Ste. Anne	0.224%	0.175%	$\mathbf{0.418\%}$	0.298%	0.671%	0.673%
Chandler	0.169%	0.115%	0.372%	0.344%	0.650%	0.622%
York River	0.164%	0.171%	0.236%	0.351%	0.631%	0.634%
General Average	0.164%	0.175%	0.264%	0.317%	0.654%	0.615%

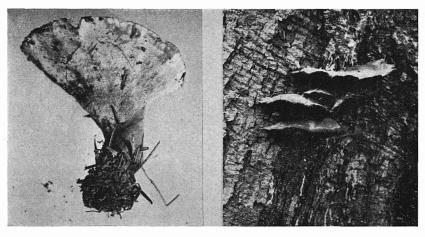
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EXPLANATION OF PLATE I

Fig. 1. Polystictus tomentosus (Fr.) Fr. Side-view to show the distinct stipe which is nearly central.

Fig. 2. Polystictus circinatus (Fr.) Cke. Side-view to illustrate the sessile, applanate fruiting bodies characteristic of the species.

Fig. 3. Map showing the distribution of *P. circinatus*. It will be observed that the species has a predominantly northern distribution.



1

2

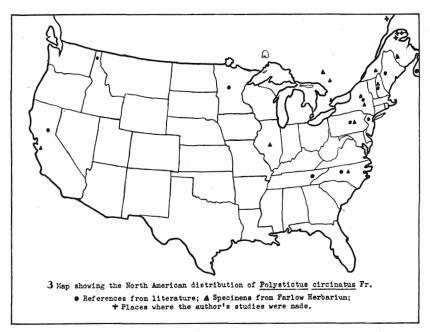
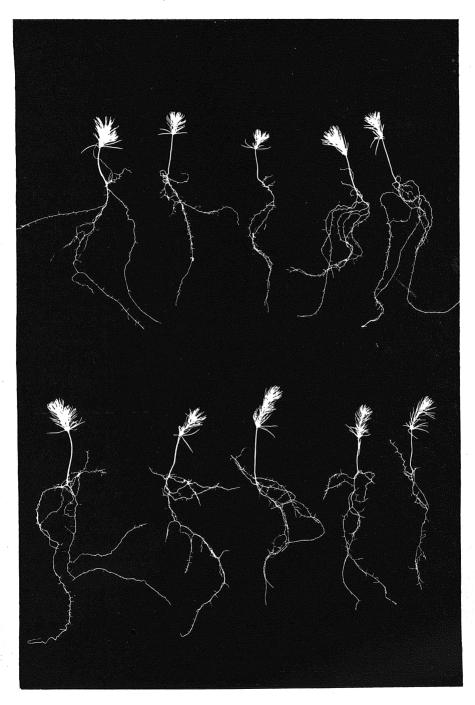


PLATE I

EXPLANATION OF PLATE II

Shadowgraph taken from seedlings of *Picea rubra* and reproduced at one-half of actual size. Specimens on the extreme left of upper and lower row show branching. Note that the inoculated seedlings (below) have longer internodes above the first year node, that the needles are more numerous and that the root system is more robust and for the most part more abundantly provided with secondary rootlets.



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PLATE II

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EXPLANATION OF PLATE III

- Fig. 1. Cross-section of rootlet of *Picea rubra* inoculated with *P. circinatus*, to show the mantle of pseudoparenchymatous tissue and the *Hartig net* which surrounds all the cortical cells.
- Fig. 2. Cross-section of rootlet of *Picea mariana* from rootlet nest from which the sporophore of *P. circinatus* had arisen. Notice the distinct pseudoparenchymatous mantle at the left, and the beginning of the formation of the *Hartig net*.
- Fig. 3. Cross-section of a small root of *Picea mariana* which has begun to show root rot. Note the accumulation of dark tannin globules in most of the cells and also the faintly showing mycelium that has penetrated into the interior of the central cells after having passed through the walls.

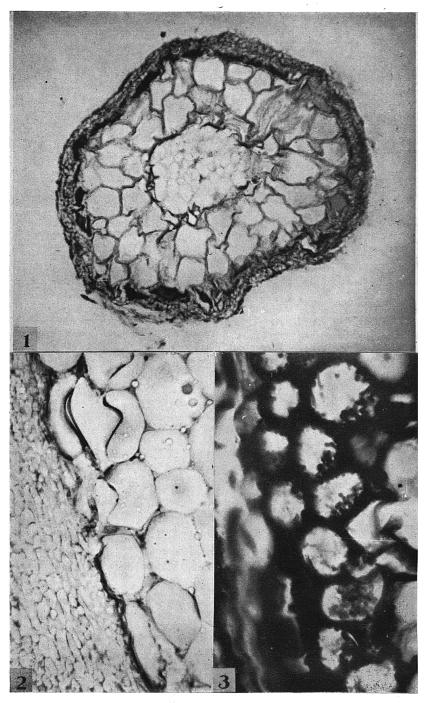


PLATE III

BIBLIOGRAPHY

Allescher, A. (1886). Verzeichnis in Süd-Bayern beobachteter Pilze. p. 74.

Ames, A. (1913). Consideration of structure in relation to genera of the Polyporaceae. Ann Myc. 11: 239, 245.

Atkinson, G. F. and H. Schrenk. (1892). Some fungi of Blowing Rock, N. C. Journ. Elisha Mitchell Sci. Soc. 9: 102.

Bennett, J. L. (1888). Plants of Rhode Island. p. 80.

Bisby, G. R. et al. (1938). Fungi of Manitoba and Saskatchewan. p. 82, 84.

Bourdot, H. and A. Galzin. (1927). Hyménomycètes de France. p. 631.

Boyce, J. S. (1938). Forest Pathology. p. 372, 393, 427.

Bresadola, G. (1920). Selecta mycologica. Ann. Mycol. 18: 67.

Burnham, S. H. and R. A. Latham. (1914). The flora of the town of Southold, Long Island and Gardiner's Island. Torreya, 14: 215.

Christensen, C. M. (1940). Observation on *Polyporus circinatus*. Phytopath. 30: 957-963.

Cooke, M. C. (1886). Praecursores ad monographia Polypororum. Grevillea, 14: 77, 82.

Curtis, M. A. (1867). Geological and Natural History Survey of North Carolina. Part III. Botany. Raleigh, North Carolina Inst. for the Deaf, Dumb and Blind. p. 97.

Dodge, B. O. (1914). List of fungi of Kewaunee County, Wisconsin. Journ. Wisconsin Acad. Sci. Arts and Let. 17 (2): 827, 829.

Donk, M. A. (1933). Revisio der Niederländischen Homobasidiomycetae-aphylophoracea. II. Amsterdam. p. 1–278.

Ellis, J. B. and B. M. Everhart. (1889). Some new species of hymenomycetous fungi. Journ. Myc. 5: 28, pl. 8.

Ellis, J. B. (1890). Catalogue of the Plants of New Jersey. p. 483.

Faull, J. H. (1922). Forest pathology, in Rept. Minister Lands and Forests, Ont. 1921: 259-266.

Finn, R. F. (1942). Mycorrhizal inoculation of soil of low fertility. Black Rock Forest Papers (N. Y.) 1 (19): 116-117.

Fries, E. M. (1821). Systema Mycologicum. 1: 341, 351.

———. (1836–1838). Epicrisis systematis Mycologici, seu synopsis Hymenomycetum. p. 474.

----. (1863). Monographia Hymenomycetum Suecia. 2: 268.

Haddow, W. R. (1941). On the history and diagnosis of *Polyporus tomentosus* Fries, *Polyporus circinatus* Fries and *Polyporus dualis* Peck. Trans. Brit. Myc. Soc. 25 (2): 179–190.

Haskell, R. J. and J. I. Wood. (1930). Diseases of plants in the United States in 1929. Plant Disease Reporter. Suppl. 75: 66.

Hatch, A. B. (1937). The physical basis of mycotrophy in *Pinus*. Black Rock Forest Bull. No. 6: 1-68.

Hay, G. U. (1903). New Brunswick Fungi. Bull. Nat. Hist. Soc. New Brunswick 5: 117.

Hennings, P. (1898) in Engler & Prantl. Die Natürlichen Pflanzenfamilien, 1^{1**}: 167, 175, 177.

Hesler, L. R. (1929). A preliminary report on Polypores of Eastern Tennessee. Journ. Tenn. Acad. Sci. 4: 9.

- Hester, J. B., J. M. Blume, and F. A. Shelton. (1937). Rapid chemical tests for coastal plain soils. Virginia Truck Exp. Sta. Bull. 95: 1433-1486.
- Hubert, E. E. (1924). The diagnosis of decay in wood. Journ. Agr. Res. 29: 551, 567.

(1929). A root and butt rot of conifers caused by Polyporus circinatus Fr. Phytopath. 19: 745-747.

-. (1931). Outlines of Forest Pathology. p. 351.

- Jørstad, I. and J. G. Juul. (1938). Ratesopper pa levende naletraer. (Rot fungi on living conifers). Meddelelser fra det Norske Skogforsøksveseen. 6 (3): 300 - 496.
- Karsten, P. A. (1889). Finlands Basidsvampar. p. 326.
- Kauffman, C. H. (1911). Unreported Michigan Fungi for 1910. Rept. Mich. Acad. 13: 230.
- (1921). The mycological flora of the higher Rockies of Colorado. Papers Michigan Acad. 1: 119.
- Konrad, P. and A. Maublanc. (1926). Icones selectae fungorum. 5: pl. 457.
- Lloyd, C. G. (1907). Letter No. 14: 5.
- (1908). Myc. Notes Polyporoid Issue 1: 2, fig. 195–199. —.
- (1911). Letter No. 30: 1, 2, 6, 11. ----.
 - (1912). Letter No. 38: 6; No. 39: 4; No. 42: 5; No. 43: 4. ____.
- (1913). Letter No. 44: 1; No. 45: 3; No. 47: 1. -----.
- -----.
- (1914). Letter No. 49: 1, 5. (1915). Letter No. 54: 1; No. 58: 1; No. 60: 1, 4, 7. (1916). Letter No. 61: 1, 6; No. 62: 3; No. 63: 2, 8. ------.
- ----.
- -----. (1920). Myc. Notes 6: 933, 949, 953, 964, 978, 979, 1014, 1018.
- ----. (1921). Myc. Notes 6: 1083.
- —. (1922). Myc. Notes 7: 1127, 1160.
- (1923). Myc. Notes 7: 1187, 1188.

Longyear, B. O. (1904). A preliminary list of the saprophytic fleshy fungi known to occur in Michigan. Rept. Mich. Acad. Sci. 4: 121.

Lowe, J. L. (1934). The Polyporaceae of New York State (Pileate species). Bull. N. Y. State Coll. For. 6: 1.

Martin, G. H. (1925). Diseases of forest and shade trees, ornamental and miscellaneous plants in the United States, in 1923. Plant Dis. Rep. Suppl. 37: 359. (1929). Diseases of forest and shade trees, ornamental and miscellaneous

plants in the United States, in 1928. Plant Dis. Rep. Suppl. 73: 370.

McKay, A. H. (1904). Fungi of Nova Scotia: a provisional list. Proc. Trans. Nova Scotia Inst. Sci. 11: 135.

-. (1908). Fungi of Nova Scotia: first supplementary list. Trans. Nova Scotia Inst. Sci. 12: 136.

Mitchell, H. L. (1934). Pot culture tests of forest fertility. The Black Rock Forest Bulletin No. 5.

Murrill, W. A. (1904). The Polyporaceae of North America. VII. Bull. Torrey Bot. Club 31: 340-348.

(1907-1908). North American Flora. 9: 1-72, 73-131.

(1915). Preliminary list of Upper St. Regis fungi. Mycologia 7: 299. (1916). North American Flora. 9: 424.

Neuman, J. (1914). The Polyporaceae of Wisconsin. p. 111-112, pl. 13, fig. 49. **Overholts, L. O.** (1916). The Polyporaceae of the Middle Western United States. Wash. Univ. Stud. 1 (3): 52-53.

(1933). The Polyporaceae of Pennsylvania. The genus Polyporus. Penn. State Coll. Expt. Sta. Tech. Bull. 298: 22.

Patouillard, N. (1900). Essai taxonomique sur les familles et les genres des Hyménomycètes. p. 100, fig. 56.

Peck, C. H. (1869). Rept. N. Y. State Bot. Museum, 22: 82.

FARLOWIA, VOL. 1, 1944

(1878). Rept. N. Y. State Bot. Museum, 30: 44. (1880). Rept. N. Y. State Bot. Museum, 32: 34. Rept. N. Y. State Bot. Museum, 46: 56. (1893). Rept. N. Y. State Bot. Museum, 47: 173-174. (1894). (1899). Plants of North Elba, Essex County. Bull. N. Y. State Museum, **6** (28) : 219.

Povah, A. H. W. (1935). The fungi of Isle Royale, Lake Superior. Papers Mich. Acad. Sci. Arts and Let. 20: 144.

Ricker, P. LeR. (1902). A preliminary list of Maine fungi. Univ. Maine Studies, 3: 64.

Rosendahl, R. O. (1941). Survey of mycorrhizae in forest nurseries of the Lake States. Univ. Wisc. Coll. Agr. Techn. Note, 21.

Routien, J. B. and R. F. Dawsón. (1943). Some interrelationships of growth, salt absorption, respiration and mycorrhizal development in Pinus echinata Mill. Amer. Jour. Bot. 30 (6): 440-451.

Saccardo, P. A. (1888). Sylloge Fungorum, 6: 208, 248.

Sartory, A. and L. Maire. (1922). Le Polyporus tomentosus Fr. Le type, ses formes, ses variétés, Assoc. Fr. Avanc. Sci. Conf. 46e Session. Montpellier. p. 773-783.

Seaver, F. J. and P. F. Shope. (1935). New or noteworthy Basidiomycetes from the central Rocky Mountain region. Mycologia 27: 646.

Shirai, Mitsutaro and Hara Kahesuke. (1927). List of Japanese Fungi. 3d ed. p. 289.

Shope, P. F. (1931). Polyporaceae of Colorado. Ann Mo. Bot. Gard. 18: 349-350.

Teng, S. C. (1932). Additional fungi from Southern China. Contr. Biol. Lab. Sci. Soc. China 8: 2, 25.

Wehmeyer, L. E. (1940). Contribution to a study of the fungus flora of Nova Scotia. Can. Jour. Res., 18: 105.

White, V. S. (1902). Some Mt. Desert fungi. Bull. Torrey Bot. Club 29: 554. Wolf, N. W. (1931). The Polyporaceae of Iowa. Univ. Iowa Studies Nat. Hist. 14: 65, pl. 4.

^{(1936).} Some Rocky Mountain Basidiomycetes. Univ. Colorado Studies **23:** 192, 195.

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