日本におけるカラマツのがんしゅ病

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摘　　要

オオシュウカラマツのがんしゅ病は英国においては19世紀初頭から問題になり，今日では広く欧州大陸に分布し，本樹種の最も重要な病害の一つに数えられ，造林木に対してはなはだしい被害を与えている。

北米合衆国では1927年にはじめて本病が発見されたが，これは英国から輸入した苗木に病原菌が潜在してもちこまれたものとされている。

欧州における永年の試験観察によれば，ニホンカラマツは本病に対して一般に抗抵性だといわれており，これがかの地で造林上わが国のカラマツが注目されている一つの理由にもなっている。

本病の病原菌がわが国に存在するかどうか長い間不明であったが，著者らが1957年長野県八ケ岳山麓で枝に寄生したものを発見したのが最初のたしかな記録である。その後長野，山梨，静岡各県下において枝に着生するものを数回にわたり採集したのであるが，当時は幹の典型的ながんしゅ状の被害をみとめることができず，わが国に本病々原菌は存在しても，実害は問題にする必要がないと考えていた。

ところが，1961年，八ケ岳山麓野辺山国有林の造林地において本病の激害を発見，その病状は欧州におけるオオシュウカラマツのそれといささかも異ならないことを知り，にわかに本病はわが国でも注目されるにいたった。それで，調査区域をひろげてしさいにしらべたところ，本病のはなはだしい被害は富士山麓にも発見され，なおこれは造林木のみならず天然林にも典型的ながんしゅ状の被害を与えていることを知った。

本病の分布は今日のところ，長野，静岡および山梨各県下の山岳地方に限られているが今後の調査によってはさらに広く本病が見い出されるであろう。現に最近北海道稚内付近のグイマツ造林木の枝に本病々原菌が採集されている。

長野県八ケ岳山麓野辺山国有林におけるカラマツの造林木（1913～1916年植栽）について，被害の解析を行なって次の結果を得た。

（1） 被害は海抜高1,500～1,700mにおいて特にはなはだしく1,400m以下では比較的軽微である。

（2） 幹がはなはだしく侵されたものは健全木にくらべて樹高および直径成長は一般におとる。

（3） 罹病木の80%以上は地上8m以下の部分にがんしゅを形成する。

（4） 幹のがんしゅは枯枝および枯死した芽（短枝）の部分から進展拡大する場合がきわめて多い。

わが国においてがんしゅ患部にみとめられる菌が，オオシュウカラマツのがんしゅ病菌と同一かまたは異種かを知るために，形態の比較および人工接種によって病原性をしらべた。その結果はこれを欧州で著

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名ながんしゅ病菌と同一とみとめ，学名として *Trichoscyphella willkommii* (HARTIG) NANNF.〔*Dasyscypha willkommii* (HARTIG) REHM〕を採用した。本菌は外国からわが国に輸入されたものとは考えられず，古くから日本に分布して天然林に存在していたのが，造林木にもうつっていったと考えるのが妥当であろう。

本病の病因としては古くから2つの説がある。その1は寒さの害を主因と考えて病原菌を副次的，補助的因子とする説であり，他は病原菌をあくまでも主因とする説である。本菌は寒さの害とは無関係に病原性を発揮することはたしかである。しかし，これだけでは本病の典型的被害の発現は説明できないようである。欧州においては，オオシュウカラマツの郷土および立地条件が本病の被害と密接な関係があるとし，特に各植栽地におけるカラマツの系統の選択を最も重視しなければならないとしている。

わが国におけるニホンカラマツではその天然分布の中心において本病のはなはだしい被害をうけていることからみると，これを欧州の学者のように，もっぱら郷土問題に帰せしめるわけにはゆかないように思われる。

欧州における観察によれば，ニホンカラマツも時に本病にいちじるしく侵される例がかなり知られている。著者らにはこれを環境因子との関連において考えるのが至当だと思われる。すなわち，気象，土壌その他の環境条件によってカラマツの樹勢がおとろえた場合に本菌がいちじるしい病原性を発揮して激害を及ぼすものであろう。それで，立地条件を無視して広く造林するならば，オオシュウカラマツにくらべてひじょうに抵抗性だとされているニホンカラマツにも，野辺山国有林に発生したような大被害が今後も発生するおそれは十分ありうる。

Larch Canker in Japan

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Introduction

European larch canker has been well known for many years in the British Isles and on the European Continent as one of the most important diseases of this tree species. According to HILEY (1919)[17] it first began to attract attention in Great Britain as a larch trouble at the beginning of the nineteenth century.

The disease came originally from the Alps, the home of European larch (*Larix decidua* MILL.). In its native habitat the canker is of little consequence. However, when introduced into the larch plantations of the lowlands of Europe, it became a destructive disease. Today in Europe, where the larch is grown extensively, the canker occurs in varying abundance in practically every plantation.

The disease is due to a fungus which has been called by a variety of names, but now generally known as *Dasyscypha* (*Trichoscyphella*) *calycina* in Britain and *Dasyscypha* (*Trichoscyphella*) *willkommii* on the Continent.

The present known distributions of the canker parasite in Europe are as follows : Austria, Belgium, Czechoslovakia, Denmark, France, Germany, Great Britain (England, Scotland, Wales), Hungary, Ireland, Italy, Latvia, Netherlands, Norway, Poland, Russia (Baltic Provinces), Sweden, Switzerland and Yugoslavia (HILEY 1919[17], SPAULDING 1961[39]).

In the United States of America the disease was first discovered in 1927, on European larch that had been imported from Great Britain as nursery stock and planted in Massachusetts many years earlier (SPAULDING & SIGGERS 1927[38]). Infections found in America on introduced larches are now believed to have been eradicated (BOYCE 1961[3]).

In Japan, as early as 1909, IDETA[19] described the European larch canker in his handbook, but never included the disease among Japanese pests. In 1933, KITAJIMA[25] presented a brief account of a cankerous disease of Japanese larch (*Larix leptolepis* GORD.) occurring in the Tohoku district, but he did not investigate its causal agent. So far as the authors can ascertain, there had been no reliable account concerning the occurrence of the larch canker fungus in Japan until 1957.

In 1957, a *Dasyscypha* was collected by the junior author on branches of Japanese larch at the foot of Mt. Yatsugatake in Nagano Prefecture, and it was identified as *Dasyscypha* (*Trichoscyphella*) *willkommii* distributed widely in Europe (ITO & ZINNO 1957[21]). This was the first discovered and recorded instance of the European larch canker parasite in Japan. More recently, serious outbreaks of the canker have been found in Japanese larch plantations in Nagano and Shizuoka Prefectures, the central part of the Main Island of Japan (ITO 1961[22], KOBAYASHI & UOZUMI 1962[26]).

In Europe, it has been generally believed that Japanese larch is almost immune or very resistant to the canker, but, unexpectedly, destructive damage of the disease has been recently discovered in plantations of our country. Now, the canker has become a major disease of

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Japanese larch. Because of the significance of the trouble, the results of the investigations that have been made by the authors are herein reported.

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Symptoms and signs

First symptoms are regular, elliptical to nearly circular bark depression, in the majority of cases a branch node or dead twig in the center. Cankers on the large branch and trunks are perennial and become open wounds forming an amphitheatre floored with dead wood and surrounded by raised tiers of swollen tissue. A copious flow of resin comes from them and may stream down the stem before hardening to a white crust. In old large cankers, the diseased barks become loose and may fall away and leave the wood more or less exposed, while the development of callus makes a more or less pronounced ridge surrounding the wood.

A single canker may girdle and quickly kill a small branch and a stem of young tree. Fructifications of the causal organism in various stages of development are to be found commonly near the edge of the canker (Plate 1 B,C,D; Plate 2 A,B,C,D; Plate 4 A,B,C, D,E).

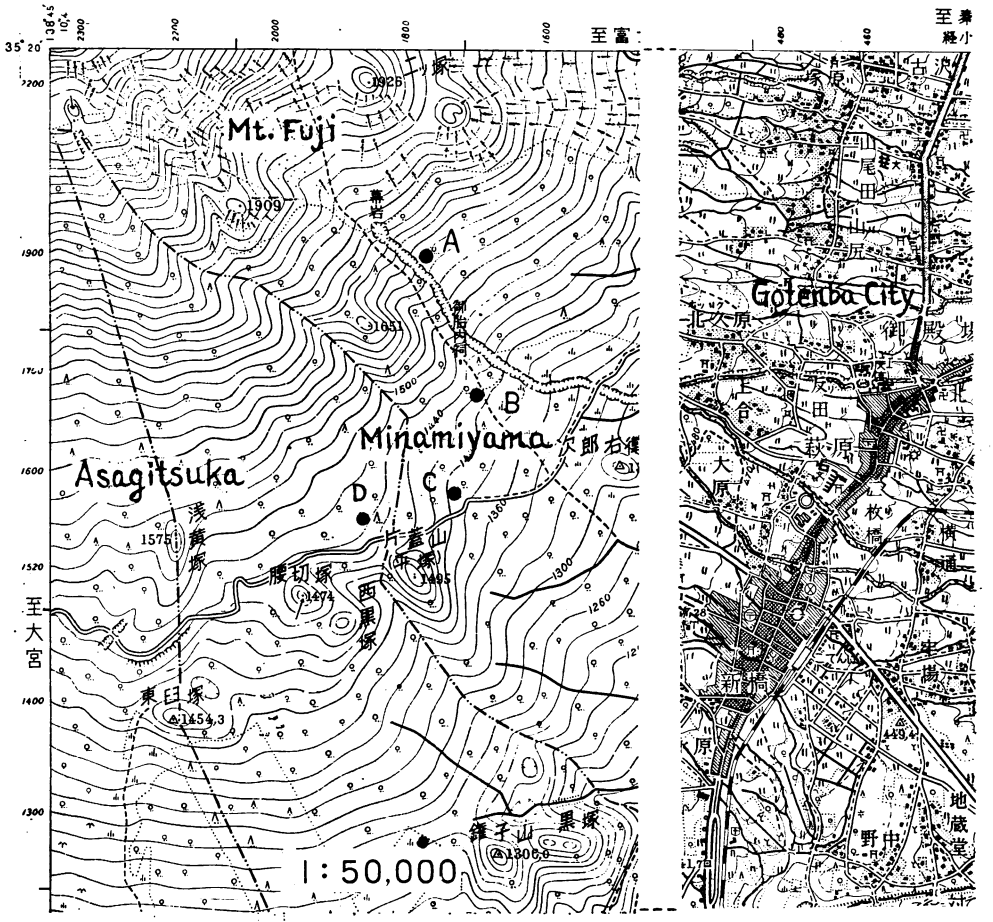
Distribution of the disease in Japan

With the discovery of the larch canker at Mt. Yatsugatake in 1957, scouting for the disease was performed to determine whether it was widely distributed in Japan. The present

Text-fig. 1. Map showing distribution of the larch canker in Japan in 1962.
a, Nobeyama National Forest, Mt. Yatsugatake, Nagano Prefecture.
b, Minamiyama and Asagitsuka National Forests, Mt. Fuji, Shizuoka Prefecture.

known distribution of the disease researched by the authors is limited to Nagano, Yamanashi and Shizuoka Prefectures, the central part of the Main Island (Text-fig. 1).

It is noteworthy that the disease occurs on trees not only in plantations, but also in natural forests at Mts. Yatsugatake, Fuji and Asama. All of these mountains are known as the center of the natural distribution of Japanese larch (Text-fig. 2).



Text-fig. 2. Map of distribution of the larch canker at Mt. Fuji, Shizuoka Prefecture, in 1962.
A, Natural forest ; B-D, Plantations.

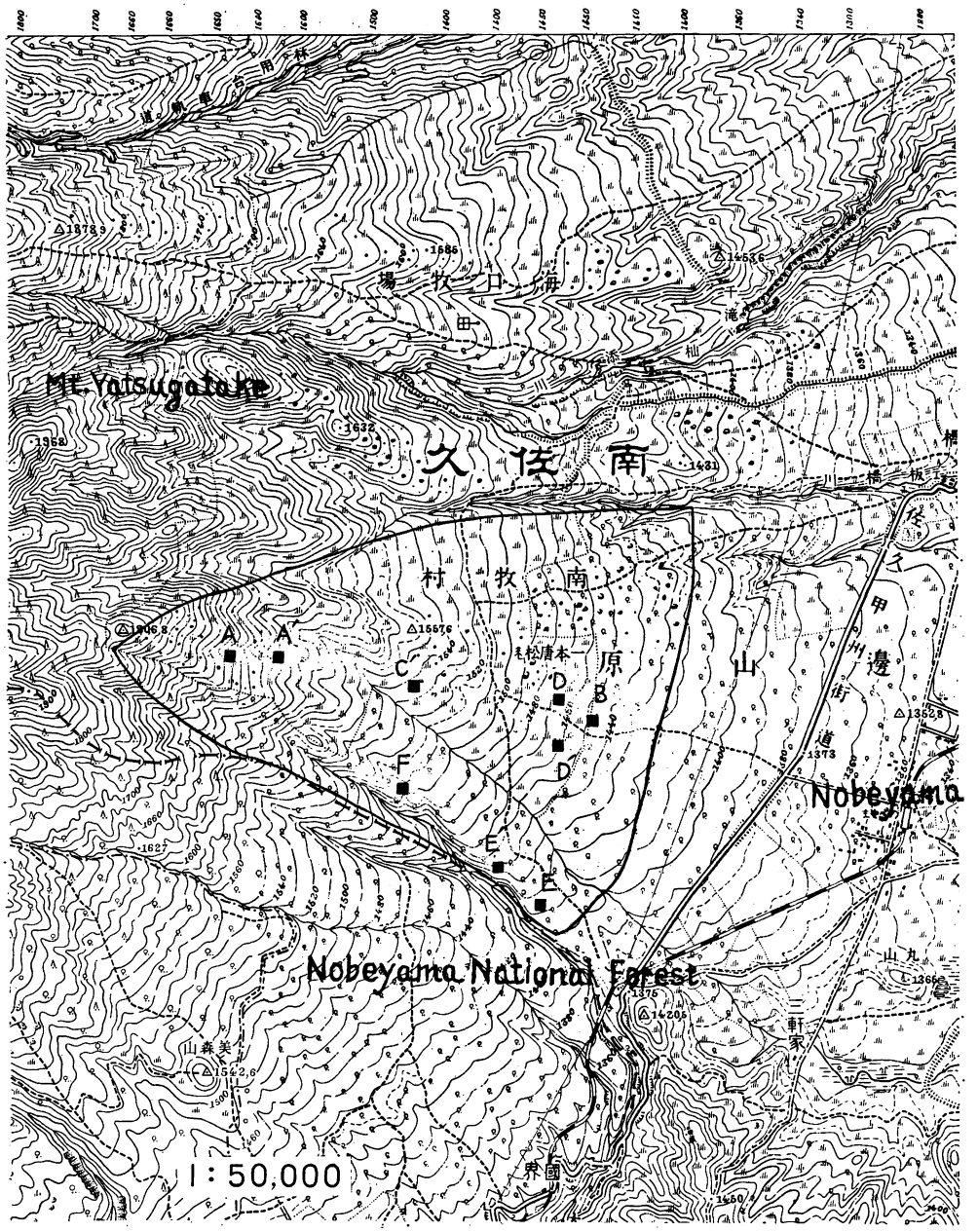
Recently, KAMEI (1961)[23] has recorded its existence on *Larix gmelinii* GORD. in Hokkaido, the northern part of Japan.

It is true that there are large areas in the district where the disease is not found, but it is probable that a more intensive search would reveal the disease in many parts of the areas which are shown on the map as free.

Damage of the disease

Since the first discovery of the larch canker parasite in 1957, the same fungus had been collected in many places on the Japanese larch branches only, and accordingly it had been considered as a minor trouble to this tree species in Japan. In 1961, however, serious damage

from stem canker caused by the fungus was found in larch plantations in the Nobeyama National Forest, Mt. Yatsugatake, Nagano Prefecture, and, in the following year, a heavy loss from the same disease attracted the authors' attention in the Minamiyama National Forest, Mt. Fuji, Shizuoka Prefecture. In these severely infected plantations practically every tree may have several cankers scattered along the trunk, making the stand worthless. Cankers also occur



Text-fig. 3. Map of the Nobeyama National Forest (the area bounded by the solid line) and the experimental plots in the Forest, Mt. Yatsugatake, Nagano Prefecture.

on branches (Plates 1～2).

Severe stem and branch cankers appeared also in natural larch stands near Mt. Asama, Nagano Prefecture, at Mts. Yatsugatake and Fuji. The destructive damage of the disease occurred generally at an elevation of 1,400 to 1,700 meters above sea level.

Analyses of the damage in the Nobeyama National Forest

During the disease survey in the Nobeyama National Forest in 1961, the authors observed extensively the destructive stem cankers, as well as branch cankers and die-backs, in larch stands, and they undertook an extensive research (KOBAYASHI & UOZUMI 1962[26]). The growth of larch stands (planted in 1913 to 1916) in this forest is not good, and its cause is considered to be largely due to adverse soil and climatic factors. Several experimental plots were selected in the forest and research on the disease was carried out in these plots (Text-fig. 2). The general view and damage of the disease in every experimental plot are summarized in Table 1.

Table 1. General view and damage of the canker in the experimental plots in the Nobeyama National Forest, Mt. Yatsugatake.

Experimental plot	A	A′	C′*	F	D′	D	B	E′	E
Altitude above sea level (m)	1,700	1,620	1,560	1,500	1,470	1,470	1,450	1,430	1,420
Age of stand	47	48	48	48	47	47	45	47	47
Number of trees per ha	2,100	1,221	761	865	1,445	1,347	1,440	563	945
Volume per ha (m^3)	93.2	48.3	77.0	305.1	155.6	143.2	105.3	139.6	256.2
Stem canker									
Number of trees tested	45	32	47	36	35	36	42	27	36
Number of non-stem cankered trees	21	9	30	20	28	27	38	22	33
Number of cankered trees	24	23	17	16	7	9	4	5	3
Percentage of stem canker infection (%)	53	72	36	44	20	25	10	19	8
Degree of branch canker infection	+++	+++	+++	+++	++	++	+	+	+

Note : * Mixed with many deciduous trees.

As shown in Table 1, the damage is generally severe from about 1,500 to about 1,700 meters in altitude. Forty to seventy per cent of larches planted at an elevation of 1,500 to 1,700 meters were damaged, in contrast to only 8 to 25 per cent in the stands grown at an altitude of about 1,400 meters.

Table 2 indicates that growth increment of the cankered trees in certain plots (A, C′, D, B and E) is clearly smaller than that of the non-cankered trees.

Number of stem cankers on the individual diseased trees in each plot were counted, and the results obtained are given in Table 3. About seventy-five per cent of the diseased trees had individually one to two cankers, and a few trees had more than seven cankers.

From Table 4, it is clear that more than eighty per cent of all stem cankers in the stands

Table 2. Growth of the stem cankered trees, comparing with the non-cankered ones. The Nobeyama National Forest, Mt. Yatsugatake.

Experimental plot	A	A′	C′	F	D′	D	B	E′	E
Height									
Non-stem cankered trees (h_1) (m)	9.64	7.70	10.92	19.65	11.72	12.86	10.87	15.02	17.16
Stem cankered trees(h_2) (m)	8.71	7.16	10.09	19.26	11.96	11.87	9.65	14.84	16.17
$h_2/h_1 \times 100$ (%)	90.4	93.0	92.4	98.0	102.0	92.3	88.8	98.8	94.2
Diameter b. h.									
Non-stem cankered trees (d_1) (cm)	11.3	11.1	15.1	15.1	14.0	14.2	12.8	19.5	20.1
Stem cankered trees(d_2)(cm)	9.9	11.0	13.4	13.4	13.8	14.2	10.3	20.8	16.4
$d_2/d_1 \times 100$ (%)	87.6	99.1	88.7	88.7	98.6	87.3	80.5	106.7	81.6

Table 3. Number of stem cankers on individual diseased trees. The Nobeyama National Forest, Mt. Yatsugatake.

Experimental plot		A	A′	C′	F	D′	D	B	E′	E	Total
Number of cankers on individual trees	1	8	8	5	11	5	7	4	2	3	53
	2	5	10	2	2	1	1		1		22
	3	4	3	3	3	1	1		2		17
	4			2							2
	5		1	1							2
	6	3									3
	7										
	8										
	9			1							1
	10		1								1
Total number of diseased trees		20	23	14	16	7	9	4	5	3	101
Total number of stem cankers		48	52	40	24	10	12	4	10	3	203
Averaged number of stem cankers per one diseased tree		2.4	2.3	2.9	1.5	1.4	1.3	1.0	2.0	1.0	2.0

Table 4. Height producing stem cankers on diseased trees. The Nobeyama National Forest, Mt. Yatsugatake.

Experimental plot		A	A′	C′	F	D′	D	B	E′	E	Total number of cankers	Ratio (%)
Height from ground level (m)	0～ 2	4	28	13	1		2		7		55	29
	2～ 4	3	5	3	3	1		1			16	8
	4～ 6	21	14	11	1	5	4		2		58	31
	6～ 8	14	3	7	2	2					28	15
	8～10	3		1	1		1	3			9	5
	10～12			2	1	1	5			3	12	6
	12～14				4						4	2
	14～16				6				1		7	4
	16～18				1						1	0.5
Total number of cankers		45	50	37	20	9	12	4	10	3	190	

Table 5. Age of stem in which the canker initiated. The Nobeyama National Forest, Mt. Yatsugatake.

Experimental plot		A	A′	C′	F	D′	D	B	E′	E	Total number of cankers	Ratio (%)
Age of stem infected (year-old)	1～10	7	4	2	1		2	1	2	2	21	14
	11～20	23	22	18	15	8	9	1	2	1	99	64
	21～30	1	7	10	2	1	1	1	2		25	16
	31～40		6	1					3		10	6

Table 6. Enlargement of cankers on stems. The Nobeyama National Forest, Mt. Yatsugatake.

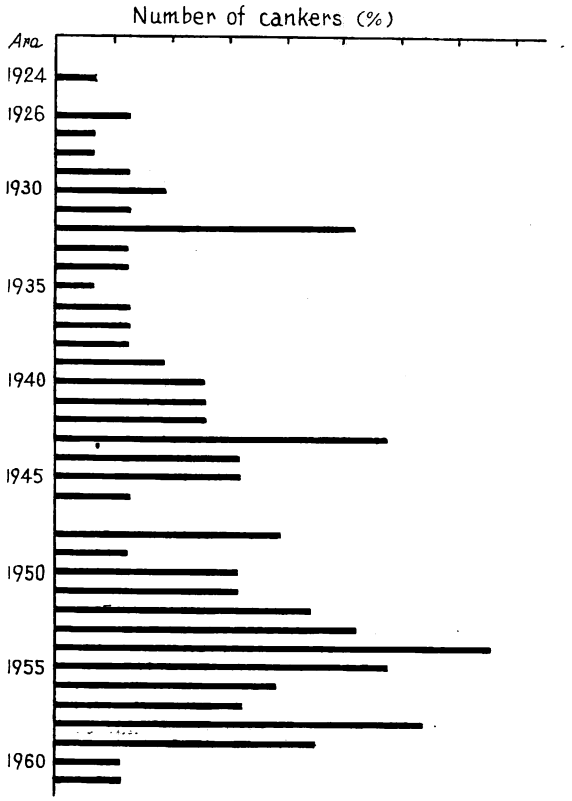
Experimental plot	A	A′	C′	F	D′	D	B	E′	E	Total	Ratio (%)
From diseased branch and twig	20	33	27	17	8	10		10	2	127	85
From bud or "dwarf shoot"	7	4	2	2	1	2	3		1	22	15

are within 8 meters above the ground level, though, of course, the authors had no knowledge of the killed and removed trees there in their younger stage.

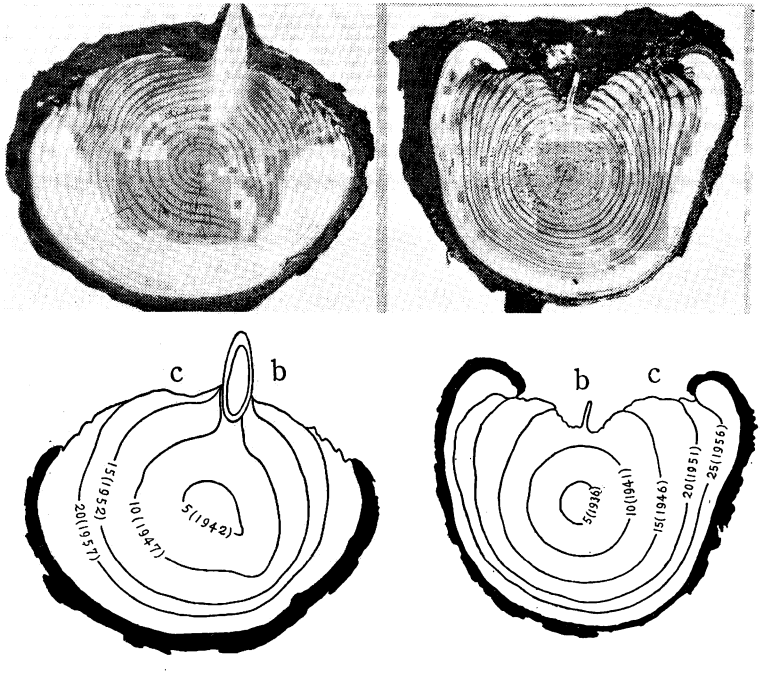
The cankers were shown through transversely and the surfaces planed and smoothed until the section was reached where the cambium had first been killed (Plate 3).

Of those in Table 5, about seventy per cent of the cankers initiated before the stem reached the age of 20 years; susceptibility to canker decreases with increasing age, and infection in trees between 30 and 40 years old is comparatively rare.

Table 6 indicates that main stem cankers occur very frequently at the base of branches which have died, and another way in which the causal fungus may gain admission to living stems without previous wounding, is through dormant buds or dwarf shoots which have died (Plate 3 A, B; Text-figs. 5～7).



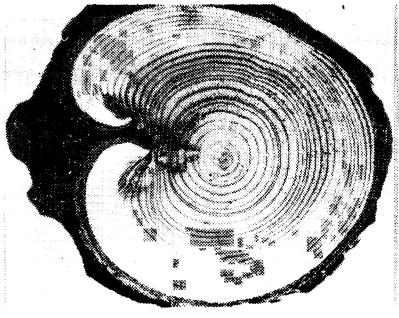
Text-fig. 4. Number of stem cankers initiated in chronological order.

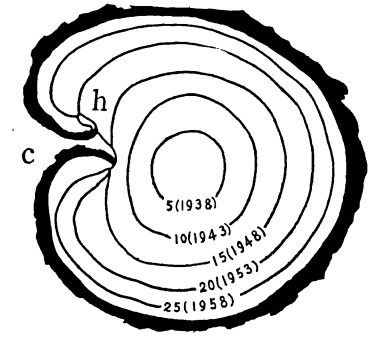


Text-fig. 5. Transverse section through the canker showing the origin from the branch. × 1
Age of section of tree in which canker occurred ……24
Age when canker began ……17(1954)
Age of branch when died …… 7(1935)
c, cankered part; b, dead branch stub.

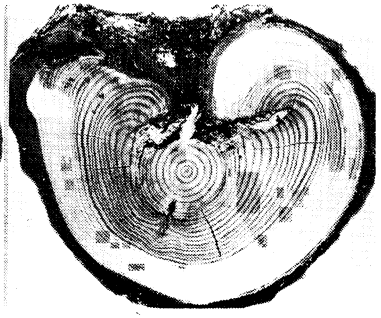
Text-fig. 6. Transverse section through the canker showing the origin from the branch. Subsequently healed on both sides. × 0.8
Age of section of tree in which canker occurred ……30
Age when canker began ……12(1943)
Age when pronounced calli developed…… 27(1958)
Age of branch when died …… 1(1943)
c, cankered pert; b, dead branch stub.

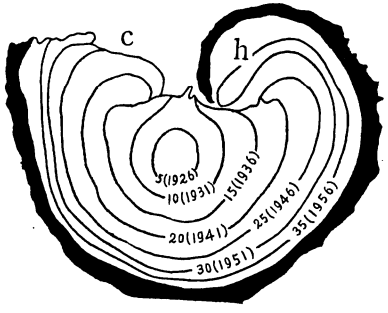
Text-fig. 7. Longitudinal section through the canker showing the base of the small branch through which infection occurred. × 0.5
Age of section of tree in which canker occurred ……49
Age when canker began ……21(1933)
Age of branch when died ……22(1934)
c, cankered part; b, dead branch stub.



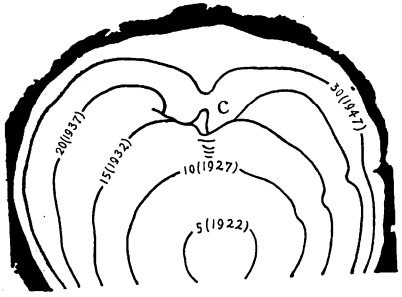


Text-fig. 8. Transverse section through the canker which is healing on both sides. × 0.6
Age of section of tree in which canker occurred ……28
Age when canker began ……12(1945)
Age when pronounced healing calli developed ……24(1957)
c, cankered part ; h, healing callus.

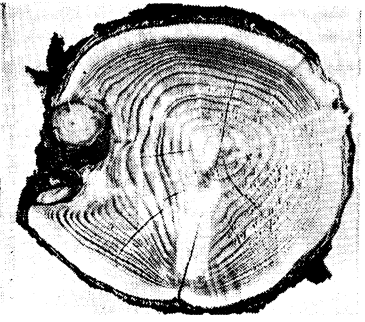


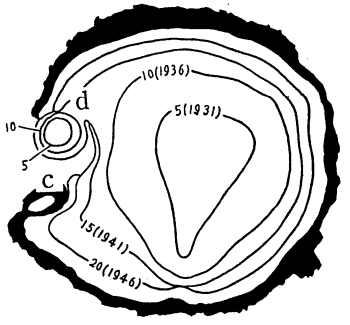


Text-fig. 9. Transverse section through the canker which is healing on one side. × 0.6
Age of section of tree in which canker occurred ……40
Age when canker began ……11(1932)
Age when pronounced healing callus developed……15(1936)
c, cankered part ; h, healing callus.



Text-fig. 10. Transverse section through the canker which was completely healed over. × 0.6
Age of section of tree in which canker occurred ……44
Age when canker began ……11(1928)
Age when canker healed over ……30(1947)
c, trace of canker.





Text-fig. 11. Transverse section through the canker occurred on a part of the lateral branch which replaced the young main stem killed by the girdling. ×0.7
Age of section of tree in which canker occurred ……35
Age when canker began ……19(1945)
Age of young main stem killed by girdling ……17(1943)
c, cankered part ; d, young main stem killed by girdling.

The inspection of the transvese sections of 155 stem cankers taken at random shows that there were three peaks of severe infection in the past, i. e. in 1932, 1943 and 1954 (Text-fig. 4). This probably means that in certain years the meteorological conditions favored the formation of cankers.

Anatomical observations on several stem cankers can be seen in Text-figs. 5~11.

Cankers on the main stem almost invariably appear at the base of a lateral branch which has died back, or near a dormant bud (Text-figs. 5~7). At first they are simply a swelling but later become open wounds forming an amphitheatre floored with dead wood surrounded by raised tiers of swollen tissue. When a main stem is attacked in a portion which is more than four or five years old, the annual growth in girth is usually sufficient to confine the canker to one side (Text-figs. 5, 6 and 9).

The cankers on the main stem are perennial and generally enlarge every year, accompanied with or rarely without the callus formation at the margin of the diseased region (Text-figs. 6, 8 and 9). A few of the canker affected parts apparently recover from the canker (Text-fig. 10).

Some of the cankers develop on a part of the lateral branch which replaced the young main stem killed by a result of the girdling (Text-fig. 11).

Causal fungus of the disease

Morphology

Apothecia scattered or grouped, erumpent, short stalked, at first globular, closed, opening in a rounded form and expanding under humid conditions to a more or less flat disk with a relatively thin chalky-white rim. Exciple white, of texture intricate, densely covered with hairs. Disk orange-yellow, 2~4 mm, mostly 2 mm in diameter (Plate 5 A).

Asci clavate, apex obtusely rounded, 100 ~ 145 × 9~12 μ. Ascospores eight, obliquely uniseriate, smooth, hyaline, continuous, commonly uniseptate upon germination, elongate-elliptic or elliptic-oblong, occasionally fusiform, obtuse or acute extremities, or acute at one end, 14~23 × 6~10 μ. Paraphyses exceeding the asci, flexuous-filiform, septate, somewhat swollen at tips, 130~190 × 2~5 μ (Plate 5 B; Text-fig. 12 A, B, C, D).

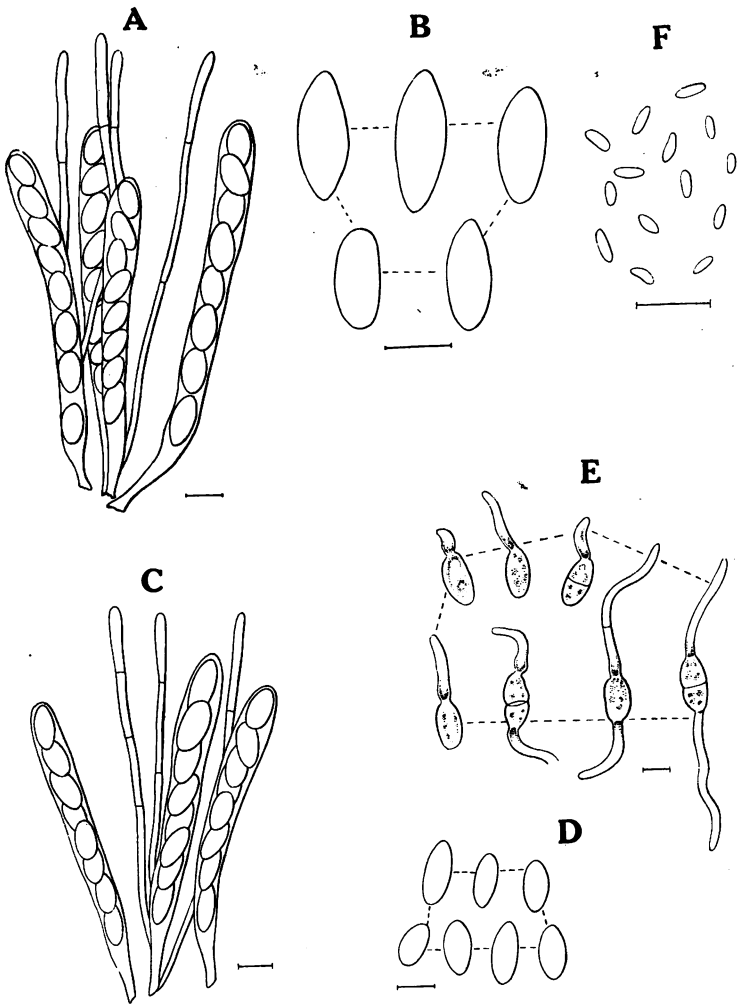
Imperfect (spermogonial) stage consisting of erumpent, fleshy, waxy whitish stromata, microconidia (spermatia) continuous, hyaline, elliptic oblong or allantoid, 3~5 × 1~1.4 μ. Germination not observed (Text-fig. 12 F).

Results of the measurement for the dimension of the fungus collected on Japanese larch are presented in Table 7.

Table 7. Dimension of the fungus on *Larix leptolepis* in Japan (μ).

Locality	Date of collection	Part of the host	Ascus	Ascospore	Paraphysis	Remarks
Mt. Yatsugatake, Nagano Pref.	Aug. 31, 1957	Branch	119~142 ×9~12	16~21×7~10	130~174×2~4	Isolate Dw-1
Nobeyama National Forest, Nagano Pref.	Oct. 20, 1961	Branch	121~146 ×10~13	16~23×7~9	150~190×3	Isolate Dw-2
		Trunk	124~143 ×10~11	17~20×7~9	150~180×3~5	
Minamiyama National Forest, Shizuoka Pref.	Sept. 8, 1962	Branch	120~145 ×10~13	16~23×7~9	150~190×3~5	Isolate Dw-3

As shown in Table 7, there are no remarkable differences in dimension of the fungus among all the materials collected by the authors.



Text-fig. 12. The canker fungus of Japan (|——| =10 μ).
A～B : The fungus collected at Mt. Yatsugatake, Nagano Prefecture, August 31, 1957.
C～F : The fungus collected in the Minamiyama National Forest, Shizuoka Prefecture, September 8, 1962.
A, C : Asci and paraphyses ; B, D : Ascospores ; E : Germinating ascospores ; F : Microconidia (spermatia).

Germination of ascospores

Fresh ascospores began to germinate in a few hours and formed usually a median septum in an initial step in germination (Plate 5 D, E ; Text-fig. 12, E). Germinated ascospore, then, produced profusely-branched, flexuous hyphae, tending to be straight (Plate 5, C).

1. Effect of temperatures upon germination

Methods : On the inner surface of the upper lid of a Petri dish containing 2 per cent dextrose agar, mature apothecia were attached quickly by means of hard vaseline in such way that the hymenial layer was hanged on the agar plate when the lid was put in position. The Petri dish in this condition was kept at 0° C. for about 24 hours. When the ascospores

Table 8. Effect of temperatures upon germination of ascospores.

Locality / Temp. (°C)	Nobeyama, Nagano, Aug. 21 '62		Minamiyama, Shizuoka, Sept. 8 '62	
	Germination percentage (%)	Max. length of germ tube (μ)	Germination percentage (%)	Max. length of germ tube (μ)
Experiment-1.				
0	45	50	23	20
10	46	60	74	100
15	95	170	88	230
20	94	270	93	270
25	87	170	90	100
30	0	—	0	—
Experiment-2.				
0	68	100	29	30
10	82	180	55	100
15	91	280	64	180
20	90	300	74	190
25	89	180	80	150
30	0.8	20	9	30

Note : While ascospores were kept at 0°C for 24 hours, the initial stage of germination occurred in a few spores, and, in this table, only the spores having longer germ-tubes than the length of spores were counted as "germinating spores".

Table 9. Effect of relative humidities upon germination of ascospores.

Relative humidity (%)	Salt in over-saturated aqueous solution	Condition tested	Experiment no.	Material collected at Nobeyama, Nagano		Material collected at Minamiyama, Shizuoka	
				Germination percentage (%)	Max. length of germ-tube (μ)	Germination percentage (%)	Max. length of germ-tube (μ)
100	Distilled water	Spores in drop*	I	81	120	75	70
			II	70	100	71	100
100	Distilled water	Spores dried	I	—	—	—	—
			II	69	120	41	80
98	K_2SO_4	Spores dried	I	29	50	3	30
			II	31	80	10	20
94	KNO_3	Spores dried	I	24	20	0	—
			II	6	30	7	30
92	K_2HPO_4	Spores dried	I	0	—	0	—
			II	0	—	13	50
87	KCl	Spores dried	I	0	—	0	—
			II	0	—	0	—

Note : * A drop of spore suspension was not dried.

had adequately fallen from the hymenium upon the surface of the agar in the dish, the apothecia were removed out, and then all ascospores were incubated at different temperatures.

Materials and results : Apothecia used in the experiments were collected at two localities, and results obtained at the end of four days are given in Table 8.

It is seen from Table 8 that garmination of the ascospores occurs at the temperatures ranging from 0° to 30° C with an optimum at about 20° C, and there are no differences in germination between the two materials collected at different localities.

2. Effect of relative humidities upon germination

Methods : Small drops of ascospore suspension were placed on clean slide-glasses. These slides were placed in desiccators (155 mm in diameter), in which the air had been controlled to the desirable constant relative humidities by using several salts in over-saturated solution. The desiccators were kept at 20° C for 24 hours, and then germination of the spores in different air-humidities was tested (ITO & HOSAKA 1952[20]).

Materials and results : Materials used in the experiments and results obtained at the end of 24 hours are summarized in Table 9.

From Table 9 it is indicated that a saturated atmosphere is most favorable for germination of the ascospores, and the spores germinate in 98 to 92 per cent humidities, while those kept at 92 per cent humidity and below show no signs of germination.

Pathogenicity

In order to make clear the pathogenicity of the fungus, several inoculation experiments were carried out on both European and Japanese larches during 1959 to 1962 in Tokyo, where frost was not severe and the chances of frost damage were therefore negligible.

The inocula used consisted of pure cultures produced from single ascospores of apothecia collected in the Yatsugatake infection area. The one (Dw-1) was isolated in August, 1957 and the other (Dw-2) done in October, 1961 (c. f. Table 7). Because of the paucity of fresh ascospores, spore inoculum was not available at this time in sufficient quantity for the investigation.

Experiment-1. Inoculatian with Dw-1 isolate (1).

Inoculations were performed on 2-year-old wood of 4-year-old saplings of both European and Japanese larches on June, 1959. The surface of the barks or the buds was carefully treated with 80 per cent alcohol, sterilized with 0.1 per cent mercuric chloride and washed several times with sterilized distilled water, then a small slit was incised with a sterilized scalpel on the barks or the buds. A burning hot scalpel was used in the case of making burned wounds. Pieces of agar bearing mycelium from pure culture of the fungus were placed on the spots to be inoculated. The parts inoculated were covered with sterilized absorbent cotton soaked in sterilized water and held in place by a band of cellophane-tape. Checks were made in a similar manner except in this instance only sterilized agar was used. During the experimental period sterilized water was supplied to the inoculated part once a week.

As shown in Table 10, all of the results obtained at the end of about a half year after the inoculation are negative.

Experiment-2. Inoculation with Dw-1 isolate (2).

In the middle of December, 1959, the healthy stems of both European and Japanese larches (4-year-old) were inoculated with the fungus by the same procedure as the previous experiment. In this experiment, however, wounds were made by cork-borer, 7 mm in

Table 10. Inoculation experiment with Dw-1 isolate of the fungus to European and Japanese larches, made on June, 1959.

Tree species	Tree no.	Inoculation or check	Treatment before inoculation	Place inoculated	Lesion formation
Larix decidua	1～2	Inoculation	Burned-wounded	Stem	—
	3～4		do.	Bud on stem	—
	5～6		Unwounded	Stem	—
	7～8		do.	Bud on stem	—
	9	Check	Burned-wounded	Stem	—
	10		do.	Bud on stem	—
	11		Unwounded	Stem	—
	12		do.	Bud on stem	—
L. leptolepis	1～2	Inoculation	Burned-wounded	Stem	—
	3～4		do.	Bud on stem	—
	5～6		Unwounded	Stem	—
	7～8		do.	Bud on stem	—
	9	Check	Burned-wounded	Stem	—
	10		do.	Bud on stem	—
	11		Unwounded	Stem	—
	12		do.	Bud on stem	—

Table 11. Inoculation experiment with Dw-1 isolate of the fungus to European and Japanese larches, made on December, 1959.

Tree species	Tree no.	Inoculation or check	Treatment before inoculation	Result	
				Size of lesion (mm)	Fruit-body
Larix decidua	1～ 6	Inoculation	Burned-wounded	15～80×6～15	+
	7～12		Unwounded	—	—
	13～14	Check	Burned-wounded	—	—
	15～16		Unwounded	—	—
L. leptolepis	1～ 6	Inoculation	Burned-wounded	10～18×6～10	+
	7～12		Unwounded	—	—
	13～14	Check	Burned-wounded	—	—
	15～16		Unwounded	—	—

diameter.

Table 11, showing the results obtained on June 3, 1960, indicates that the fungus is clearly pathogenic to the larches and produces many spermogonial (microconidial) stromata on the lesions induced (Plate 6 A, B, C, D ; Plate 7 A, B).

Experiment-3. Inoculation with Dw-1 isolate (3).

On December 24, 1960, the inoculation with the fungus was made on 2-year-old wood of the 5-year-old larches. Inoculation technique used in this experiment is the same as in Experiment-2. Results obtained on June 27, 1961 are summarized in Table 12. It is clear, from Table 12, that the fungus produces distinct lesions and spermogonial stromata on both

Table 12. Inoculation experiment with Dw-1 isolate of the fungus to European and Japanese larches, made on December, 1960.

Tree species	Tree no.	Inoculation or check	Treatment before inoculation	Result	
				Lesion	Fruit-body
Larix decidua	1～2	Inoculation	Burned wounded	+	+
	3～4		Wounded	±	−
	5～6		Unwounded	−	−
	7	Check	Burned wounded	−	−
	8		Wounded	−	−
	9		Unwounded	−	−
L. leptolepis	1～3	Inoculation	Burned wounded	+	+
	4～6		Wounded	+	+
	7～8		Unwounded	−	−
	9～10	Check	Burned wounded	−	−
	11～12		Wounded	−	−
	13～14		Unwounded	−	−

Table 13. Inoculation experiment with Dw-2 isolate of the fungus to European and Japanese larches, made on December, 1961.

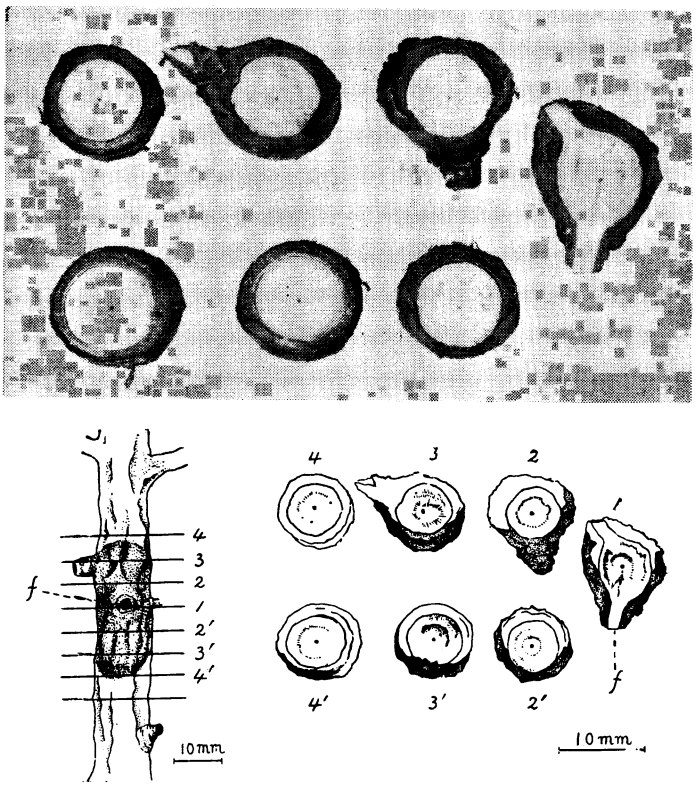
Tree species	Tree no.	Inoculation or check	Treatment before inoculation	Result	
				Lesion	Fruit-body
Larix decidua	1～2	Inoculation	Burned wounded	+	−
	3～4		Wounded	+	+
	5	Check	Burned wounded	−	−
	6		Wounded	−	−
L. leptolepis	1～2	Inoculation	Burned wounded	+	+
	3～4		Wounded	+	+
	5	Check	Burned wounded	−	−
	6		Wounded	−	−

European and Japanese larches, and it is virulent especially in the case of burned-wounded inoculation.

Experiment-4. Inoculation with Dw-2 isolate.

On December 20, 1961, stems of the 4-year-old European and Japanese larches were inoculated with the fungus which had been isolated and cultured shortly before. By the method noted already, the inocula were placed on burned or unburned wounds on 3-year-old wood of the trees. From Table 13 showing the results of the experiment obtained on April 20, 1962, it is indicated that the fungus causes canker lesions starting from both burned and unburned wounds, and produces numerous spermogonial stromata on the lesion (Plate 6 E ; Plate 7 C, D, E).

An example of anatomical view in the lesion made by artificial inoculation is shown in Text-fig. 13.



Text-fig. 13. Transverse section through the lesion of Japanese larch produced by artificial inoculation with the fungus (Dw-2) (December 20, 1961～April 20, 1962).
f: Inoculated part; dotted portions, diseased parts judged by naked eye.

When first inoculated in June, 1959, the trees failed to be infected, because, during the summer, all of the wounds inoculated healed over (Experiment-1). On the trees inoculated by wounding in winter, however, infection was successful, and many spermogonial stromata were produced on the lesions (Experiments 2～4). In pathogenicity there have heen observed no remarkable differences between the two isolates used in the investigation.

Taxonomy

Literature on the European larch canker has become much confused by the variety of names which have been applied to the causal organism.

HILEY (1919)[17] pointed out that in 1859 BERKELEY was the first to ascribe the cause of the canker to a fungus. BERKELY treated it under the form of *Peziza calycina*. Seven years later, WILLKOMM (1866) ascribed the cause to a Discomycete which he profusely illustrated but incorrectly called *Corticium amorphum* (PERS.) FRIES. HOFFMAN (1868) corrected WILLKOMM's error and adopted the same name for the fungus as BERKELEY.

HARTIG (1880)[16] likewise recognized WILLKOMM's mistake, but in correcting the error he made a new name, *Peziza willkommii* HARTIG, for he believed the larch canker parasite to be a new species.

In 1889 SACCARDO[36] placed HARTIG's new fungus as a synonym of *Dasyscypha calycina* FUCKEL. REHM in 1871 issued a specimen, *Dasyscypha calycina* (SCHUM.) FUCKEL, collected

by himself. REHM (1871) referred to this collection and applied the combination, *Dasyscypha willkommii* (HARTIG) REHM. In 1896 REHM published the first complete description of *D. willkommii* (HARTIG) REHM with illustrations of a large-spore form with filamentous paraphyses unswollen at the tip as figured by HARTIG (1880)[16].

Dasyscypha cylicina sensu FUCKEL has filamentous paraphyses, while the other species named have lanceolate paraphyses. *Lachnum* KARSTEN (1971) is based on characters similar to those of *Dasyscypha*, but was limited to include only species with lanceolate paraphyses. Species with filamentous paraphyses, including *D. calycina*, were removed to the genus *Helotium* FR.

BOUDIER (1885) placed stalked species with lanceolate paraphyses in *Dasyscypha*, ignoring *Lachnum*. He created the genus *Trichoscypha* for species with filamentous paraphyses, with a single species, *T. calycina* (SCHUM. ex FR.) BOUD. REHM (1887～1896) accepted *Lachnum* for species with lanceolate paraphyses, placing related species with fiiliform paraphyses in *Dasyscypha*. NANNFELDT (1932)[33] pointed out that *Trichoscypha* BOUD. was a homonym of the older *Trichoscypha* HOOKER, and he substituted his new name *Trichoscyphella*. He revived *Lachnum* KARST. for species with an exciple of "textura prismatica" and usually lanceolate paraphyses. HAHN and AYERS (1934)[12] followed REHM and accepted *Dasyscypha* as the genus name. DENNIS (1949), however, followed NANNFELDT in accepting *Trichoscyphella*, but used *Dasyscypha* in place of NANNFELDT's *Lachnum*. MANNERS (1953)[30] accepted *Trichoscyphella* as the generic name of the larch canker fungus and related species.

The larch canker fungus has been generally called *Dasyscypha calycina* (SCHUM.) FUCK. in Great Britain and *D. willkommii* (HARTIG) REHM on the European Continent and in the United States of America. HILEY (1919)[17] and other European workers held the opinion that the European larch canker organism was a heterogenous species, comprised of a number of intermediate forms between the parasitic and saprophytic types. They regarded these two species as members of a polymorphic species, and recognized that the forms differed physiologically, but not morphologically.

In the exhaustive studies on Dasyscyphae on conifers, HAHN and AYERS (1934)[12] concluded that *D. calycina* FUCKEL (nec. *Peziza calycina* SCHUM.) was distinct morphologically and physiologically from *D. willkommii* (HARTIG) REHM, and should be recognized as separate species. It was the opinion of HAHN and AYERS (1934[12], 1943[14]) that the organism causing European larch canker should be called *D. willkommii* (HARTIG) REHM, and not *D. calycina* (SCHUM.) FUCKEL which could not infect healthy larch and showed saprophytic nature. They (1934)[12], furthermore, described two new species of the genus *Dasyscypha*, *D. oblongospora* and *D. occidentalis*, inhabiting *Larix* in the United States of America.

SEAVER (1951)[37] used *Lachnella* established by FIRES (1835) as the genus name of the European larch canker fungus and allied species. He adopted *Lachnella willkommii* HARTIG for the former, and newly named *L. hahniana* SEAVER for the fungus known as *Dasyscypha calynina*.

In the taxonomic study of the larch canker parasite and related fungi, MANNERS (1953)[30] an English worker, reported that his findings confirmed those of HAHN and AYERS (1934[12] 1943[14]) and *Trichoscyphella willkommii* (HARTIG) NANNF. should be accepted as the name of the parasite and the new combination *T. hahniana* (SEAVER) MANNERS was proposed for the related saprophyte usually known as *Dasyscypha calycina*. He recognized also that *Trichoscyphella willkommii* and *T. hahniana* were shown to be distinct both morphologically and pathologically. Recently, DENNIS (1960)[8] followed MANNERS' opinion.

At about the same time as MANNERS (1953)[30], ROBAK's (1952[34], 1953[35]) studies on the larch canker fungus (*Dasyscypha willkommii*), based on material from Norway, led to the conclusion that the saprophytic ("calycina") and parasitic ("willkommii") races were morphologically and culturally distinct from each other. He considered that SEAVER's (1951)[37] *Lachnella* (*Dasyscypha*) *hahniana* for the saprophytic fungus should be denominated *D. willkommii* var. *hahniana*.

The fungus that has been hitherto collected from the cankers of living Japanese larch in Japan should be morphologically considered as a single species (Table 7, Text-fig. 12).

In comparison with the four fungi of *Larix* studied by HAHN and AYERS (1934)[12], the morphological characteristics of the authors' fungus are similar to *Dasyscypha willkommii* in ascospore dimension, to *D. willkommii* and *D. calycina* in paraphysis length, and to *D. willkommii* and *D. occidentalis* in mode of ascospore germination (Plate 5,C). In shape of paraphysis the authors' fungus is rather similar to *D. willkommii* and *D. occidentalis*, and not to *D. calycina* (Text-fig. 12).

As determinative characteristics of *Trichoscyphella willkommii* (*Dasyscypha willkommii*) and *T. hahniana* (*D. calycina*), MANNERS (1953)[30] pointed out the color of fresh apothecia and the presence or absence of submoniliform paraphyses. According to MANNERS' opinion, the authors' fungus is very similar to *T. willkommii* in the color of fresh apothecia, and is intermediate between *T. willkommii* and *T. hahniana* in the shape of paraphyses, which are usually very slightly swollen at the tips.

In pathogenicity, as noted already, HAHN and AYERS (1934[12], 1943[14]) reported that *Dasyscypha willkommii* is only the species parasitic to larch and the other three fungi containing *D. calycina* are wholly saprophytic. MANNERS' (1953)[30] inoculation experiments showed that *Trichoscyphella willkommii* could cause cankers, but not *T. hahniana*, excepting one strain which was in certain respects intermediate between the two species. The authors' fungus was usually found on active cankers and caused the disease by artificial inoculations.

From the facts mentioned above, the fungus occurring on the cankered larch in Japan may be identified as *Trichoscyphella willkommii* (HARTIG) NANNF. [*Dasyscypha willkommii* (HARTIG) REHM].

Discussion and conclusion

The home of the larch canker parasite which is widely distributed throughout the European Continent and Great Britain has been considered to be the Alps. In the first decade of the twentieth century, the fungus was introduced into the United States of America by nursery stocks imported from Great Britain (SPAULDING & SIGGERS 1927)[38].

In Japan, the first collection of the disease on Japanese larch (*Larix leptolepis*) was made at Mt. Yatsugatake in 1957 (ITO & ZINNO 1957)[21]. Since that time, further surveys of the regions around Mt. Yatsugatake, Mt. Fuji and Mt. Asama showed a more extensive distribution of the disease in the central part of the Main Island of this country. The disease affects severely larch trees not only in plantations but also in natural forests (ITO 1961[22], KOBAYASHI & UOZUMI 1962[26]).

From the results of the authors' morphological and parasitological studies, the causal organism of Japanese larch canker may be identical with *Trichoscyphella willkommii* (HARTIG) NANNF. [*Dasyscypha willkommii* (HARTIG) REHM] occurring on European larch (*Larix decidua*).

Considering the fact that the larch canker fungus is commonly distributed in the natural stands far distant from plantations, it is probably native to Japan, and not introduced from abroad.

Several European and American workers (HILEY 1919[17], HOPP 1957[18], BOYCE 1950[2], GREMMEN et *al.* 1961[10], etc.) said that Japanese larch is almost generally very resistant or immune to the canker. As a cause of high resistance of Japanese larch to the canker, HILEY (1919)[17] noted that Japanese larch has a more pronounced faculty for making cork layers than the European larch. While, on the contrary, other many investigators reported that Japanese larch was also susceptible to the disease (BOYCE 1941[1], DAY 1950[6], FOWLER 1953[9], HAHN & AYERS 1934[12], 1936[13], 1943[14], HAHN 1951[15], KHAN 1955[24], LANGNER 1952[28], MANNERS 1955[30], MILLARD 1949[31], VAN VLOTEN 1954[40], ZYCHA 1959[41]). But, generally speaking, it may be true that Japanese larch is more resistant than European larch to the canker. In the mountain region of Japan at high altitude, the severe canker occurs on both naturally reproduced and plantation-grown trees of Japanese larch within its native range, and this indicates probably that Japanese larch may become susceptible to the disease under unfavorable conditions for growth of this tree species. DAY (1950[6], 1955[7]), in Britain, pointed out that the occurrence of the die-back and canker of Japanese larch was accompanied with severe frost injury.

Among European researchers it is generally known that the disease has appeared only when the vigor of the host has been reduced by some environmental factors or complex of factors. In Britain, the European larch is susceptible to frost injury in the spring and again in the autumn. The former period coincides with the renewal of cambial activity and the new cambium starting from the buds and progressively developing downwards is particularly liable to suffer from frost. Frost injury reduces the vitality of the larch (HILEY 1919[17], LANGNER 1936[27], etc.).

From the time of HARTIG (1880)[16] onwards the real cause of the canker has always been a matter of discussion. Some investigators (DAY 1931[4], 1937[5], 1955[7], LATOUR 1950[29], etc.) concluded that frost plays an important part in the formation of larch cankers and the fungus, *Trichoscyphella willkommii* (*Dasyscypha willkommii*) is not the sole cause of them, while, on the contrary, other workers (HARTIG 1880[16], HILEY 1919[17], HAHN & AYERS 1943[14], MANNERS 1953[30]) reported that the fungus induces cankers under frost-free conditions.

HAHN and AYERS (1943)[14] have demonstrated that cankers can be initiated by the absence of frost injury. It may be concluded that, even though larch canker is usually initiated by frost, the presence of the fungus is necessary for the development of cankers to a large size over years.

The authors' inoculation experiments have shown that *Trichoscyphella willkommii* can cause cankers in the absence of frost, but it is not yet clear for how long such cankers may persist and grow in the absence of frost.

European silviculturists (DAY 1937[5], 1955[7], GRIMM 1937[11], MÜNCH 1936[32]) believe that the extensive losses caused in many plantations by this disease have mainly been possible because of unsuitable provenances, and the disease will become of much less importance when these are eliminated. There is a marked correlation between latitude of origin and severity of damage. BOYCE (1961)[3] says that the larch canker in Europe causes negligible damage if suitable races of larches are established on sites that favor vigorous growth. In Britain the best control of canker is said to lie in extending the propagation of the Scottish

larch in suitable localities, just as in Germany a type from the Sudeten border of Bohemia appears to enjoy comparative immunity from the canker injury in certain areas with a similar climate to its original habitat. Having in mind that the severe cankers occur widely in the central part of Japan, the native habitat of Japanese larch, the cause of damage is probably something other than "provenance problem".

Though it is very difficult to determine exactly the soil conditions which favor cankers and the reverse, the edaphic factors seem to be also important. It is believed that soil conditions which favor larch-growing in other respects are generally least conductive to canker, and if the trees are growing vigorously there is a good chance of their remaining free from canker (HILEY 1919[17]). According to MATSUI et *al.* soil conditions, especially physical properties, in the cankered area of the Nobeyama National Forest are unfavorable for larch-growing.

From the foregoing, the authors conclude that the fungus must be the primary cause of the canker and, environmental factors, such as unfavorable climatic and soil conditions, may probably play an important rôle in the canker formation of Japanese larch, which hitherto has been generally believed to be very resistant to the disease. From this it follows that if the tree is more widely planted without regard to selecting site, the damage of the disease might well occur severely elsewhere.

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Explanation of plates

Plate 1

A : A part (Plot A', 1620 m in altitude) of the severely cankered Japanese larch plantation in the Nobeyama National Forest, Mt. Yatsugatake, Nagano Prefecture. Photo. Sept. 25, 1961.

B : Amphitheatre-like canker on the main stem of 48-year-old Japanese larch in the Nobeyama National Forest, Mt. Yatsugatake. × 0.3

C～D : Destructive canker on the main stem of Japanese larch in the Nobeyama National Forest, Mt. Yatsugatake. × 0.5
C, Front view ; D, Side view.

Plate 2

A～B : Canker on the main stem of 45-year-old Japanese larch in the Nobeyama Natioal Forest, Mt. Yatsugatake. × 0.5
A : Front view ; B : Side view.

C : Canker on the main stem of Japanese larch in the Nobeyama National Forest (Plot F, 1550 m in altitude). × 0.5

D : Canker on the main stem of 10-year-old Japanese larch in the Minamiyama National Forest, Mt. Fuji, Shizuoka Prefecture. × 0.5

Plate 3

Transverse sections through the main stem cankers of Japanese larch in the Nobeyama National Forest, Mt. Yatsugatake.

A : Section of the cankered stem at the height of 8 m above the ground, showing the base of the small branch through which infection probably occurred. × 1.5
Age of the stem 17 years, age of canker 5 years.

B : Section of the cankered stem at the height of 7 m above the ground. × 1.3
Age of the stem 16 years, age of the canker 6 years.

C : Section of the cankered stem at the height of 8.1 m above the ground, showing the base of the small branch through which infection probably occurred. ×1.3
Age of the stem 20 years, age of the canker 11 years.

D : Section through the old canker. In this canker, a part of the wood is exposed by falling away of the dead bark. × 0.9
Age of the stem 47 years, age of the canker about 30 years.

E : Section of the canker, containing copious resin. × 0.7
Age of the stem 29 years, age of the canker 11 years.

F : Section through the cankered stem in which double infections had occurred. The

one canker which had been infected 41 years ago (a) was completely healed over, and the other which had been infected 29 years ago has been healing. × 0.6

Plate 4

A : Apothecia of the canker parasite on the canker accompanied by heavy exudation of resin on the branch of 43-year-old Japanese larch, collected at Mt. Yatsugatake, August 31, 1957. × 1.2

B : Apothecia of the canker parasite on the die-backed twig of 6-year-old Japanese larch, collected in the Asagitsuka National Forest, Mt. Fuji, August, 1958. × 1

C : Apothecia of the canker parasite on the branch of 12-year-old Japanese larch, collected in the Minamiyama National Forest, Mt. Fuji, Sept. 8, 1962. × 1.7

D : Ditto. × 1

E : Apothecia of the canker parasite on the die-backed branch of Japanese larch, collected at Mt. Nyugasa, Nagano Prefecture, Aug. 20, 1960. × 2

Plate 5

A : Apothecia of the canker parasite. × 4.5

B : Section of hymenium of the canker parasite. × 400

C : Germinating ascospore of the canker parasite. × 180

D : Initial stage of ascospore germination. × 310

E : Ditto. × 660

Plate 6

Results of the inoculation experiments with the canker parasite to European larch.

A : Lesion produced by burned-wounded inoculation with the fungus (Dw-1). × 0.9 Photo. May 24, 1960.

B : Ditto. Check.

C : Lesion produced by wounded inoculation with the fungus (Dw-1) (right) and check (left). × 1 Photo. April 20, 1960.

D : Enlargement of the lesion shown in D. Numerous spermogonial stromata can be seen. × 1.5

E : Lesion produced by burned-wounded inoculation with the fungus (Dw-2) (right) and check (left). × 1. Photo. April 20, 1962.

Plate 7

Results of the inoculation experiments with the canker parasite to Japanese larch.

A : Lesion produced by burned-wounded inoculation with the fungus (Dw-1). × 1.7 Photo. May 24, 1960.

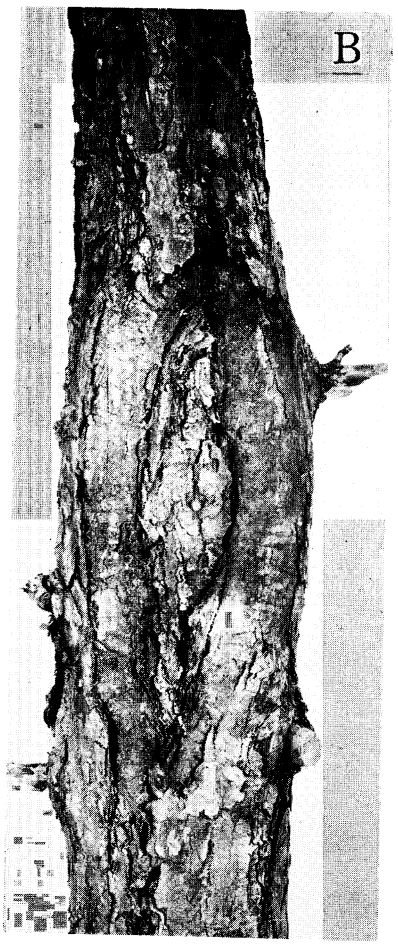
B : Ditto. Check × 0.9

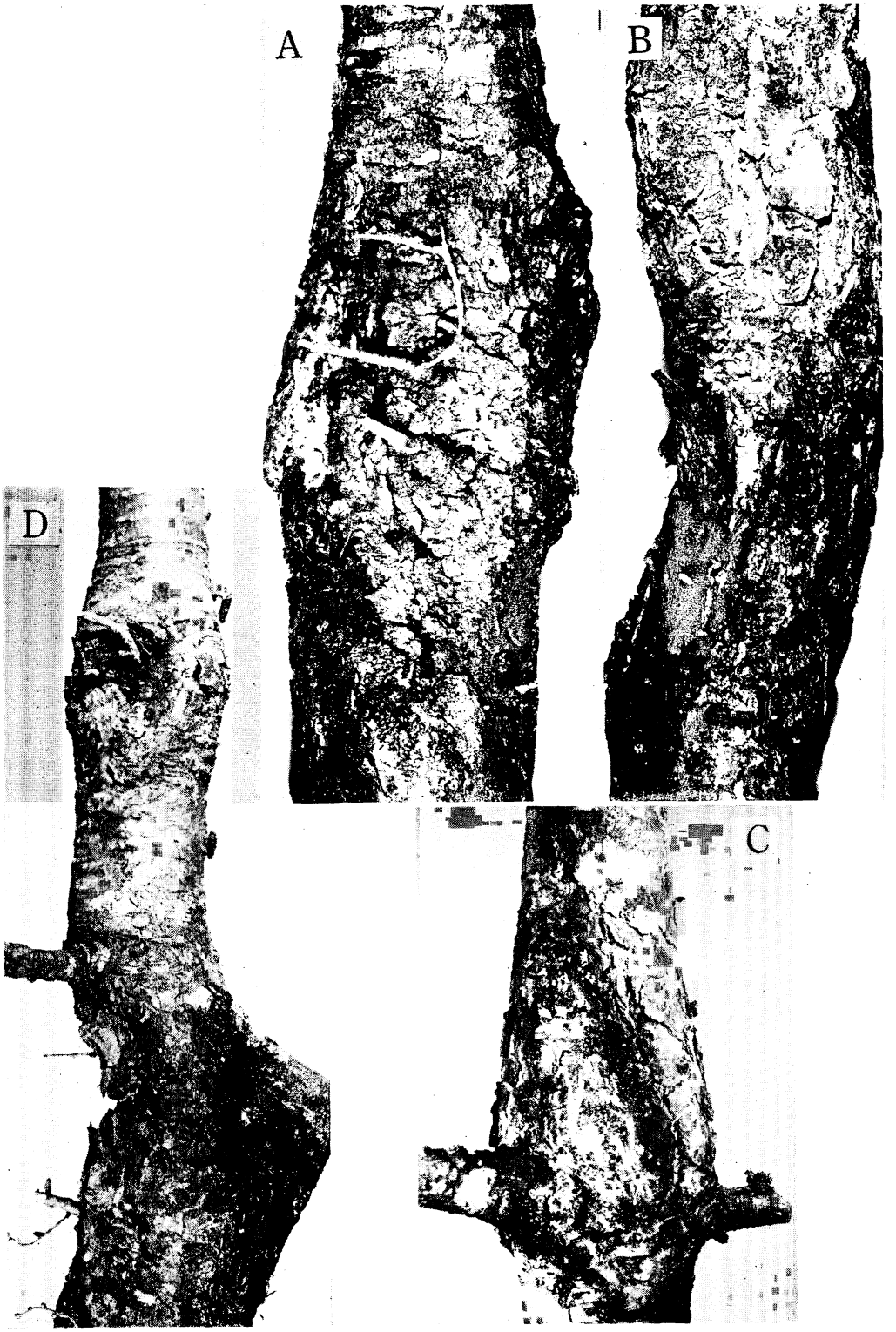
C : Lesion produced by burned-wounded inoculation with the fungus (Dw-2) (right) and check (left). × 0.9 Photo. June 27, 1962

D : Lesion produced by wounded inoculation with the fungus (Dw-2) (right) and check (left). × 0.9 Photo. June 27, 1962

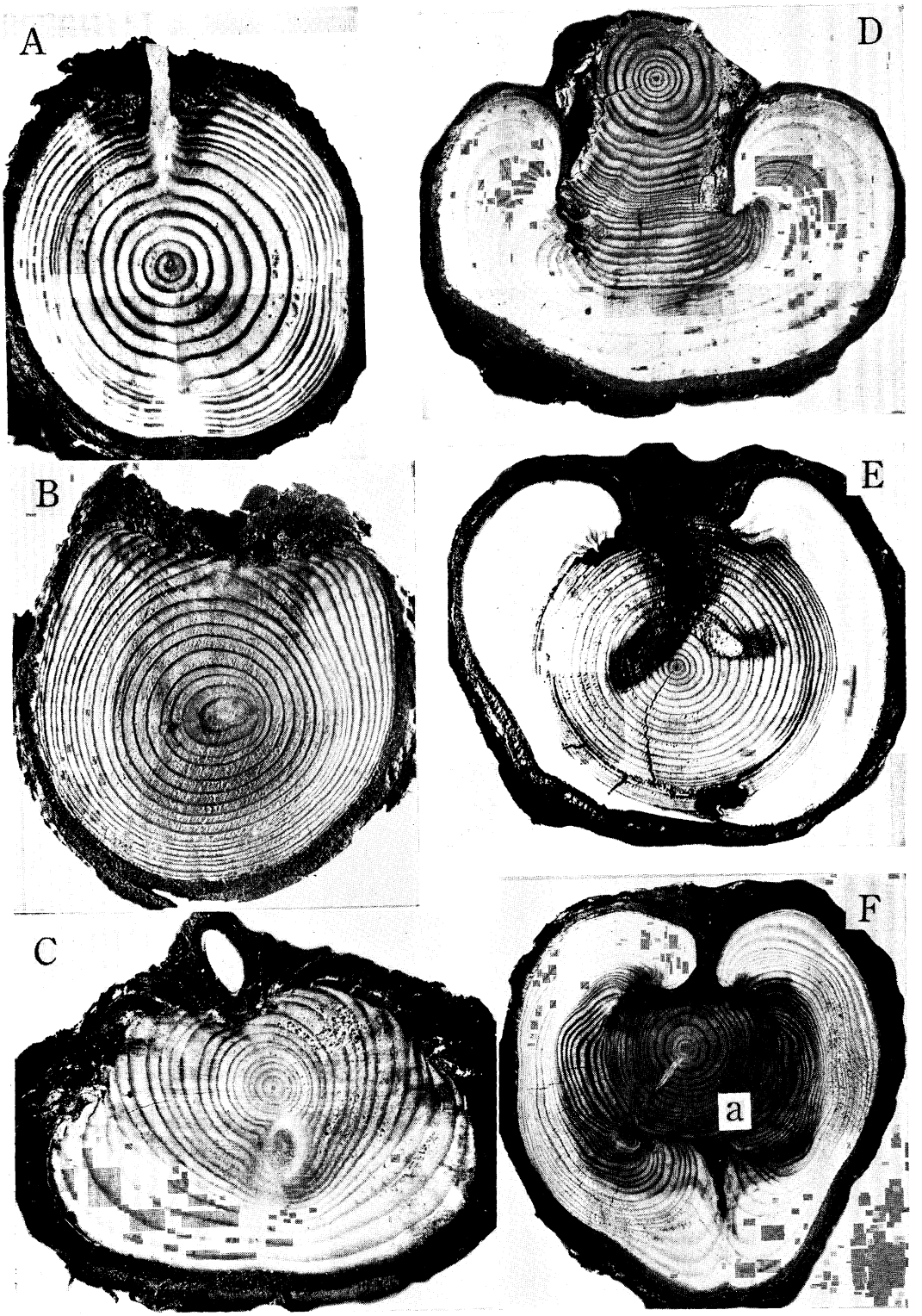
E : Lesion produced by burned-wounded inoculation with the fungus (Dw-2) to the dormant bud (right) and check (left). × 0.9 Photo. June 27, 1962

— Plate 1 —




A
B
C
D

— Plate 3 —




A

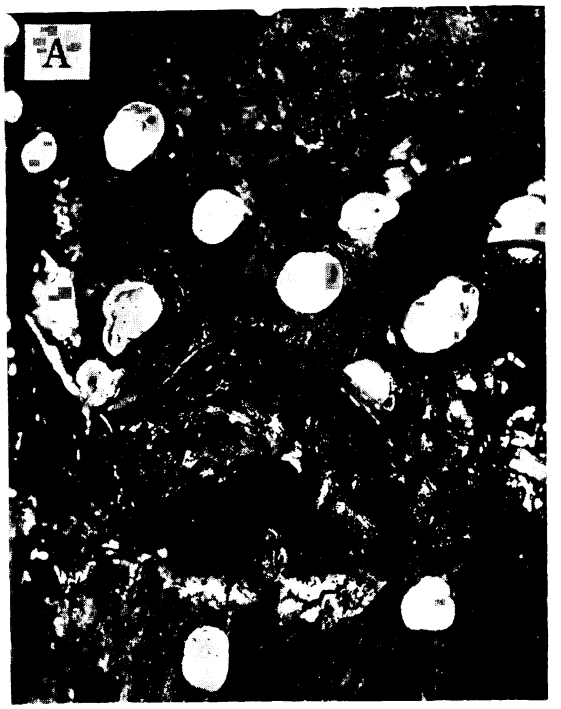

B

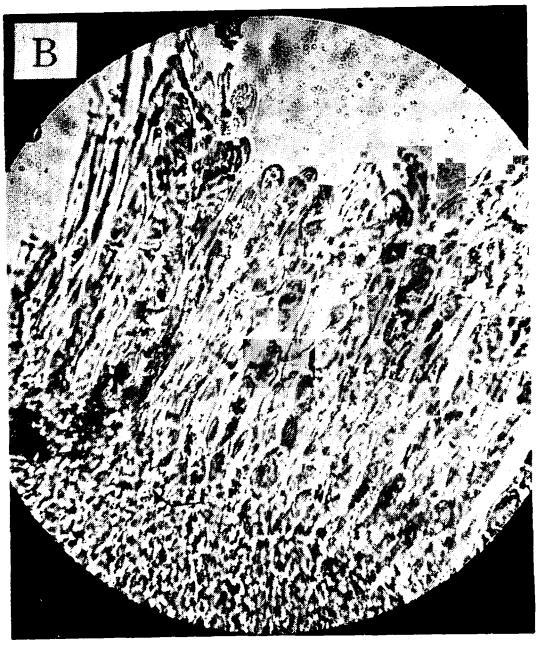

E

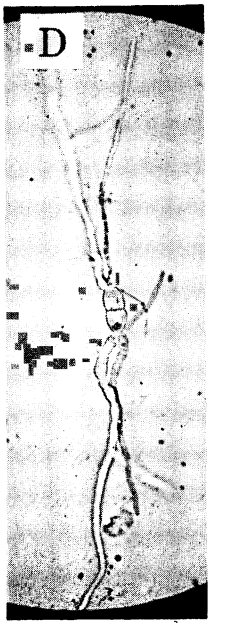

C

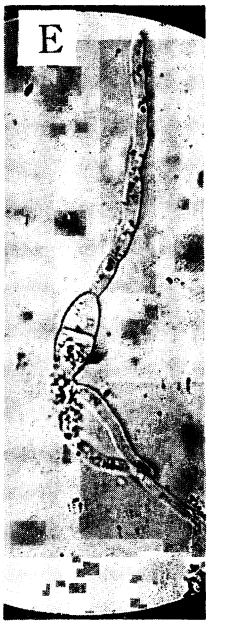

D

— Plate 5 —










A
B
D
C
E

— Plate 7 —