

Immunity of the Gramineae to Violet Root Rot Caused by *Helicobasidium mompa* TANAKA

By

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Introduction

The violet root rot caused by *Helicobasidium mompa* TANAKA which has been well known under the name of "Murasaki-monpa" disease among Japanese phytopathologist and growers is one of the most important soil-borne diseases in Japan, Taiwan (Formosa) and Korea. *Helicobasidium mompa* TANAKA was first described as a fungus affecting mulberry trees (*Morus alba* L.) by N. TANAKA⁽¹⁰⁾ in 1891.

Helicobasidium mompa is an aggressively parasitic fungus which causes a destructive root rot in woody and herbaceous plants, and it has now a known host range of more than 100 wild and cultivated species (Itô 1949)⁽⁴⁾.

Although the violet root rot has been investigated since 1891, comparatively few resistant plants have been found. As early as 1895, FUNAZU⁽²⁾ advocated the rotation of crops on diseased soil, and he said: "Maize, Italian millet and other members of the grass family do not die from this cause, and consequently should be used in soil infested by the disease." Then, MIYAKE (1917)⁽⁶⁾, YASU (1927)⁽¹²⁾, BOKURA (1934)⁽¹⁾, TOCHINAI (1938)⁽¹¹⁾, HIURA (1939)⁽⁹⁾ and others noted, in their handbooks, that gramineous plants were immune or highly resistant to the disease. On the contrary, *Saccharum officinarum* L., sugar cane (SAWADA 1919)⁽⁷⁾, and *Pleioblastus (Arundinaria) simoni* NAKAI, a bamboo grass (SUEMATSU 1930)⁽⁸⁾, belonging to the Gramineae, have been listed as hosts of *Helicobasidium mompa*.

Many species of the Gramineae have been generally considered to be immune or completely resistant to the disease, but the nature of resistance still remains obscure. Since 1946, the author has made some efforts to study the nature of immunity of the gramineous plants to the disease, and a brief note on this study has already been published in a preliminary report (Itô 1952)⁽⁵⁾. While the results of this study are not wholly conclusive at this time, the purpose of this paper is to present data accumulated to date as an aid to other investigators who may be studying this disease.

The author wishes to express his special appreciation to the late Emeritus Professor Dr. Hazime YOSHII, of Kyushu University, under whose direction this study was made, for advice and criticism so willingly given. Thanks are due to Mr. Haruzo ÔGANUKA, of Tohoku Branch of the Government Forest Experiment Station, for assistance in field works.

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Field observations on *Arundinaria chino* (FR. et SAV.) MAKINO

As pointed out by SUEMATU (1930)⁸⁾, sporophores of *Helicobasidium mompa* are frequently formed on culms and leaf sheaths of bamboo grasses.

In November 1943, the author first found well-developed sporophores on *Arundinaria chino* (FR. et SAV.) MAKINO (*Pleiblastus chino* MAKINO), a bamboo grass, in the field of the Government Forest Experiment Station, Meguro, Tokyo (Plate 1, A). A number of sporophores of the fungus were produced on culms and leaf sheaths of the same species in the forest of the Station under moist conditions in 1948 (Plate 1, B). Typical purplish brown strands of the fungus frequently got entangled on rhizomes of the bamboo grass, but that did not necessarily prove that the fungus got nourishment from such rhizomes. Some parts of the root system, especially fibrous roots, were blackened and killed by the fungus, but no visible symptoms of the disease above ground or no remarkable retardation in growth were found in such plants (Plate 1, C, D). However, roots of *Sambucus racemosa* L. subsp. *sieboldiana* HARA, *Mallotus japonica* MÜLLER, ARG., and fleshy roots of snake-gourd, *Trichosanthes cucumeroides* (SER.) MAIX, which were very susceptible to the disease were so completely rotted by the fungus that the bark or skin could be easily removed from the central part (Plate 1, E).

From the field observations it may be said that *Arundinaria chino*, a bamboo grass, is highly resistant to the violet root rot.

Inoculations in the field

In 1946 and 1947, the inoculation experiments were conducted in the field at Koma, Iwate Prefecture. Precipitation, air and soil temperatures in the plots were recorded throughout the experimental period.

Experiment-1 (1946)

Wooden-boxes (32×32×30 cm) were filled with the field soil and steamed for one hour. After cooling down, on May 20th, the fungus was inoculated to the soil in the boxes. The inoculum was a pure culture of *Helicobasidium mompa* (Strain M-1) (ITO 1949)⁴⁾ grown on steamed barks of paper mulberry (*Broussonetia kazinoki* SIEB.) in 300 cc Erlenmayer flasks for about 60 days at 20~25° C. The inoculum was removed from the flask and placed in the soil approximately 1 cm deep from the surface. As checks, steamed barks of paper mulberry which were not cultured with the fungus were used.

On May 27 th, seeds of the following plant species were sown in the boxes: Maize (*Zea mays* L.), rice (an upland rice) (*Oryza sativa* L.), Italian millet (*Setaria italica* BEAUR.), wheat (*Triticum sativum* LAM.), oats (*Avena sativa* L.), Japanese barnyard millet (*Echinochloa crus-galli* var. *frumentaceae* W.F. WIGHT), and soy bean (*Glycine max* MERRILL). According to the macroscopic observation all of the gramineous plant species tested which had been inoculated with the fungus were normal in growth and fructification, and, there were no remarkable differences between the inoculated plant and the uninoculated one (Plates 2~3). In soy bean, the inoculated plant bearing yellowish green leaves was inferior to the uninoculated one in growth and fructification (Plate 4, A, B).

In the middle part of October, all plants tested were carefully excavated and examined.

The gramineous plant species which bore no visible symptoms of the disease above the ground were found to have purplish brown strands of the fungus on their roots, but showed no distinct pathological changes. However, on the contrary, roots of soy bean inoculated were heavily damaged, and a number of sclerotia of the causal fungus were produced on the surface of the infected roots.

Experiment-2 (1947)

In the growing season of 1947, another inoculation test was made by the same procedure as in the previous experiment. Plant species used in this experiment were as follows: Maize, Italian millet, perso-millet (*Panicum miliaceum* L.), oats, Japanese barnyard millet, soy bean, and sweet potato.

Results obtained in the cases of the gramineous plants and soy bean are very accordant with those in Experiment-1 (Plate 3, E, F). Some of the roots and the fleshy roots of sweet potato inoculated were covered with networks of the rhizomorphs of the fungus and were completely rotted.

Results of the field inoculations made in 1946 and 1947 showed that the gramineous plants were immune from the violet root rot, at least, at maturity under field conditions, whereas soy bean and sweet potato which had been recorded as being very susceptible were heavily affected by the disease.

Inoculation *in vitro*

Artificial inoculations with the fungus were made to very young seedlings growing under aseptic conditions *in vitro*. The gramineous plant species used in the experiments were as follows: Maize, rice, Italian millet, perso millet and Japanese barnyard millet.

Methods Seeds of the gramineous species were surface-sterilized by treatment with 80 per cent alcohol, mercuric chloride solution (0.1 per cent), washed several times in sterile water, and then placed on sterile 2 per cent glucose agar in Petri dish. As soon as the majority of seeds in any given lot had produced seedlings with primary roots (radicles) from several mm long, all dishes were examined carefully for the presence of possible contaminating organisms. Contaminated plates were discarded; the remainder were inoculated by placing near or on the roots of each seedling with a small piece of mycelium, taken from a pure culture of the fungus (Strain M-1). The cultures were then placed on the desk in the laboratory at room temperature (18~25° C).

Results From the inoculated parts the mycelia of the fungus crept down or up on the surface of root of the gramineous seedlings. Young primary roots inoculated became purplish brown in color, being more or less withered and necrotic. Apical parts, especially root caps and fibrous roots, were heavily affected by the fungus and became dark purplish brown in color, slender and necrotic. The basal parts of the main roots became slightly discolored, but they were not withered and necrotic at all (Plates 4~6, Figs. 1~2). Though mycelial strands of the fungus were frequently formed on the surface of adult main roots of the gramineous plants, no remarkable pathological change was observed in plant tissue beneath the fungus mycelium.

From infected roots of the gramineous seedlings adequate material was preserved for anatomical study.

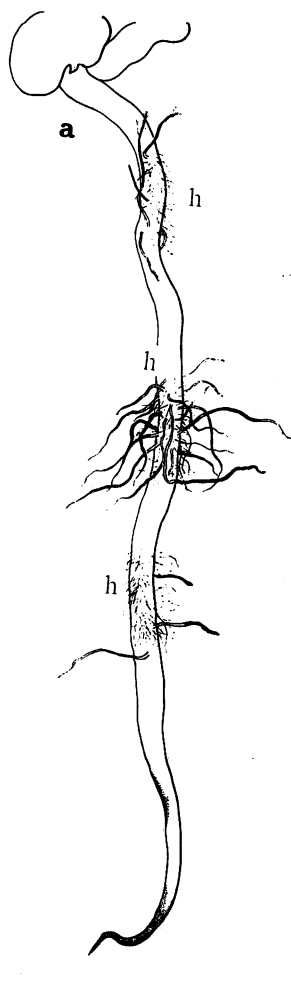


Fig. 1 Primary roots of maize seedlings inoculated with *Helicobasidium mompa*.

A week after inoculation at room temperature (18~25°C). × 2
a, main root b, lateral root
h, hyphae of the fungus



Fig. 2 Young seedlings of rice, persimmon and Japanese barnyard millet inoculated with *Helicobasidium mompa*.

A week after inoculation at room temperature (18~25°C). × 2
a, rice b, persimmon c, Japanese barnyard millet
h, hyphae of the fungus

Patho-anatomical observations

Materials and methods Various infected primary roots of the young gramineous seedlings cultured under aseptic conditions *in vitro* were removed and fixed in chromo-acetic acid solution (chromic acid 1 g., glacial acetic acid 1 cc., sterile water 100 cc.). All material was embedded in paraffin by ZIRKLE'S (1930)¹⁴⁾ n-butyl alcohol method and sectioned serially at 8~10 μ . Two staining techniques were employed; the Flemming's triple stain, and YOSHII'S (1933)¹⁵⁾ Sudan III-methyl green method for microchemical test.

Results In patho-histological characters, there were observed no remarkable differences

among five species of the Gramineae examined, and maize, one of them, was chosen for detailed observation.

The hypha of the fungus penetrates usually the suture of epidermal cell of the root. It is not rare to observe the hypha actually piercing the epidermal wall. The original penetration from the outside may or may not be attended with constrictions of the hyphae at the point of entrance. Fragments of the fungus hypha are frequently observed in the root hairs developed from the epidermal cells (Fig. 3).

The hyphae which penetrated the epidermal cell develop intercellularly as well as from cell to cell in the cortex. As penetration of the cortical cell wall is sometimes effected, a

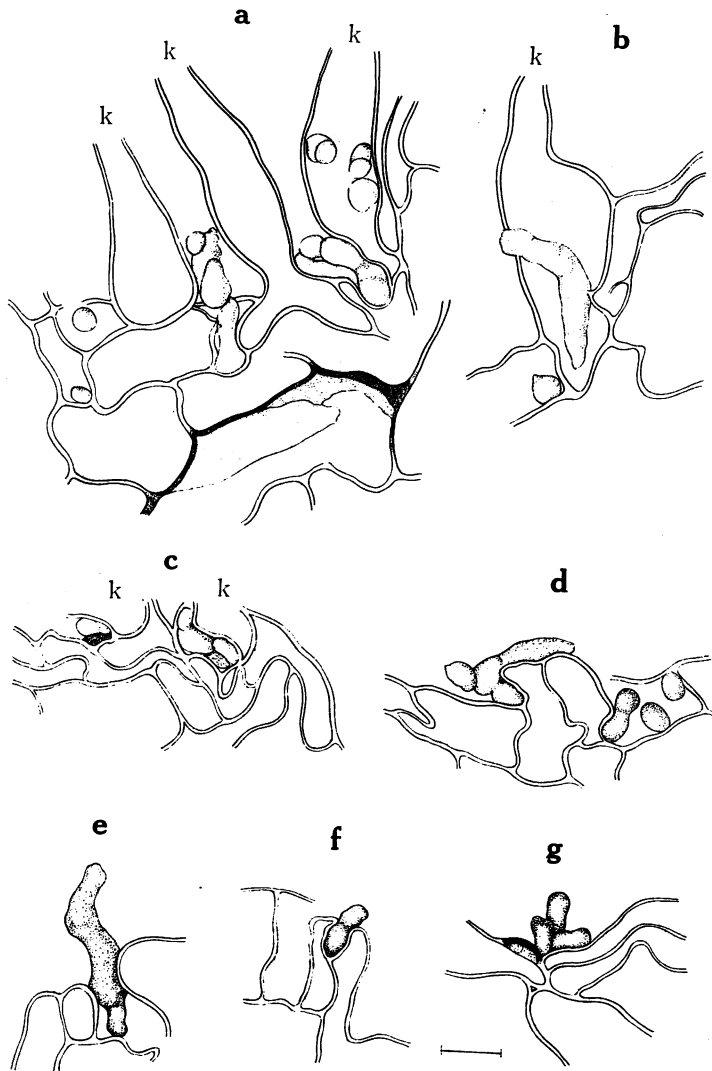


Fig. 3 Penetration of hyphae of *Helicobasidium mompa* through the epidermal cells of primary or lateral roots of maize seedling (— = 10 μ).

k, root hair

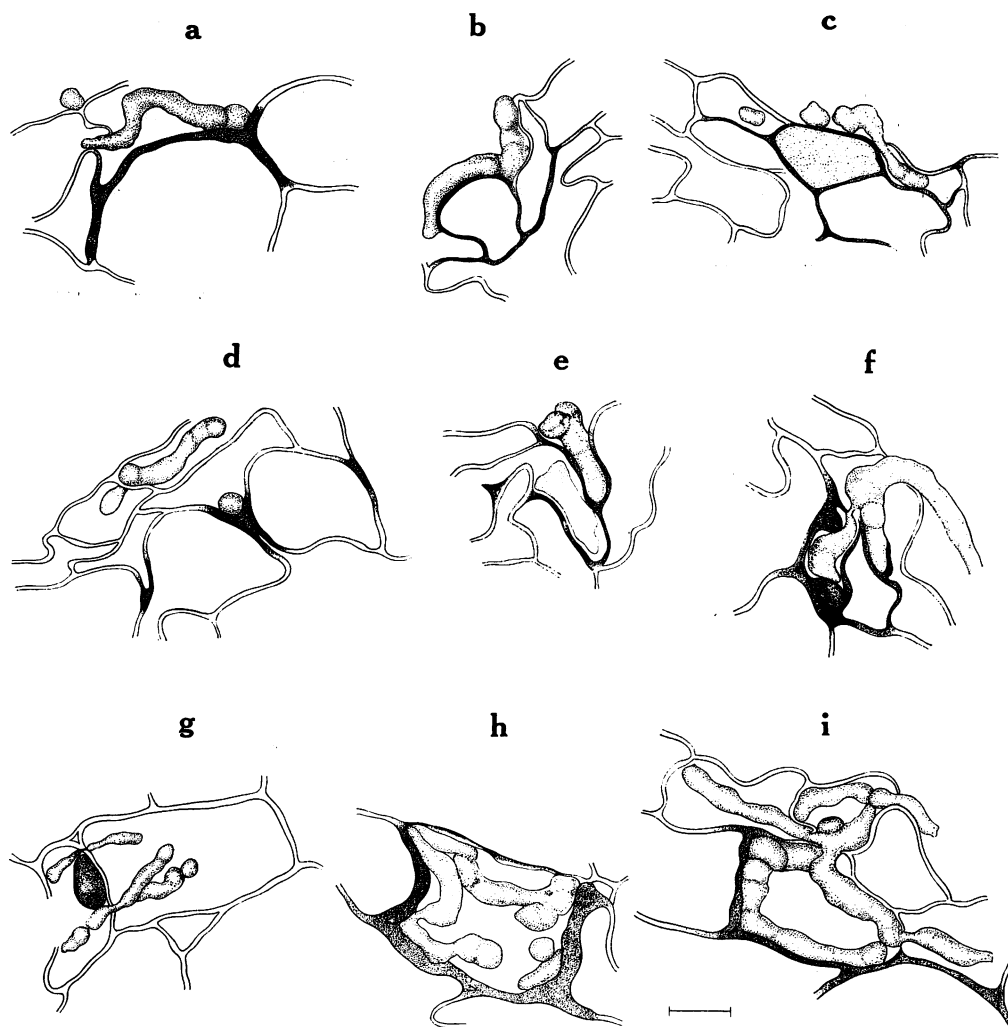


Fig. 4 Hypae of *Helicobasidium mompa* in or near the cortical cells of primary or lateral roots of maize seedling (— = $10\ \mu$).

marked constriction occurs in the penetrating hypha.

Shortly after or even before the entry of hypha into a cortical cell its wall becomes thickened. In some cells the hyphae become aggregated much more than in others. The wall of a cell thus filled with hyphae becomes greatly thickened, making it difficult for the hyphae to pass from it to the next cell. In main and lateral young roots, the author has never seen a case in which the hyphae have penetrated the other cortical cells beyond the thickened cell wall even at the end of 18 days from the original penetration. In fibrous roots, however, the fungus penetrates the epidermis, passes through the cortex and its progress is hindered by the endodermis (Fig. 4).

The thickened cell wall of the cortex stained strongly with safranin shows wound gummy reaction by Sudan III-methyl green staining. Plasmolysis, degeneration and wound-gummi-

fication occur in the cells infected as well as in those beyond the fungus hyphae.

In the gramineous plants, the hyphae of the fungus infect only young roots, and they are unable to penetrate the well developed exodermis of adult roots.

Consideration and conclusion

Without any experimental proof it has been generally considered from field observations that the Gramineae are immune or highly resistant to the violet root rot caused by *Helicobasidium mompa* TANAKA, a polyxenic pathogen. Results of the field inoculations made by the author showed that the gramineous plant species were immune from the disease at maturity under field conditions, although mycelial strands of the fungus were observed on the surface of their underground parts. As to the artificial inoculation in field and *in vitro*, the secondary or permanent roots were completely free from the disease, but the primary roots were infected by the fungus. Fibrous roots in seedling stages were very readily affected by the disease. These facts show that the causal fungus is unable to attack adult root systems, except fibrous roots.

Hyphae of the fungus penetrated the epidermal cells of the primary root of the gramineous plants, developed intercellularly, and penetrated adjacent cortical cells in the same manner as reported in sweet potatoes and soy beans by ITO (1949)⁴⁾. The wall of the cortical cell thus filled with hyphae became greatly thickened and wound-gummified or lignified, making it very difficult for the hyphae to pass from it to the next cell. In sweet potatoes, it seemed likely that the advance of the parasite was checked, for no further development of the hyphae beyond the barrier was noted (ITO 1949⁴⁾, SUZUKI 1957⁹⁾). But, in the gramineous plants, the hyphae in the cortical cell which had been completely enclosed by the thickened and wound-gummified wall were probably unable to pass out of the cell. This may be due to the difference between sweet potato and gramineous plant in quantity as well as in quality in the thickening of the cell wall. Hyphae enclosed in the cell are probably pushed out and leave the diseased host tissue.

The general immunity of the gramineous plants to the violet root rot is considered to be due at least in part to the local necrosis by a hypersensitive reaction in the cortical cell of primary roots of these plants, and, possibly, this restricts the infection to a limited part.

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Explanation of plates

Plate 1

- A. Sporophore of *Helicobasidium mompa* on *Arundinaria chino*, a bamboo grass. $\times 0.5$
f, sporophore of the fungus.
- B. Ditto. $\times 0.8$
- C~D. Rhizomes and roots of *Arundinaria chino* tangled with mycelium of *Helicobasidium mompa*. $\times 0.8$
- E. Fleshy roots of snake-gourd, *Trichosanthes cucumeroides*, attacked by *Helicobasidium mompa*. $\times 0.9$
h, healthy fleshy root.

Plate 2

Artificial inoculation with *Helicobasidium mompa* to the gramineous plants in the field.

- A. General view of inoculation test. Photo. June 13, 1946.
- B. Ditto. Photo. September 3, 1946.
- C. Maize inoculated with the fungus. Photo. September 3, 1946.
- D. Maize uninoculated (control). Photo. September 3, 1946.
- E. Rice inoculated with the fungus. Photo. September 3, 1946.
- F. Rice uninoculated (control). Photo. September 3, 1946.

Plate 3

Field inoculations with *Helicobasidium mompa* to the gramineous plants.

- A. Italian millet inoculated with the fungus. Photo. September 3, 1946.
- B. Italian millet uninoculated (control). Photo. September 3, 1946.
- C. Oats inoculated with the fungus. Photo. September 3, 1946.
- D. Oats uninoculated (control). Photo. September 3, 1946.
- E. Perso millet inoculated with the fungus. Photo. October 23, 1947.
- F. Perso millet uninoculated (control). Photo. October 23, 1947.

Plate 4

- A. Field inoculation with *Helicobasidium mompa* to soy bean. Photo. September 3, 1946.
- B. Ditto. Uninoculated soy bean (control). Photo. September 3, 1946.
- C. Primary and lateral roots of maize seedlings inoculated with *Helicobasidium mompa*.
Five days after inoculation at 18~20°C. $\times 1$

Plate 5

- A. Primary roots (radicles) of maize seedling inoculated with *Helicobasidium mompa*. $\times 2$
Four days after inoculation at 18~25°C.
h, uninoculated one (control)
- B. Primary and lateral roots of maize seedling inoculated with *Helicobasidium mompa*.
 $\times 3.5$
Eighteen days after inoculation at 18~25°C.
- C. Primary roots (radicles) of rice seedlings inoculated with *Helicobasidium mompa*. $\times 2$
Four days after inoculation at 18~25°C.
h, uninoculated one (control).

Plate 6

- A. Primary roots (radicles) of perso millet seedling inoculated with *Helicobasidium mompa*.
× 1.2
Five days after inoculation at 18~25°C.
- B. Primary roots (radicles) of perso millet seedling inoculated with *Helicobasidium mompa*.
× 2
h, uninoculated one (control)
- C. Primary roots (radicles) of Japanese barnyard millet seedling inoculated with *Helicobasidium mompa*. × 2
Four days after inoculation at 18~25°C.
h, uninoculated one (control).

紫紋羽病に対する禾本科植物の免疫性

(摘 要)

伊 藤 一 雄⁽¹⁾

紫紋羽病菌 *Helicobasidium mompa* TANAKA は代表的な多犯性土壌伝染病菌の一つとして知られているもので、多くの科、属にわたる木本性および草本性植物を侵し、その寄主の数は100以上に及んでいる(伊藤 1949)。

本菌は禾本科植物を侵しがたいことはすでに古くから知られており、本病被害跡地にはこれらを輪作することによって、その後の被害をまぬがれると述べられていた(船津 1895)。そして、その後も同様の記述が散見されるのであるが(三宅 1917, 保 1927, 卜蔵 1934, 柄内 1938, 樋浦 1939), これらはもとより圃場観察によるいわば経験的な記述で、実験的に確認されたものではない。一方、禾本科に属すサトウキビ(沢田 1919)およびメダケ(末松 1930)が本菌の寄主植物としてあげられている記録もある。

著者は本病に対する禾本科植物の免疫性(強抵抗性)を実験的に明らかにする目的で野外観察、圃場接種試験および無菌状態における人工接種試験を行ない、さらに病態解剖観察によって細胞・組織の病変経過を追跡した。

ニワトコ、アカメガシワ、カラスウリなどとともに群生しているアズマネザサの稈および葉鞘に本菌の子実体がおびただしく形成され、夏季には担子胞子の生成をみることはしばしば認められる(Plate 1 A, B)。そして一見するところ、ササははなはだしく罹病しているように思われるが、いちじるしい成長阻害も枯死も起こらず、土を掘ってよく観察すると、近接するニワトコ、アカメガシワおよびカラスウリの地下部は本菌によってはなはだしく侵されて腐敗しているにもかかわらず、ササの地下茎・根部には菌糸束はからまりついてはいるが、細根(毛根)をのぞき、ほとんど全く何らの病変も認められない。ただし細根は黒色壊死状を呈し、本菌の侵害をうけていることは明らかに察知された(Plate 1 C, D, E)。

圃場において2か年間本菌の培養菌糸を接種源として人工接種試験を行なった。供試禾本科植物としてはトウモロコシ、アワ、ヒエ、リクトウ、エンバク、コムギおよびキビの7種、それに対照として本病に罹病しやすい(伊藤 1949)サツマイモとダイズを用いた。2か年間の結果を総括すると、供試禾本類はいずれも、接種区、無接種区を問わず、正常な成長をとげて開花結実し、その間に差異は認められなかった(Plate 2~3)。ただし接種区では地下部に本菌の菌糸束がからまりついてはいることは明らかに認められた。一方、本病にきわめて感受性のサツマイモおよびダイズの地下部は、はなはだしく侵されて腐敗し、菌糸束および菌核が根の表面に多量に形成されていた。ダイズの接種区では成長が不良になり、葉は黄変し、結実も不良になり、無接種区と明らかな対照を示した(Plate 4 A, B)。

トウモロコシ、アワ、キビ、リクトウおよびヒエの5種について、これらの無菌培養子苗に本菌を人工接種すると、接種点を中心にして菌糸は蔓延し、発芽後間もない幼根は紫褐色に変じて萎凋壊死し、これ

1969年4月23日受理

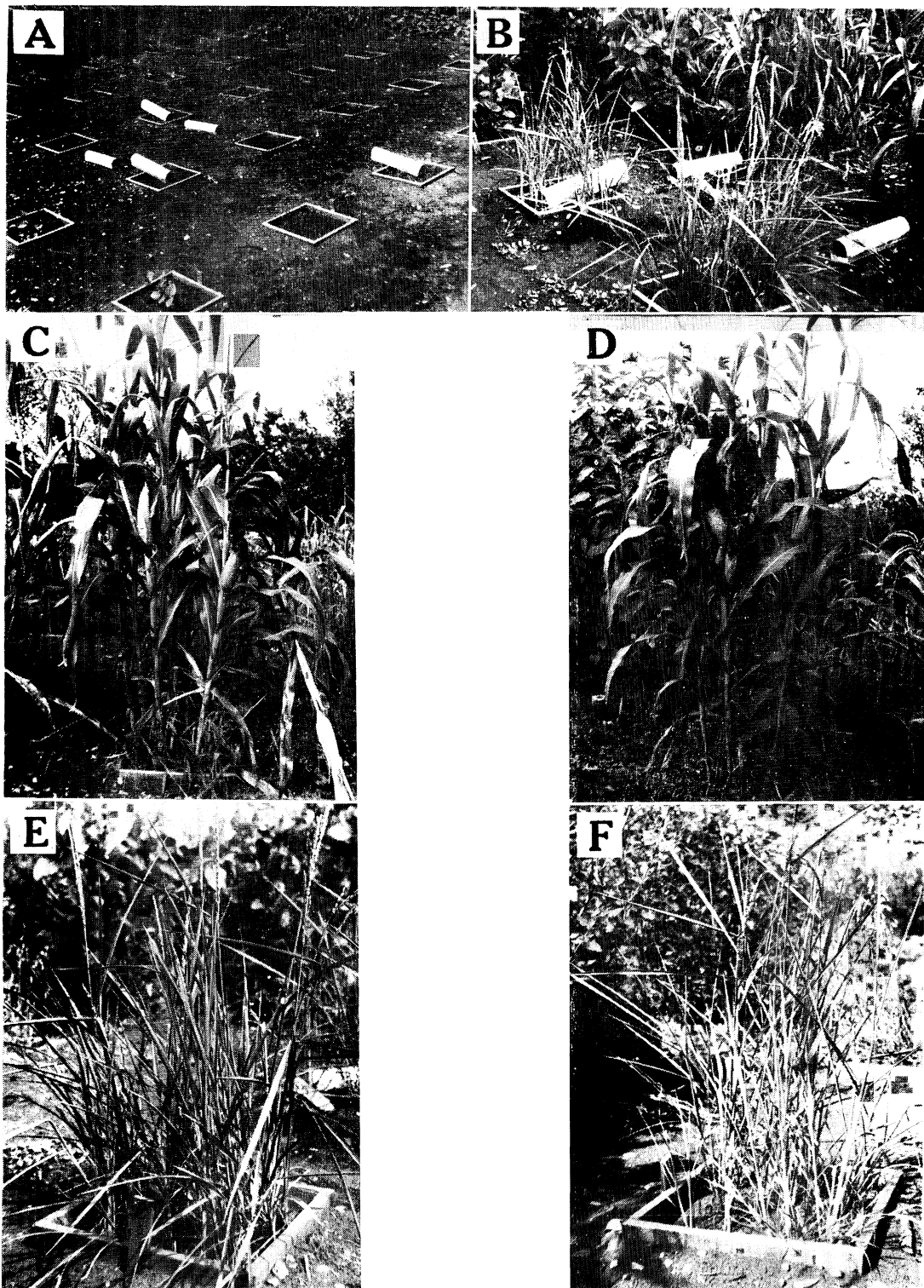
(1) 保護部長・農学博士

は根端およびこれに近い部分ほどはなはだしく、基部は軽微である。すなわち、根冠付近および細根（毛根）は濃紫褐色を呈して軟化萎縮壊死する。しかし幼根基部では変色は認められるが、はなはだしく陥凹軟化することはほとんどなく、したがって幼苗は発育をつづける。老成根には菌糸束がその表面にほふくすることはあるが、顕著な病変は認められない（Plate 4 C, Plate 5, 6, Fig. 1~2）。

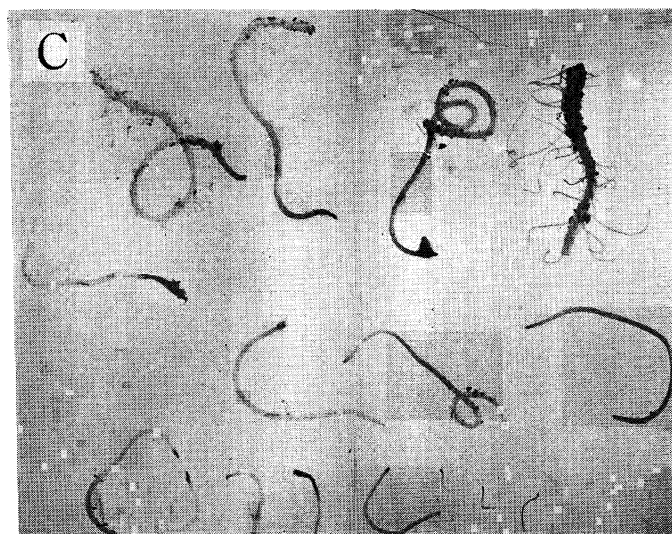
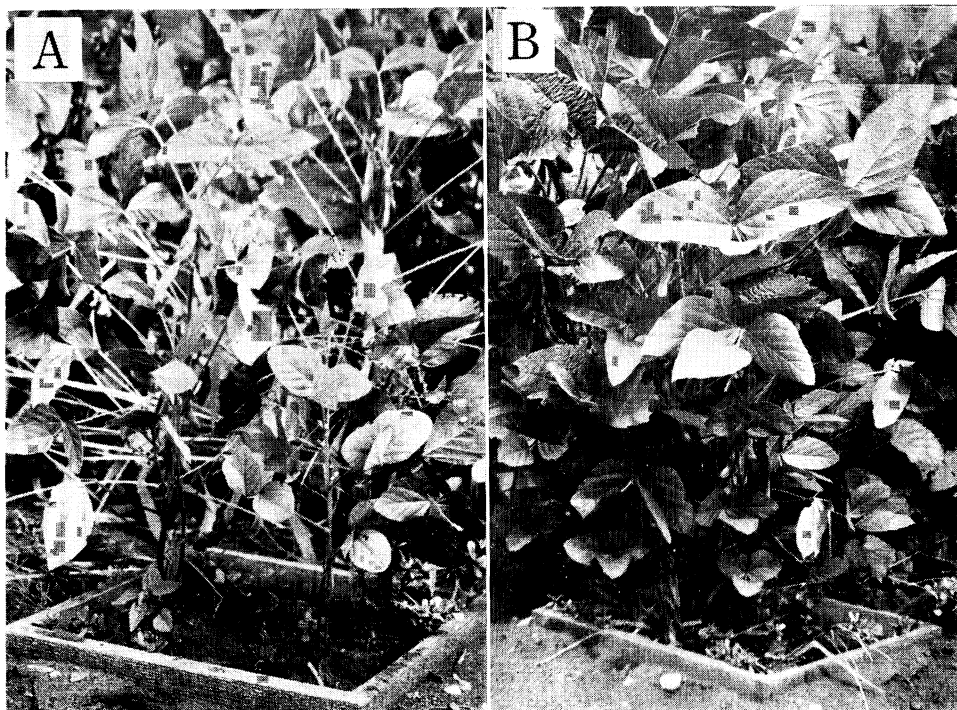
本菌の禾本科幼根への侵入方法およびその後の細胞・組織病変経過は各種とも大同小異なのでトウモロコシについてくわしく調べた。菌糸は幼根の表皮細胞縫合部から侵入することが多く、また表皮細胞膜を直接貫通することもある。貫入にさいして菌糸はややその太さを減じ、貫通後ふたたび復元し、はなはだしく細くなることはほとんどない。菌糸はさらに表皮直下の皮層細胞に侵入し、侵入と同時に、あるいは侵入に先だってこの部分の細胞膜は急激に肥厚する。この場合には菌糸は貫通にあたりその太さをいちじるしく減ずる。菌糸の侵入をうけた皮層細胞膜ははなはだしく肥厚し、サフラニン濃染性で、Sudan III-メチルグリーン反応からみると傷痕ゴム化（木質化）したものである。幼主根および幼側根においては肥厚した細胞の内腔に菌糸は緘封され、侵入後18日経過したものでも菌糸がこの細胞膜を通過してさらに内方に蔓延したものは全くなかった。しかし毛根ではやや趣きを異にし、さらに内方まで侵され、同様に皮層細胞膜も傷痕ゴム化して肥厚するが、これも内皮まででとどまり、中心柱は変化がない。侵入をうけた細胞およびこれに近接する細胞は原形質分離を起こし、なお傷痕ゴム質が小塊状に生成されることもある（Fig. 3~4）。本菌菌糸の侵入は幼組織に限られ、すでに外皮が完成された老成根を貫通して侵入することは全くない。

以上のことから、禾本科植物は本病に全然罹病しないのではなく、幼根は本病病原菌の侵入の対象となり、細胞・組織の病変をもたらすことは明らかである。本菌の菌糸が皮層細胞に侵入するとその細胞膜は急速に肥厚し、かつ木化（傷痕ゴム化）し、菌糸は肥厚細胞腔内に緘封されて脱出蔓延することができない。肥厚細胞腔内にとじこめられた菌糸はその細胞とともに押し出されて離脱するか、あるいはそのまま死の運命をたどるものと思われる。すなわち、本菌の侵入にあった禾本科の幼根細胞は一種の過敏性壊死を起こし、侵害を局所的にとどめるとも解され、この現象が禾本科植物の本病に対する免疫性（強抵抗性）の少なくとも一部にはなっているものと考えられる。









Appendix

Supplement to host plants of *Helicobasidium mompa* TANAKA

Host plant*		Author
Scientific name	Japanese name	
Pinaceae		
1. <i>Larix leptolepis</i> GORDON	Karamatsu	Ito (1959) ³⁾
2. <i>Pinus taeda</i> L.	Têda-matsu	Ito (1961) ⁵⁾
Palmae		
3. <i>Trachycarpus fortunei</i> (HOOK) H. WENDL.	Shuro	FUNAZU (1895) ¹⁾
Crommelinaceae		
4. <i>Commelina communis</i> L.	Tsuyukusa	SUZUKI & ABUMIYA (1963) ⁸⁾
Liliaceae		
5. <i>Asparagus officinalis</i> L.	Oranda-kijikakushi (Asuparagasu)	SUZUKI & ABUMIYA (1963) ⁸⁾
Betulaceae		
6. <i>Alnus katoana</i> YANAGITA var. <i>microphylla</i> NAKAI	Kobano-yamahannoki	SATO (1962) ⁷⁾
Polygonaceae		
7. <i>Rumex japonicus</i> HOUTTUYN	Gishigishi	SUZUKI & ABUMIYA (1963) ⁸⁾
Leguminosae		
8. <i>Lespedeza cuneata</i> G. DON.	Medohagi	Ito (1962) ⁶⁾
9. <i>Medicago sativa</i> L.	Rûsan	SUZUKI & ABUMIYA (1963) ⁸⁾
10. <i>Trifolium repens</i> L.	Shiro-tsumekusa	SUZUKI & ABUMIYA (1963) ⁸⁾
Rutaceae		
11. <i>Phellodendron amurense</i> LUPR.	Kihada	Ito (1960) ⁴⁾
Cucurbitaceae		
12. <i>Trichosanthes cucumeroides</i> (SER.) MAXIM.	Karasuuri	Ito (1952) ²⁾
Compositae		
13. <i>Sonchus brachyotis</i> DC.	Hachijôna	SUZUKI & ABUMIYA (1963) ⁸⁾
14. <i>Sonchus oleraceus</i> L.	Nogeshi	SUZUKI & ABUMIYA (1963) ⁸⁾
15. <i>Paraxacum officinale</i> WEBER	Seiyô-tanpopo	SUZUKI & ABUMIYA (1963) ⁸⁾

* In using the scientific and Japanese names of the host plants the author chiefly followed OHWI, J. (1965). Flora of Japan. Tokyo.

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