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A Contribution on the Mechanism of Disease Development in Todo-fir Canker Caused by *Trichoscyphella calycina* (SCHUM. ex FR.) NANNFELDT

By

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Summary: In this paper, the authors deal with an outline of the mechanism of disease development in Todo-fir canker, based on the physiological and pathological experiments results and on field observations. The mechanism of canker development is not simple; in fact it is rather complicated. The causal fungus is always colonized macroscopically healthy parts of the trees establishing the latent infection.

If necrotic tissues are made, for example, by cold damage, they will serve as a propagating area for the causal fungus previously infected latently, resulting in rapid increase of aggressiveness to the host trees. These necrotic tissues are also produced by snow pressure, resulting in the bending of the stem or the shedding of branches.

Decrease of the activity of Todo-fir trees is hastened by various environmental factors; dewatering resulting from soil freezing and wind-blowing in early spring, sucking action by aphides, pathogenic fungi injurious to the root system, injuries made at weeding, and so forth.

When the equilibrium between the host and the causal fungus is broken by the influence of environmental conditions, resulting in an increase of aggressiveness of the fungus and a decrease in the activity of the host, the canker will develop.

Based on the mechanism of canker development, it is important to consider beforehand the site conditions to be afforested, because it may be impossible to improve the site conditions in any attempt to eliminate or suppress the disease.

Introduction

It has been generally recognized that wounds on the surface of host trees, in many cases, serve as an entrance for the pathogenic fungi causing canker or dieback. In Hokkaido, canker disease develops in relatively young Todo-fir (*Abies sachalinensis* MAST.) plantations, and destructive damage by the disease has been encountered for some time. It has been believed without any doubt that the causal fungus, *Trichoscyphella calycina* (SCHUM. ex FR.) NANNFELDT, invades host trees through wounds and then induces the canker.

The authors continued the survey on the transition of the damage caused by the attack of the fungus for 3 years, and, at the same time, the causal fungus itself, and conducted physiological and pathological experiments relating to the development of the canker.

Based on the results obtained, the authors in their investigation into the mechanism of canker development, found that the establishment of the disease and the reason for its occurrence was not easy to determine; it is possible to appear when some environmental factors specific for the plantations act upon Todo-fir trees liable to predispose the disease.

If it is true that a wound, for instance, a mass of necrotic cells on the surface of trees

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serves as an entrance for the canker pathogen, the disease will not develop readily. Whether the canker develops or not may depend mainly on the results of interaction among the host, the pathogenic fungus, and environmental factors.

To ascertain this assumption, the authors have conducted further experiments and observations especially on the manner of existence of the causal fungus. In this paper the authors give in outline the mechanism in canker development based on some results hitherto obtained.

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Observation in relation to canker development

1. Distribution of the causal fungus, and of severely damaged Todo-fir plantations

To clarify how the causal fungus and severely damaged Todo-fir plantations caused by the attack of the fungus are distributed in Hokkaido, a field survey was conducted. As shown in Fig. 1, the causal fungus is widely distributed in Todo-fir plantations and in natural forests all over Hokkaido. In the manner of its existence, the fungus is seen to be mostly saprophytic, and it is macroscopically found all the year round, even under the snow, as cup-shaped apothecia on dead branches at the lower part of Todo-fir. Occasionally, many apothecia

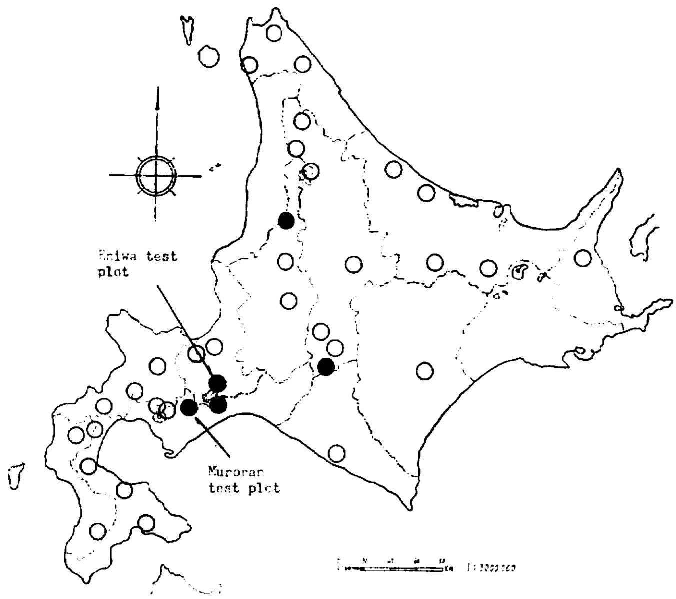


Fig. 1 Distribution of the causal fungus (○), *Trychoscyphella calycina* (Schum. ex Fr.) Nannf., and severely damaged Todo-fir plantations (●), and the locality of test plot.

appear on the whole dead trunk. Though some Todo-fir plantations such as those belonging to each of the Muroran[18], Eniwa[18)34], Tomakomai, Horokanai[18], and Kanayama[18] District Forestry Offices were severely damaged by the causal fungus, the number of damaged plantations is fewer than that of localities in which the existence of the causal fungus is ascertained.

The canker appears frequently in many plantations, but, in most cases, it is sporadic and becomes rarely epidemic. It is noteworthy that the development of the disease is limited to younger plantations, mostly less than 10 years after afforestation.

2. **Survey on the disease development relating to environmental conditions in the test plot**

2-1. Outline of the test plot and the method for the survey

The authors continued the survey on the disease develoment relating to environmental conditions for 3 years at the test plots belonging to Muroran and Eniwa District Forestry Offices, being located as shown in Fig. 1, the outline of which were as follows:

Muroran test plot: The Todo-fir plantation including the test plot was in 67 Division, afforested in 1961, the altitude of which is about 680m, facing the southwestern direction with 10° in slope. As for the climatic conditions, southwestern wind was prevalent and frequently fog appeared, resulting in the shortening of solar radiation time in the summer season. In winter, strong northwest wind blew and snowfall reached 2 m or more. Soil was sandy loam of B_D-type, and soil freezing was observed till late spring.

In early June, 1965, the test plot was established in the plantation. It was a square of 25m × 25m in size, containing 140 numbered Todo-fir trees.

Eniwa test plot: The Todo-fir plantation including the test plot was in 328 Division, afforested in 1957. It is flat in topography with a part of 5° in slope. Soil was of immature volcanic ash containing pumice stones, shown as Im-type. This area including the test plot was characterized by frequent occurrence of cold damage due to little snow, and by aphides' parasite (*Cinara todocola* (INOUYE)).

In mid-May, 1965, the test plot was established in the plantation. It was rectangular in shape with 9 planting rows containing 177 numbered Todo-fir trees.

At the time of every survey, tree height, amount of current growth, position and size of cankered lesions, appearance of apothecia on cankered lesions or on dead branches, position of wounds on trunks, and of tents made by ants for the protection of aphides parasitizing to Todo-fir trees, and the cause of death of each numbered tree, were recorded. The survey was conducted 2 times in each year from 1965 to 1967.

From these records, the authors wanted to derive possible predisposing factors for the development of the disease.

2-2. Some results obtained from the survey

a. Relationship between wounds and the disease development

As regards the relationship between wounds newly produced on the trunks and the canker development, an interesting result was obtained in Muroran test plot, where the development of the canker was increasing at that time. As shown in Table 1, the position of the wounds on the trunks in early June (just after the melting of snow) coincided with that of newly developed cankers found in early November in the same year. As far as the results are concerned, it is natural to draw the conclusion that the wounds provided an entrance for the causal fungus, followed by the development of the disease.

Table 1. Relationship between wounds on trunks and canker development
(Muroran District Forestry Office, 67, planted in 1961)

No. of trees surveyed	Wounds discovered in June 8, '65	Canker development in Nov. 2, '65	No. of trees surveyed	Wounds discovered in June 8, '65	Canker development in Nov. 2, '65
477	7B	6•4•f	537	10B	10•4•1/2•F
479	10B; 40BBr	10•5•f•F; 35•1•1/4	542	35W	35•3•1/2
489	7W	5•3•1/2	544	15B	15•1.5•1/5
502	15B	12•1•1/4•F; 15•3•1/4	549	25B	25•3•f
515	10B	10•3•1/2	558	12W	12•3•f•F
519	10W	10•2•1/2	566	10B	10•3•1/2•F
526	10W	10•4•1/2•F	573	20W	20•3•1/2•F
534	8BrBr; 15B	7•1•1/4; 15•1•1/2	575	23B	22•2•1/2
536	16BrBr	16•BB2•3/4•F			

(Note) 1. Concerning the wounds:

B: Bending of trunk, BrBr: Broken branch,
BBr: Bending of branch, 15B: Bending of trunk occurring 15cm above the ground.
W: Wounds,

2. Concerning the canker development:

10•5•f•F: Indicates a canker lesion of 5 cm in length, surrounding the stem with fruit bodies at 10 cm above the ground.

15•3•1/4: Indicates a canker lesion of 3 cm in length, appearing in a quarter of the stem without fruit bodies at 15 cm above the ground.

BB: At the base of the branch.

b. Comparison of actual state of disease development in different environmental conditions

In the next year, comparisons of the actual state of disease development observed in both plots and the nearby Todo-fir plantation of presumably different environmental conditions from the plots were made. For the purpose of comparison, a small area of the plantation facing a southeastern direction was selected in Muroran, where the northwestern prevailing wind was far weaker than in the test plot due to the difference of slope direction. In Eniwa, a small area of the plantation, where chemical control of aphides was conducted in a recent year, adjacent to the test plot, was selected. The same survey was conducted in these two selected areas, together with the test plots.

As shown in Table 2, difference of actual state of canker development in relation to the difference of environmental conditions were obvious. The cause of the difference was possibly due to that of slope direction in Muroran, and due to aphides parasitizing on Todo-fir trunks in Eniwa, resulting in the decrease of activity of the host trees, as will be discussed later. It was assumed that the predisposing factor was mainly climatic in Muroran, and was both biological and climatic in Eniwa.

3. **Recovery of cankered lesion**

Diseased individuals do not necessarily die. In the test plots, the authors frequently encountered test trees recovering by callus formation during the growing season (Plate 1, A).

In the campus of the Branch Station, where environmental conditions are considered to be beneficial for the growth of Todo-fir trees, the authors could not find the natural canker development, though apothecia of the causal fungus were usually seen on dead branches of

Table 2. Relationship between damage status and site conditions

Location and surveying plot		Eniwa District Forestry Office, 328		Muroran District Forestry Office, 67	
		Test plot (Not controlled)	Aphides control plot adjacent to test plot	Test plot (WNW slope)	SE slope adjacent to test plot
Surveyed in		May 13, 1966		June 10, 1966	
Total No. of trees surveyed		177	30	140	30
Healthy trees		117	29	23	19
Diseased trees		19	1	70	11
Infection percent (%)		10.7	3.3	50.0	36.7
Per one diseased tree	No. of lesion	1.3	1.0	1.5	1.3
	Length of lesion (cm)	4.7	3.0	4.1	3.6
	Circumference of lesion	0.59	0.50	0.49	0.46
Mean tree height (cm)		90.4	105.1	66.0	75.8
Mean current growth (cm)		10.5	14.4	18.0	26.3
Rate of growth (%)		13.1	15.9	37.5	53.1
No. of dead trees by the disease		18	0	31	0
Planted in		1957		1961	

the host trees. When the causal fungus was inoculated during the dormant season of the host trees, the canker developed in the following spring, and then many cankered lesions recovered by callus formation during the growing season (Plate 1, B).

These observation results suggest that the progress of the disease might be greatly influenced by the activity of the host trees, which will be decided by the action of environmental conditions surrounding the host trees.

Experimental

1. Some physiological characteristics of the causal fungus, relating to infection and development of the disease

1-1. Discharge and germination of ascospores under various temperatures

Materials and methods

Apothecia collected from dead Todo-fir trees in the campus of the Branch Station were attached to the under-surface of the lid of Petri-dishes for single spore isolation containing water agar. These dishes were kept under various temperatures. Discharge of ascospores and their germination were examined after 3 and 6 days.

Results

As shown in Table 3, discharge of ascospores took place in the temperature range between 0～2°C and 30°C after 6 days, though no discharge was observed at the temperatures of 0～2°C and 5°C after 3 days. No ascospores were discharged at 35°C. In the temperature range between 15°C and 25°C, ascospores were discharged actively.

As for the germination of discharged ascospores, the same tendency as in the case of the

Table 3. Discharge of ascospores and their germination under various temperatures

	Temperature (°C) / Repeat	0~2		5		10		15		20		25		30		35	
Discharge	1	−	±	−	+	+	+	+	+	+	+	+	+	±	±	−	−
	2	−	±	−	±	±	+	+	+	+	+	+	+	±	±	−	−
	3	−	±	−	±	±	+	+	+	+	+	+	+	±	±	−	−
	4	−	±	−	+	+	+	+	+	+	+	+	+	±	±	−	−
Germination	1	−	+	−	+++	−	+++	+++	+++	+++	+++	+++	+++	−	−	−	−
	2	−	+++	−	+++	−	+++	+++	+++	+++	+++	+++	+++	−	−	−	−
	3	−	+++	−	+++	−	+++	+++	+++	+++	+++	+++	+++	−	−	−	−
	4	−	+	−	+++	−	+++	+++	+++	+++	+++	+++	+++	−	−	−	−

Left column: After 3 days; Right column: After 6 days.
Discharge: + Recognized with naked eye as white deposit,
± Recognized by microscopic observation,
− Not discharged.
Germination: +++ Abundantly germinated, ++ Moderately germimated,
+ Slightly germinated, − Not germinated.

discharge was observed. They germinated in the range between 0~2°C and 25°C, with the optimum between 15°C and 25°C after 6 days, but no germination occurrd at 30°C.

1-2. Mycelial growth under various temperatures

Materials and methods

Fungus cultures used in the experiment were isolated from ascosporous origin collected in Nakayama-tôge and the campus of the Branch Station, respectively. Mycelial colonies with a bit of agar medium were cut from the margin of fungus colonies, preliminarily cultured on potato sucrose agar. These inocula were transferred to the center of Petri-dishes containing potato sucrose agar and Saito's soy agar, and then they were kept at given temperatures. Diameters of mycelial colonies were measured twice at definite intervals, and the differences of the diameters were used for the measure of mycelial growth.

Results

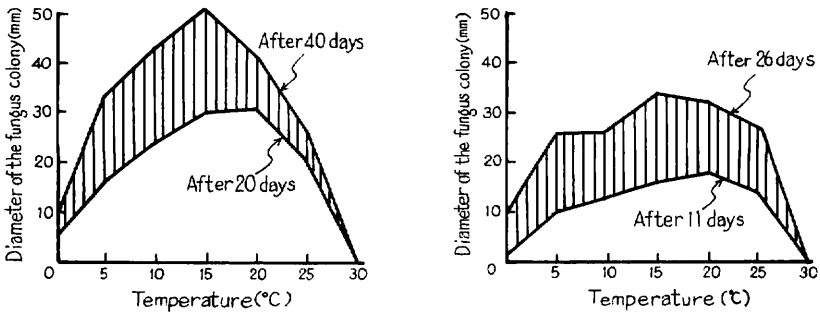
Fig. 2 shows that the growth of mycelial colonies occurred in the temperature range between 0°C and 25°C, with the optimum of 15°C, and not at 30°C. In the range between 0°C and 15°C, the growth rapidity of the colonies was linear, then it decreased suddenly with increase of temperatures. According to these results, it seems probable that the mycelia of the causal fungus grow even under the snow.

1-3. Survival of apothecia after exposure to low temperatures

For the purpose of examining the survivability of the causal fungus after exposure to low temperatures, because apothecia periodically encounter severe cold in winter, the following experiments were conducted.

Materials and methods

Todo-fir cuttings 3 cm in length, bearing apothecia of the causal fungus, were prepared, half of which were water-soaked and supplied with adequate water. These cuttings were then put into low temperature rooms, and after definite hours they were left in room temperature of 20°C for 24 hours. Apothecia were removed from cuttings and discharge of ascospores and their germination after 3 days were examined in the same manner as described above.



Culture medium: Saito's soy agar.
Left: Isolate from the campus.
Right: Isolate from Nakayama-tôge.

Fig. 2 Growth of fungus colonies at various temperatures.

Results

Results are shown in Table 4. It is clear that under the severe conditions of -20°C for 24 hours, dried apothecia discharged ascospores which germinated normally. Wet apothecia exposed in -20°C for 4 hours also discharged ascospores, and they germinated well. These results show that apothecia are highly tolerable to very low temperatures in the field.

2. **Comparison of water content of bark between the tree parasitized by the aphides and the healthy one**

If predisposing factors, induced from field survey, act upon host trees, their activity will be decreased and presumably become liable to develop into the disease. As for an index estimating the tree activity, amount of water contained in the bark was considered. The concept "relative turgidity", proposed by Weatherley[33], was introduced into forest pathological field by Bier[5][6]. The present authors applied this idea for an index expressing the tree acti-

Table 4. Survival of apothecia after exposure to low temperatures

Materials with	Exposure (°C) (hours)	Discharge			Germination		
		1	2	3	1	2	3
Dried apothecia	−5 →+20 (5) (24)	+	−		+	−	
	−10→+20 (2) (24)	+++	+++	+++	+	+++	++
	−20→+20 (5) (24)	+++	+++	+++	++	+	++
	−20→+20 (24) (24)	+++	+++	+++	+++	+++	+++
Moistened apothecia	−5 →+20 (4) (24)	+++	+++	+++	+	++	++
	−10→+20 (4) (24)	+++	+++	+++	++	+++	++
	−20→+20 (4) (24)	+++	+++	+++	++	++	++

Discharge: +++ Abundantly discharged,
++ Moderately discharged,
+ Slightly discharged,
− Not discharged.

Germination: +++ Abundantly germinated,
++ Moderately germinated,
+ Slightly germinated,
− Not germinated.

** Significant in 1% level.

vity of Todo-fir parasitized by the aphides and of the healthy one.

Materials and methods

Bark samples used in this experiment were taken from Eniwa test plot and Tomakomai plantation situated near Eniwa, respectively.

Fresh weight (1) of the bark disks was measured, then they were transferred to distilled water for 24 hours, and their weight saturated with water (2) was measured. The bark samples were oven-dried and weighed again (3). From these three weighings, percentage relative turgidity will be obtained by the following calculation:

(1)−(3) (weight of water in a bark sample) ×100/(2)−(3) (weight of water required to saturate the sample)

Results

Table 5 show that the water content of the bark was higher in the healthy trees than those parasitized by the aphides, and that the colonization of aphides became an important agent in decreasing the host activity.

Table 5. Comparison of water content of bark expressed by relative turgidity between the tree parasitized by aphides (*Cinara todocola*) and healthy one

Date of examination	Localities where samples were taken	Age of stand	Relative turgidity (%)	
			Healthy	Parasitized
May 14, 1966	Eniwa Dist. For. Office, 328	9	85.2**	76.2
Sept. 20, '66	Tomakomai Dist. For. Office, 99	4	82.3**	70.0

** Significant in 1 % level.

3. **Inoculation experiment**

3-1. The time of inoculation

Materials and methods

Inocula were prepared from mycelial colonies with a bit of agar medium, and from ascospores. The culture was the same as that used in the experiment on mycelial growth, isolated from ascospores in the campus of the Branch Station. Ascospore suspension was prepared as follows: fresh apothecia were crushed in sterilized water and then the water containing ascospores was filtered with two sheets of cheesecloth. The filtrate was used for inoculum.

Healthy Todo-fir trees 5 and 10 years old, grown in the campus, were used for the experiment. A wound, about 5mm×5mm in size, was made with a sterilized scalpel or a heated iron rod on the trunk at about 10 cm or 15cm above the ground, to which the fungus mycelia or ascospore suspension were inoculated. At the inoculation point, absorbent cotton was fixed with cellophane tape and was supplied distilled water to avoid the rapid desiccation of the inoculum. Five trees were inoculated each time.

Inoculation was conducted 7 times from May to November, 1965, and the development of the canker was examined the following year.

Results

As shown in Table 6, it is clear that inoculation tests conducted in the growing season (May and August) gave negative results, where inoculated wounds recovered with callus tissue as described previously (Plate 1, C), and positive results were always obtained in the

Table 6. Inoculation experiments conducted at various times (surveyed in 1966)

Date of inoculation (1965)	Source of inocula-tion	No. of dis-eased indi-viduals	Lesions formed (mean) (length mm) × (circumf.)			Appearance of apothecia		
			May 10	June 16	Aug. 11	May 10	June 16	Aug. 11
May 22	M	0						
Aug. 10	M	0						
Sept. 21	M	5	34×3/4	36×3/4	45×3/4	−	−	+
Oct. 18	M	5	29×3/4	36×3/4	43×3/4	−	±	+〜+++
do. (*)	S	5		36×1/2	42×1/2	−	−	++
Nov. 20	M	5	27×3/4	36×3/4	41×3/4	−	±	+〜+++
do.	S	5	15×1/4	20×1/2	27×3/4	−	−	+〜++

(Note) Each set contained 5 trees of 5 years of age, inoculated to burned wound, except in the case of 10 years of age, inoculated to fresh wound marked *.
M: Mycelial colony with a bit of agar medium.
S: Ascospore suspension.

tests conducted in the dormant season of Todo-fir, forming apothecia on cankered lesion (Plate 1, D). Cankered lesions produced by the inoculation with ascospore suspension were smaller than those with mycelia.

It was observed that cankered lesions, formed by inoculation made in the dormant season of the host trees, recovered gradually by callus formation during the next growing seasan in the campus, where environmental conditions were considered to be advantageous for the growth of Todo-fir trees (Plate 1, B).

3-2. Relationship between enlargement of cankered lesion and the aphides' parasite

Based on the consideration that the aphides' parasite possibly had an accelerating effect on the enlargement of cankered lesion, owing to the decrease of tree activity, four sets of inoculation experiments were conducted.

Materials and methods

Mycelial colonies with a bit of agar medium were used for inoculum. The culture of the causal fungus was the same as in the previous inoculation experiment. The following 4 sets of treatment were conducted:

Treatment A. Five-year-old Todo-fir seedlings were potted on November 11, 1966, and left out of doors. Fresh wounds made by sterilized scalpel at the base were inoculated on August 1, 1967, and then they were kept at 15°C in a separated greenhouse.

Treatment B. Potted seedlings similar to those in A were parasitized with aphides, collected in the campus, on July 27, 1967; then fresh wounds made in the same manner as for those in A were inoculated with the causal fungus on August 1, 1967, and then kept at 15°C in a separated greenhouse.

Treatment C. Potted seedlings similar to those in A were inoculated at the fresh wound with the causal fungus on November 25, 1966, and left out of doors. The canker developed in the following spring. Seedlings with the cankered lesion were kept at 15°C from July 27, 1967, in a separated greenhouse.

Treatment D. Seedlings the same as those in C were parasitized with aphides on July 27, 1967, and kept at 15°C in a separated greenhouse.

Five pots were used in each set of inoculation. Enlargement of cankered lesions was examined on October 4, 1967.

Table 7. Relationship between the enlargement of cankered lesions and the aphides' parasite

Treatment	At the start of the experiment (August 1, 1967)		Results in October 4, 1967		
	Colony of aphides	Largeness of lesion (mean)	Colony of aphides	Largeness of the canker	
				Mean	Range
					mm circumf.
A	−	0	−	18 × 0.38	16~20 × 0.25~0.5
B	+	0	++	58 × 1.00	50~80 × 1.00
C	−	26 mm × 0.75 circumf.	−	28 × 0.75	25~30 × 0.75
D	+	32 × 0.75	++	53 × 1.00	30~60 × 1.00

Results

Results are shown in Table 7. Compared the results between the treatment A and B, and between the treatment C and D, respectively, it is clear that the enlargement of cankered lesions was hastened by aphides' parasite. As far as the present results are concerned, it cannot be said that the aphides' parasite is an indispensable factor in inducing the development of the canker, because the canker developed in the treatment A without aphides' parasite. To date, the authors have no data to determine whether the lesions resulting from sucking by aphides provide an entrance for the causal fungus.

3-3. Enlargement of cankered lesions under the snow

The temperature under deep snow will be estimated to be 0°C. To ascertain whether the causal fungus can be active under the condition of 0°C, the following inoculation experiments were conducted.

Materials and methods

Three-year-old Todo-fir seedlings were used. They were inoculated on October 7, 1967, with the fungus mycelia in the same manner as described above, and were left out of doors. Later, 5 seedlings were arbitrarily dug out from the snow at 2-month-intervals, and the enlargement of cankered lesions was examined.

Results

Results are shown in Table 8. It is clear that, even under the snow, cankered lesions enlarged constantly.

4. Ecology of the causal fungus, especially the manner of existence in the host —— latent infection ——

Because, in artificial inoculation experiments, an unnaturally large amount of inoculum of higher infection potential will be provided to the wound to be inoculated, there will be no difficulty to explain the relationship between cause and effect on the develoment of the disease. In some cases, nevertheless, apothecia of the causal fungus happen to appear on the whole trunk after the death of trees without any cankered lesions. For example, healthy trees were cut into disks for the purpose of taking their growth measurement in autumn, and after the measuring, the disks were left overwintering in polyethylene bags. In the following spring, many apothecia appeared on the bark of all the disk. This phenomena will be explained only by introducing the assumption that the causal fungus already infected latently into apparently healthy trees before they were cut into disks.

Table 8. Enlargement of cankered lesions under the snow

Date of observation	Largeness of lesions (length mm × circumf.)	Remarks
Dec. 20, '68	7.0 × 0.25	Many apothecia were formed from early May
Mar. 12, '69	16.2 × 0.5	
Apr. 30, '69	23.0 × 0.5	

To verify the assumption of latent infection, the authors conducted the following experiments.

4-1. Isolation experiments of the causal fungus from the bark and leaf scars of apparently healthy Todo-fir trees

Materials and methods

Pieces of about 5 mm square were prepared from Todo-fir bark collected from apparently healthy trees. They were surface sterilized with 20 times' diluted sodium hypochlorite aqueous solution, and ten of each were put onto potato sucrose agar in Petri-dishes. Isolation experiments were done at the temperatures between 0°C and 5°C or between 10°C and 15°C. At the same time isolation from leaf scars was conducted.

Results

According to the results shown in Table 9, fungus colonies closely resembling the causal fungus were always isolated, though isolation percentage was low, in each trial of isolation. In the isolation experiment performed in November, 1969, with the leaf scars collected from Sôbetsu, a larger isolation percentage of 41% was obtained. This may be due to the fact that, as far as this isolation is concerned, leaf scars to be isolated were taken from the lower part of a trunk.

4-2. Ascertaining the isolated fungi closely resembling the causal fungus to be the authentic causal fungus.

To ascertain whether the isolated fungi in the previous isolation experiment closely resembling the causal fungus are identical with the authentic canker fungus, the following experiments were conducted.

Materials and methods

Cuttings of Todo-fir stem 10cm in lenght and 1.0～1.5cm in diameter were steam-sterilized in plugged glass tubes with a small amount of water. They were inoculated with isolated cultures closely resembling the causal fungus on January 10, 1970, and kept at 10～15° C in a glass room. Cultures used for inoculation were the isolates from the bark of Todo-fir collected at Shimizu and Tomakomai, and from leaf scars collected at Sôbetsu, respectively.

Results

Several months after inoculation, spermatia were exuded abundantly, followed by appearance of apothecia successively. Unexceptionally apothecia were produced on cuttings inoculated with every isolate (Plate 2, A and B). With matured apothecia, dimension of asci and ascospores was measured on December 24, 1970. Table 10 shows that the dimension in each isolate coincided with that of the known causal fungus, and that cultures used in this experiment were undoubtedly the causal fungus itself.

4-3. Appearance of apothecia on dead trunks by girdling treatment

As already mentioned, natural canker development is never seen in the campus of the

Table 9. Isolation of fungi from

Materials used for isolation					Healthy
Localities where samples were collected	Tomakomai				Shimizu
Age of stands (years)	7	8	8	8	10
Date of isolation	X, '69	XI, '69	V, '70	V, '70	VI, '69
Isolation temperature (°C)	0~5	0~5	0~5	10~15	0~5
Trichoscyphella calycina	5%	2%	1%	%	5%
Phomopsis sp.	10	37	47	10	20
Ascocalyx sp.	+				+
Cytospora sp.				+	
Phacidium sp.					
Fusarium spp.	+	15	1	3	+
Botrytis sp.	+	+	+	1	+
Rhachodium sp.		+	+	+	+
Pestalotia sp.		3		+	
Others **	85	43	51	86	75

* Pieces of leaf scar to be isolated were collected from the lower part of the trunk.

** Others contained two dominant species unidentified.

Branch Station, though the causal fungus is usually found saprophytically. The authors concluded that the causal fungus must be establishing the infection latently in the bark of Todo-fir growing apparently healthy in the campus, hence the following experiment was undertaken.

Materials and methods

Twenty Todo-fir saplings 8 years of age were transplanted in November, 1969, in the birch plantation situated at a corner of the campus to avoid further infection by the causal fungus after the treatment. Soon after the transplanting, they were girdled near the base of the trunk about 1 cm in width. From then on, they were left under the natural condition.

Table 10. Dimension of apothecia appearing by inoculation with fungi isolated from apparently healthy bark and leaf scar

Locality fungi isolated	Date of inoc.	Date of measurement	Asci (μ) (Mean)	Ascospores (μ) (Mean)
Shimizu	Jan. 10, '70	Dec. 24, '70	50.0~62.5×4.5~5.0 (55.0×4.7)	5.0~7.5×2.5~3.0 (6.5×2.5)
Sôbetsu	〃	〃	43.2~48.0×4.1~4.3 (47.8×4.3)	4.3~7.2×2.4~3.1 (6.0×3.0)
Tomakomai	〃	〃	47.5~57.5×4.3~5.0 (53.0×4.8)	4.5~6.8×2.5~3.3 (5.5×2.8)
		May 20, '27*	42.9~65.0×3.9~5.2	3.9~7.1×2.3~3.0
		Apr. '64 **	43.0~70.0×3.3~5.0	4.5~7.5×2.0~3.3

* Measured by Kamei [18] with the specimens collected in Sapporo.

** Measured by the authors with the specimens collected in the campus.

healthy bark and leaf scar

bark			Leaf scar						
Campus of the Branch Station			Sôbetsu		Tomakomai		Campus of the Br. Sta.		Sôbetsu
8	8	8	10	10	8	8	8	8	10
I, '70	IV, '70	IV, '70	VI, '69	XI, '69	V, '70	V, '70	IV, '70	IV, '70	XI, '69
0～5	0～5	10～15	0～5	0～5	0～5	10～15	0～5	10～15	0～5
3%	%	−%	5%	4%	+%	+%	2%	2%	* 41%
7	25	20	10		29	31	21	12	
			+		+				
	+								
3	3	5	10		8	5	2	5	
+	4	+	+		+	+		+	
	1	+	+		+	+	3	+	
2	1	2				+		+	
85	66	73	75	96	63	64	72	76	59

Results

In the following summer, they began to die successively, and, as shown in Table 11, apothecia appeared unexceptionally soon after the death of treated trees (Plate 2, C). This being the case, the tendency that the lower the position girdled, the more the number of apothecia, was recognized (Plate 2, D). At the same time, Table 11 shows that the dimension of these apothecia coincided with that of the causal fungus.

From these results, it is highly probable that apparently healthy Todo-fir is infected latently by the causal fungus.

Discussion and conclusion

HEMMI[13] reporting on the development in some kinds of plant disease, suggested that under natural conditions, host plants would probably contain pathogenic fungi in living state in their tissues without showing any symptoms, and if the equilibrium condition between the host and the fungi was broken by some environmental factors toward increasing the aggressiveness of the fungi, then diseases would develop. This state of affairs is latent infection.

On the latent infection of citrus fruits, BAKER and WARDLAW[4] ascertained this phenomena by isolation experiments from the skin of grapefruit. They could isolate constantly four pathogenic fungi containing *Phomopsis citri* and *Glomerella cingulata*, well-known storage pathogens. In Japan, the latent infection of citrus black spot fungus was ascertained by KODAIRA and SATO[20], TOKUNAGA[31], and SUEDA[27]. Later, TOKUNAGA and YOKOHAMA[32] reported on the latent infection of pathogenic fungi causing citrus black spot, anthracnoses of citrus and certain tropical fruits, and ripe rot of grapes, and commented as follows:"……… It has been confirmed that the

Table 11. Appearance and dimension of apothecia on the dead stem around the girdled zone

A. Appearance of apothecia (1970)

No. of trees girdled	Appearance of apothecia		No. of trees girdled	Appearance of apothecia	
	Aug. 17	Nov. 26		Aug. 17	Nov. 26
1	+	+++	11	++	++
2	+	+++	12	++	+++
3	+++	+++	13	−	+
4	+++	+++	14	+	+++
5	+++	+++	15	+	++
6	−	+	16	++	+++
7	−	+	17	++	++
8	+++	+	18	−	++
9	−	+	19	−	+
10	−	+	20	−	++

Girdling: November, 1969.

B. Dimension of apothecia (December 24, 1970)

No. of sample	Asci (μ)	Ascospores (μ)
1	42.5～47.5 × 3.8～5.0 (44.8 × 4.5)	5.0～6.8 × 2.5～3.3 (5.8 × 3.0)
2	42.5～50.0 × 4.5～5.3 (46.5 × 5.0)	5.0～6.8 × 2.5～3.8 (5.8 × 3.3)

( ) : Mean

latent infections were present in tissue of certain fruits on which the anthracnose should never develop even in the stage of over-ripening. ……… In the case of leaves and shoots, the anthracnose fungi were found latently in the apparently healthy tissue, although the disease developed usually upon such parts on trees weakened by root injury or stem borer or upon leaves fallen or partially dead. ……… It may be possible to consider that though the infection has become established already, the aggressiveness of these organisms is comparatively reduced, but in the tissue deteriorated in vitality their pathogenicity becomes increased."

On the mechanism of the disease development and ecology of *Diaporthe Nomurai* HARA, the causal fungus of mulberry-blight, AOKI[2)3)] found that this fungus mycelia existed constantly in the lenticel of the host plants grown in both localities where snowfall was heavy and severe damage by the fungus always occurred, and where snowfall was usually scanty and rarely the damage happened, and proved experimentally that, when the snow covered the latently infected hosts, keeping them in dark and moistened conditions for longer period, the resistant ability of the host against the aggressiveness of the causal fungus would be reduced considerably, followed by the development of the disease.

Later, latent infection was discovered on European larch canker by DAY[9)]. He reported that living larch bark contained constantly a microflora, sometimes included *Dasyscypha willkommii*, the infected center of which was mainly a small group of dead cells occurring commonly in living host, and the microflora would possibly stimulate the development and extension of the canker, when some injuries happened to the host, resulting in the decrease of its activity.

Some kinds of anthracnose disease of black locust and acacia were recognized to be transmitted by seeds, already infected latently by causal fungi by SATÔ and SHÔJI[26], and HASHIMOTO[11], respectively. TERASHITA[28] isolated various kinds of fungi, including damping-off fungi, from apparently healthy rootlets of Japanese red pine (*Pinus densiflora* SIEB. et ZUCC.), and recently it was ascertained by ONO[25] that a root rot fungus, *Armillaria mellea* (FR.) QUÉLET, was frequently parasitizing to the root of apparently normally growing larch trees.

As mentioned above, the fact that there occurs no symptom after the establishment of fungal infection, where host tissues contain the causal fungus in a living state for a longer period, has been known in some diseases. As shown in Fig. 1, it is found that there is no more than a few damaged plantations, despite wide distribution of the causal fungus throughout Hokkaido. This is probably due to a low aggressive potential of the causal fungus, lack of some environmental conditions necessary to predispose Todo-fir trees to the disease, or both.

From Table 1, the reader might get the impression that the causal fungus invaded from wounds caused in spring and the canker developed *in situ* in the following autumn. In Table 6 and Fig. 2, however, it was shown that the results of artificial inoculation during the growing season of Todo-fir were negative, inoculated wounds recovering by forming callus tissue, and the velocity of mycelial growth very slow. Based on these facts, it is rather difficult to conclude that a cankered area of several centimeters in diameter developed by autumn, starting from landing and germination of ascospores of the causal fungus on wounds newly established in spring. And further, considering the fact that, under natural conditions, the causal fungus of slow growing characteristic should live among many other microorganisms[1,7,8,9], it will be still more difficult to explain the establishment of infection, and extensive growth of the causal fungus on the wounds. The thought that the causal fungus had established the infection in the dead or collapsed tissues of the host bark before wounds or injured parts were made, and the fungus thus already existed propagated extensively into them, followed by the production of the cankered area *in situ* till autumn, will offer a better explanation for the canker development. Because the fact that apothecia of the causal fungue exist all the year on dead branches or cankered lesions, discharge and germination of ascospores take place at a wide range of temperature, and mycelial growth may occur in the lower temperature range, there may exist always the chance to establish the latent infection (Tables 3, 4 and Fig. 2).

Results of isolation, girdling experiments conducted to ascertain the latent infection showed the probability of latent infection to the bark or leaf scars of apparently healthy Todo-fir (Tables 9, 10, and 11, and Plate 2, C and D). In Todo-fir plantations, dead tissues such as leaf scars, naturally died branches, and lesions caused by early or late frost are always present. For some kinds of tree disease, such as canker or die-back, these dead tissues are recognized by many workers to provide the entrance for pathogenic fungi, and when the host activity is decreased by the influence of environmental conditions, diseases will develop[2,3,9,10,12,14,16,17,18,19,21,22,23,24,29,30].

If this idea on the latent infection in Todo-fir canker is true, it may be said that the causal fungus has always the chance to establish the latent infection, and adversely the host trees are always liable to become the carrier of the canker disease. So, consideration should be given to what environmental factors are necessary to develop the disease for the carrier.

Table 2 shows that the status of the canker development is not even in a plantation; the appearance of the disease is different in relation to site conditions. In Eniwa test plot, degree of the damage by the canker is likely to be decided by whether aphides' parasite exists. Regarding the influence of aphides' parasite on Todo-fir, INOUYE and YAMAGUCHI[15] reported that Todo-firs lost their vitality and became liable to be attacked secondarily by pathogenic fungi and pests. Table 5 shows that the water content of the Todo-fir bark expressed by relative turgidity in parasitized trees is significantly lower than that in healthy trees, suggesting decrsease of tree activity in the former. The relationship between canker development and the water content of the host bark is thought to coincide with BIER's[5)6)] idea that canker diseases caused by facultative parasites easily develop when values of relative turgidity of the host bark fall below a definite level, being 80% in the case of deciduous trees. As regards the extension of cankered lesion, Table 7 shows that the aphides' parasite clearly accelerated it as compared with non-parasitized trees. From these results, it may be true that aphides' parasite weaken the tree activity and make it easy to develop the canker disease and to extend cankered lesions, though whether the lesions of sucking by aphides serve as an entrance of the causal fungus is not clear. Though the treatment A and B were done in August (mid-summer), canker lesions were produced. This was probably due to the fact that inoculated seedlings were kept in the lower temperature of 15°C.

Aphides' parasite, by the way, was seldom found in the Muroran test plot, where the depth of snow in winter reaches frequently about three meters, and soil freezing continues till late May, with strong prevailing wind. The test plot, facing a southwestern direction, is directly in the path of strong winds during the cold season. Despite the rapid increase of transpiration of Todo-fir soon after the snow is melted by the influence of strong wind, succeeding water supply from the root system must be intercepted, followed by considerable decrease of tree activity. Conversely, in the southeastern slope, this phenomena combined with soil freezing and strong wind does not take place. The authors consider that the difference of the damage state in two plots in the Muroran test plot is traceable mainly to the difference of such site conditions.

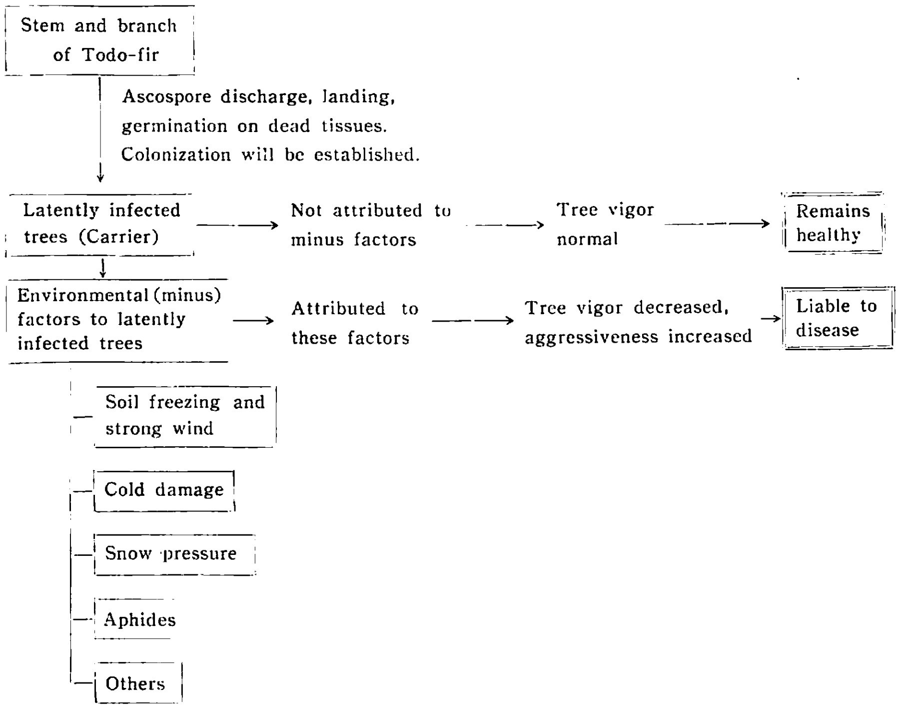
In both areas, Eniwa and Muroran, the canker is prevailing, and it is thought that the latent infection will readily take place in naturally dead tissues. Moreover, Eniwa test plot is in an area in which cold damage occurs because of less snowfall, and lesions easily occur on the trunk of Todo-fir near the ground surface. In Muroran test plot locating in a cold, heavy snowfall area, the crook of the trunk, and shedding of branches caused by the snow pressure, and lesions by cold damage are usually found.

As shown in Table 8, where cankered lesions extend under the snow, and because cold damage does not occur during mid-winter due to high resistant ability of the host against cold damage, it may happen in late autumn or mid-spring, when the temperature at those times is not so severe, that the causal fungus already infecting latently in the bark or leaf scars of the host trees will begin to propagate rapidly into such locally dead or collapsed tissues as mentioned above. This is suggested to some extent by the results of experiment on survivability of the causal fungus against low temperature as shown in Table 4. At that time, if the tree activity is decreased by the parasitic action of aphides or compelled dewatering, the resistant power of the host trees against the disease will also decrease, and the aggressiveness of the causal fungus will increase, relatively. As a result, the canker will develop in a relatively shorter period of time.

Though the authors postulated predisposing factors such as snow pressure, soil freezing, cold damage, strong prevailing wind, and parasitic action of aphides, other conditions to decrease the tree activity may also prove to be the inducing factors, namely, pathogenic fungi injurious to root systems, wounds made at weeding, and injuries caused by rodents, and so forth.

Based on the considerations mentioned above, the following diagrammatic scheme on the mechanism of canker development will be obtained.

Diagrammatic scheme of the mechanism of disease development in Todo-fir canker



The scheme suggests the importance of the selection of sites to be afforested, because the survival of planted seedlings against the disease will be decided mainly by the environmental conditions, many of which will be impossible to be improved after the establishment of afforestation.

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Explanation of plate

Plate 1.

A. Test tree No. 576 in Muroran test plot. The cankered lesion was recognized until the last survey in the spring, 1967, then healed by callus formation (Photo: October 18, 1967).

B. Healed cankered lesion by callus formation. This was inoculated with the mycelia on October 7, 1968, in the campus, and the canker once developed the next year; then it recovered (Photo: January 19, 1970).

C. Healed wound by callus formation to which the mycelia were inoculated on May 22, 1965, in the campus (Photo: August 19, 1966).

D. The cankered lesion and apothecia produced by inoculation with a bit of mycelium of the causal fungus to a fresh wound on October 18, 1965, in the campus (Photo: August 19, 1966).

Plate 2.

A. Apothecia appearing on a Todo-fir cutting in a tube inoculated with the isolate from Shimizu (Photo: November 27, 1970).

B. Ditto (enlarged).

C. Apothecia appearing just after the death of a treated tree around the girdled zone (Photo: November 27, 1970).

D. Apothecia appearing on dead trunks around the girdled zone. The lower the girdled position, the bigger the number of apothecia (Photo: November 27, 1970).

トドマツがんしゅ病の発病機構に関する一考察

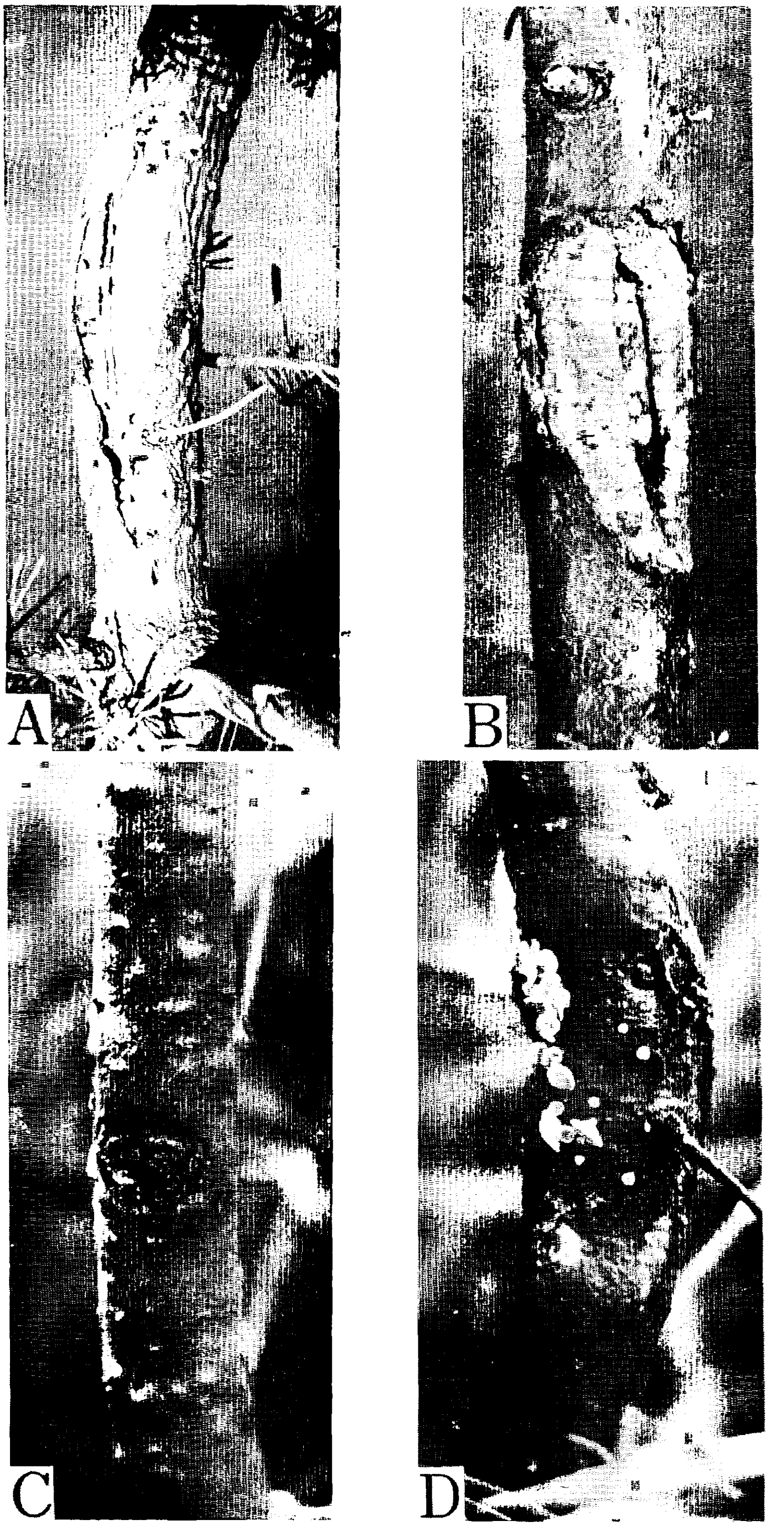
横田俊一[1]・松崎清一[2]

摘要

トドマツがんしゅ病による激害林分は，本病原菌の広い分布に比べて意外に少ない。筆者らは被害造林地における発生環境解析，本病病原菌の諸性質に関する実験および観察を行なった結果，本病の発生は単に傷から病原菌が侵入して起こるという単純なものではなく，環境条件に大きく左右されるものであることが明らかとなった。すなわち，本病病原菌は，外観健全に見える造林木に対して潜在的に感染を起こしており，このような保菌木が環境条件の影響をうけて樹勢が低下すると発病に至るものである。

造林木に自然に生ずる枯枝，葉こんその他の壊死部に病原菌は腐生的に生存しているが，それだけでは発病しない。しかし，たとえば早春あるいは晩秋の霜害などで生じた凍傷こんなどは潜在的に存在している本病菌の繁殖の場となる。このように増殖した場合には病原菌は高い侵害力を有するようになるであろう。いっぽう，土壌凍結が春おそくまで続き，強い季節風に吹かれると，トドマツは強制的に脱水作用をうけ樹勢は急速に低下する。このような場合には，すみやかにがんしゅ病が発生する。凍傷痕に限らず，雪圧による樹幹の曲がりや枝折れ，枝ぬけなども同様に病原菌の急速な繁殖の場を提供する。トドマツの樹勢の低下を来たす条件は，アブラムシの寄生，根部障害，下刈り時の傷その他が考えられるが，要するに，潜在的に存在する本病菌の増殖と宿主の活力の低下によって，寄主と寄生者間の平衡が破れると速やかに発病に至るものと解される。このよのな被害を回避するためには，とくに造林立地の選定が重要であると考えられる。

1970年12月14日受理
(1)(2) 北海道支場保護部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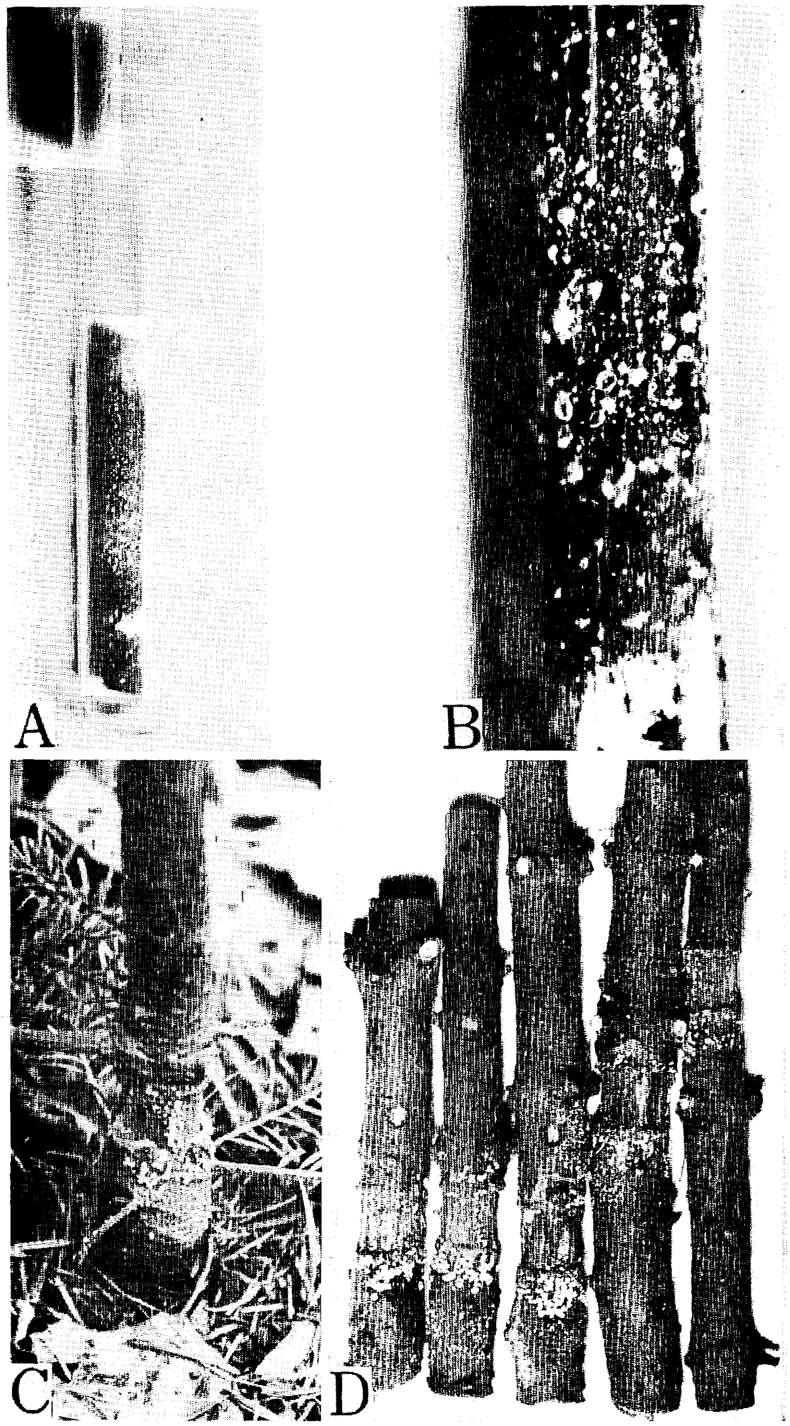
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