

キリの枝枯をおこす *Phomopsis* および その完全時代 *Diaporthe* について

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ま え が き

筆者らは、まえにキリ(*Paulownia tomentosa* STEUD.)の枝枯をおこす *Physalospora paulowniae* 菌についての報告 (ITÔ & KOBAYASHI 1951)⁽¹⁾ のなかで、キリの枝枯部にはおおくの菌類がみつめられるが、そのなかでは *Phomopsis*, *Fusarium*, および *Physalospora* が重要な菌と考えられることをのべておいた。そのごひきつづいての調査において *Phomopsis* 菌の寄生している枝のうえに、しばしば *Diaporthe* 菌が混生するのを観察し、キリにみられたこの2つの菌は同根関係にあるのではないかと予想した。この報告においては、これらの点を確かめるためにおこなった若干の実験結果と、これらの菌の所属についておこなった検討の結果についてのべる。

この研究をおこなうあいだ、激励と助言をいただいた保護部長今関六也氏にお礼もうしあげるとともに、原図作製に助力していただいた中川道夫氏に感謝の意を表する。

菌 の 形 態

1951 年秋から翌年春にかけて、あたらしく枯れた、あるいは枯れかかっている枝にたいして、観察をつづけたところ、おなじ枝のうえに *Phomopsis* の柄子殻および *Diaporthe* の子のう殻がつくられ、それらはいずれも2月下旬ないし3月上旬にいたって完熟した。*Phomopsis* の柄子殻は半球形の隆起として生じ (Plate 1, C), 成熟すると中央が裂開して孔口を生ずる。*Diaporthe* の子のう殻は樹皮内につくられるが、黒色の頸が樹皮を通じて外にいくらか突きだし、皮目を小さくしたような隆起となる (Plate 1, B)。春から秋にかけての雨のあと、あるいは多湿期には、*Phomopsis* の柄子殻から淡黄色の胞子角を生ずる。

1. *Phomopsis* (Fig. 1)

柄子殻は径約0.7mm、樹皮下につくられる子座のなかに不規則な2室となつて生ずる。分生子梗は細く、分岐はなく、無色、長さ5~8 μ 。柄胞子は2つの型をもち、ひとつはA-胞子で、橢円型ないし紡錘型、単胞、無色、大きさ7~10 \times 2.5~3 μ 。自然の柄子殻および培養基上の柄子殻内につくられる。いまひとつはB-胞子 (stylospore) で、釣針型あるいは針状で無色、単胞、細長く24~38 \times 0.7~1.1 μ の大きさをもち、培養基上の柄子殻内にのみつくられる。

2. *Diaporthe* (Fig. 2, Plate 1: D, E)

子のう殻はひとつ、または数個が集まつて樹皮下につくられ、樹皮を通じて表面にでる黒色の頸をも

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つ。頸の長さは 60~90 μ 。子のう殻の球形部の直径は 340~450 μ で、殻壁は黒色膜状、厚さ 17~28 μ 。子のうは長こん棒状、無色、大きさ 38~44 \times 6.5~8.5 μ 。子のうのなかには 8 個の子のう胞子が不規則 2 列にふくまれる。子のう胞子は無色、2 胞、楕円形ないし紡錘形で隔膜部でくびれる。大きさ 11~14 \times 2.5~4 μ 。

Phomopsis と *Diaporthe* の同根関係

1. 2, 3 の培養実験

柄胞子 (*Phomopsis*) および子のう胞子 (*Diaporthe*) からそれぞれ単胞子分離をおこなった。2% 素寒天培養基上 25°C において両者ともに数時間で 100% ちかくの発芽をしめた。柄胞子はどこからでも発芽管をだし、子のう胞子は両端から発芽管をだして発芽した。

柄胞子および子のう胞子からそれぞれ単胞子分離した培養はまったくおなじ特徴をしめし、この両菌株をもちいて、数種の培養基上における発育経過、特徴を調べたが、いずれもおなじ特徴をしめた。実験した 5 種の培養基上における培養特徴をしめすと、つぎのとおりである。

a. ジャガイモ寒天培養基：もちいた培養基のなかでは麦芽汁寒天、斎藤氏しろう油寒天培養基とともに菌の発育はよかつた。菌そうは緊密で、白色のあらい綿状気中菌糸におおわれ、内部菌糸は淡紫褐色。約 1 カ月ごとに菌そう表面に数個の柄子殻をつくり、やがてそれから淡黄色の胞子角を生ずる。このなかには A- 胞子と B- 胞子がふくまれている。

b. 斎藤氏しろう油寒天培養基：菌そうはたいらに発育し、はじめ白色、のち淡褐色にかわり、表面は白色綿状の気中菌糸で密におおわれる。やはり約 1 カ月ごとに菌そう上に柄子殻がつくられ、A- 胞子と B- 胞子をふくんだ胞子角を生ずる。

c. 麦芽汁寒天培養基：菌そうははじめたいらにのびるが、やがて周辺部に皺を生じ、白色。表面は短毛状のあらい気中菌糸でおおわれる。約 1 カ月ごとに柄子殻をつくり、A- 胞子と B- 胞子をふくんだ淡黄色の胞子角をおしだす。

d. ワツクスマン氏培養基：菌そうは発育ややおそく、緊密で白色、表面綿状の気中菌糸で密におおわれる。柄子殻は約 2 カ月ごとに菌そう表面につくられる。

e. キリ枝煎汁寒天培養基：菌そうは発育わるく、まわりは波状に不規則にのび、たいらで、周辺部に生ずるわずかの白色の気中菌糸をのぞいて、ほとんど無色である。2 カ月ごとにおいても柄子殻をつくらない。

以上いずれの培養基上においても、子のう殻の形成はついにみとめられなかつた。またつぎに、菌そうの発育と温度との関係をしらべたが (Table 1)、それにおいても、両菌株はまったくおなじ発育度と特徴をしめた。Table 1 にみられるように、発育温度は 9~30°C、適温は 25°C にあり、0°C および 35°C では発育しない。また、より高温の区においては、菌そう周辺部で波状不規則な発育をしめた (Fig. 3)。

2. 接種試験

培養実験において、*Phomopsis* および *Diaporthe* からの両菌株はともに同様の特徴をしめし、区別することはできなかつたが、さらにこのことを確かめまた病原性を調べるために、1951 年 4 月、8 月および 1953 年 9 月の 3 回にわたって接種試験をおこなった。接種は当年生枝および 2~3 年生褐色枝をもちい、それぞれ三角刀によつて焼傷接種および切傷接種をおこなった。接種は各区 5 本ずつとり、対照比

較区は2本ずつとした。接種ごの観察によると、本菌は接種してから1～2カ月のあいだに寄主のカルス形成により、傷口はほとんど、あるいはまったく閉塞するが、秋に接種したものの一部は翌春になつて枝枯をおこし、いずれも *Phomopsis* の子実体を生じた (Table 2)。それからの再分離は接種にもちいた母菌株とおなじ培養を生じた。発病枝はそのごの観察をつづけたが *Diaporthe* を生じなかつた。

自然においては、キリの枝枯は *Phomopsis* によると思われるものをもつとも多いが、接種試験の結果からみると、傷痕寄生をするとはいえ、その病原性は強いものではないようである。

以上の培養、接種実験や観察の結果からみて、キリに寄生する *Phomopsis* 菌と *Diaporthe* 菌は同根関係にあり、前者は後者の不完全時代であると考えられる。

菌 の 分 類

外国においてはキリに記載されている *Phomopsis* の記録はないが、原²⁾ は 1913 年にキリから採集したとして *Phomopsis imperiales* Sacc. et Roum. を記録している。しかし形態や引用文献がなく、また Saccardo によるこの菌の原記載をみつけられなかつた。しかしながら、Saccardo の *Sylloge Fungorum*¹²⁾ にはキリに *Phoma imperiales* Sacc. et Roum. という種が記載され、この菌は *Diaporthe* の不完全時代であるとのただし書がついている。このことからみると、原はこのただし書によつて *Phoma imperiales* の属名を *Phomopsis* 属に移して紹介したものと考えられる。*Phoma imperiales* の記載はもともとそう詳しいものではないが、筆者らのえた *Phomopsis* 菌の形態に一致するので、やはりそのただし書によつて *Phoma imperiales* Sacc. et Roum. と同定してよいものとする。

また、*Diaporthe* 菌もキリに記載されているものはない。Wehmyer は 1933 年に *Diaporthe* 属菌のモノグラフ¹⁴⁾ を発表したか、そのなかで *Diaporthe medusaea* Nit., *D. eres* Nit., *D. beckhausii* Nit. および *D. strumella* (Fr.) Fck. がキリの *Diaporthe* に近いようであつた。これらのうち *D. medusaea* と *D. eres* はきわめて大きい種で、各種の広葉樹に記載されていたおおくの *Diaporthe* 菌が Wehmyer によつてこの2種のなかに異名として移されている。しかし *D. medusaea* は柄子殻世代の形態や子のう殻の形態、形成状態などあきらかに本菌とは異なるものであり、また *D. beckhausii* と *D. strumella* もまたその柄子殻世代とくに B-胞子の形態によつて本菌とは異なるものである。*D. eres* はその基本種および異名とされたおおくの種の形態が本菌の形態にきわめてよく一致する。

Wehmyer のモノグラフ以降発表され、あるいはまたわが国において存在の知られているおおくの *Diaporthe* 菌 (*D. vaccinii* Shear¹⁵⁾, *D. moriokaensis* Sawada¹³⁾, *D. Take Hara*³⁾, *D. nomurai* Hara⁴⁾, *D. Aucubae* Sacc.⁵⁾¹¹⁾, *D. leiphaemia* (Fr.) Sacc.⁵⁾¹⁴⁾, *D. umbrina* Jenkins⁵⁾⁷⁾ など) はいずれもキリの *Diaporthe* とは形態的に異なるものである。

以上各種の *Diaporthe* 菌との比較の結果、筆者らは Wehmyer がカエデ、ウツギ、カバ、シデ、クリ、キッサゲ、ボブラ、トネリコ、ウルシなどおおくの広葉樹の *Diaporthe* を集めて1種とした *D. eres* Nit. 菌に形態的一致をみるので、キリの菌も *D. eres* Nit. と同定する。したがつて *Phoma imperiales* Sacc. et Roum. および原がこれを *Phomopsis imperiales* Sacc. et Roum. として紹介した菌は、今後その不完全時代としてとりあつかわれることになる。

要 約

キリの枝枯病をおこすと考えられる菌のうち、しばしば混生する *Diaporthe* および *Phomopsis* 菌について若干の実験をおこない、その同根関係をあきらかにし、またその分類学的所屬を検討した結果 *Diaporthe eres* NIT. と同定した。

本菌は自然においては、枝枯部にもつともしばしばみられるが、その病原性は強いものではない。

図 版 説 明

Plate 1

A : 枝枯をおこしているキリ

B : *Diaporthe eres* NIT. の子のう殻を生じているキリ被害枝 ×1

C : *Diaporthe eres* NIT. の柄子殻 (*Phomopsis*) を生じているキリ被害枝 ×1

D : *D. eres* の子のう殻 ×90

E : 同上 ×150

***Phomopsis* and its Perfect Stage *Diaporthe* causing a Die-Back of the Paulownia Tree**

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Introduction

In the previous paper⁹⁾ dealing with a die-back fungus, *Physalospora paulowniae* ITÔ et KOBAYASHI, the writers mentioned that *Phomopsis*, *Fusarium* and *Physalospora* were considered to be the more important among the many fungi inhabiting the dead twigs of *Paulownia tomentosa* STEUD.

In the course of examining further materials, the writers have frequently found a *Diaporthe* on the same die-back twigs bearing *Phomopsis* pustules, and have presumed a correlation between them.

Culture experiments and inoculation tests were undertaken to ascertain their genetic connection, and from the results of these experiments the writers came to the conclusion that the *Phomopsis* was the imperfect stage of the *Diaporthe*.

It is the purpose of the present paper to report the genetic relation between the *Diaporthe* and the *Phomopsis* collected on the dead twigs of paulownia trees.

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Morphology of the fungus

The examinations carried out at varying intervals on the newly dead twigs from the fall of 1951 to the following spring showed that an ascomycetous fungus belonging to the genus *Diaporthe* often appeared together with *Phomopsis* on the same lesions, and that they matured in late February to early March.

During the moist period or just after the rainfall in spring to fall, pale yellowish tendrils were pushed out from sphaeric pustules of the *Phomopsis*. Besides these *Phomopsis* pustules there were also found smaller bodies which were conical ostioles of the perithecia of *Diaporthe*.

Morphological characteristics of these two fungous forms are as follows:

1. **Conidial stage (*Phomopsis*)** (Fig. 1, Plate 1: C)

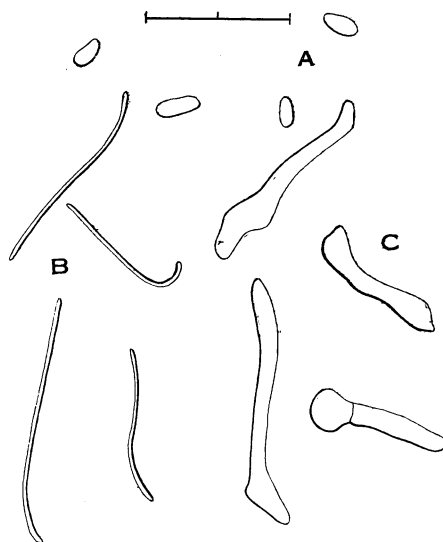


Fig. 1
Imperfect stage of *Diaporthe eres* NIT. (= *Phomopsis*) on paulownia tree
A: A-spores B: B-spores (stylospore)
C: Germinating A-spores
(|—————| = 20 μ)

compact with a few aerial mycelia. Later, they become greenish olive to purplish brown. About a month after at 25°C, several fruit bodies of *Phomopsis* were generally produced on the surface of the compact mycelia. Shortly after, it was usually found that from these fruit bodies pale yellowish and viscous masses consisting of nature conidia or A-spores and stylospores or B-spores oozed out. In these cultures, however, formation of the ascigerous structures has not been detected at all.

By the following experiments it was confirmed that there were no differences between the isolates obtained from pycnospore and those from ascospore.

a. Relation of mycelial growth and kinds of agar medium

By a sterile scalpel, inocula of about 5 mm square isolated from both conidium and ascospore were trasplanted respectively on the several kinds of agar medium*¹ in PETRI dish. Mycelial growth and characteristics of the fungus on each agar medium were observed for a month. In this experiment the fungus grew well on soy agar, malt agar and potato-sucrose agar, but poorly on the others, especially paulownia decoction agar. During the experiment, both isolates originating from ascospore and conidium grew similar in appearance and could not be distinguished from each other. Cultural characteristics of the fungus on various agar media are summarized as follows:

On potato-sucrose agar: Colonies are compact and flat with rough, white and cottony aerial hyphae. Inner mycelia are purplish brown, "Light Cinnamon Drab" to "Fuscous" in color. About a month after, several pycnidia are produced on the surface of the colony and then yellowish conidial masses, cosisting of A-spores and B-spores, ooze out from them.

On SAITO's soy agar: Colonies are flat and white, but later turn to pale brown, "Haie Brown" to "Chaetura Drab", in color. Surface of the colonies are covered densely with white and cottony aerial hyphae. Pycnidial formations are also found the same as on potato-sucrose agar.

On malt agar: Colonies grow flat at first and later develop with some radial wrinkles. They are white in color and covered with rough cottony aerial hyphae. Pycnidial formation is similar to those of the above cases.

On paulownia decoction agar: Colonies grow slowly, irregularly and flatly. They are colorless except for a few white aerial mycelia at the margin of the colonies. No pycnidial formation is observed.

On WAKSMAN's solution agar: Colonies are compact and white with dense cottony aerial mycelia. Pycnidia are produced on the surface of the colonies about two months later.

b. Relation between temperature and mycelial growth

Comparison of both isolates in relation to temperature and mycelial growth were tested by PETRI dish method using potato-sucrose agar. Diameter of the mycelial colonies

*¹ 1) Potato-sucrose agar: Distilled water 1 l, potato 200 g, sucrose 20 g, agar-agar 20 g.

2) SAITO's soy agar: Distilled water 850 cc, onion decoction 100 cc, Japanese soy 50 cc, sucrose 50 g, agar-agar 20 g.

3) Malt agar: Distilled water 1 l, malt 200 g, agar-agar 20 g.

4) Paulownia decoction agar: Distilled water 1 l, paulownia twig 100 g, sucrose 20 g, agar-agar 20 g.

5) WAKSMAN's solution agar: Distilled water 1 l, glucose 10 g, peptone 5 g, KH₂PO₄ 1 g, MgSO₄ · 7H₂O 0.5 g, agar-agar 20 g.

Table 1. Relation between temperature and mycelial growth of the fungus

Origin of isolates	Temperature (°C)		Diameter of mycelial colony					
	0	9	15	20	25	28	30	35
<i>Diaporthe</i>	0	20	49	74	85	67	35	0
<i>Phomopsis</i>	0	19	49	72	85	64	25	0

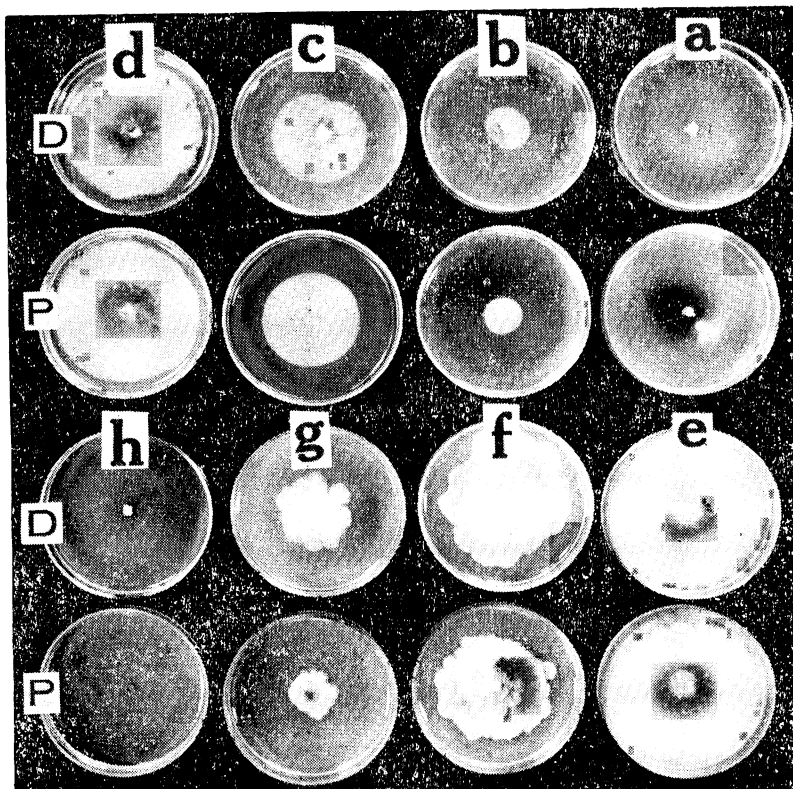


Fig. 3 Relation between the mycelial growth of the fungus and temperatures
 D: Isolate from ascospore of *Diaporthe eres* NIT., P: Isolate from pycnospore of *D. eres*
 a: 0°C, b: 9°C, c: 15°C, d: 20°C, e: 25°C, f: 28°C, g: 30°C, h: 35°C

after a week of incubation at each temperature are shown in Table 1.

As shown in Table 1, both isolates developed much the same as each other, and they grew at from 9°C to 30°C with an optimum at 25°C, but could not grow at 35°C or 0°C. At higher temperatures they grew irregularly at the margin of the colonies (Fig. 3).

2. Inoculation experiment

In order to confirm similarity in the two fungus forms and to determine their pathogenicity, inoculation tests were made to green current shoots and brown old twigs with both isolates from *Diaporthe* and *Phomopsis*. The surface of the current year's shoots was treated with 80 per cent alcohol, sterilized with 0.1 per cent solution of corrosive sublimate and washed with sterile water, and then small slits were incised

with a sterile scalpel on the shoots. In the case of making burned incisions, a burning hot scalpel was used. The bits of the colonies from each of two fungus forms were introduced into these treated slits. The wounds were covered with moist absorbent cotton and paraffin paper for 10 days. As a check sterile agar was used instead of the mycelial colonies.

Inoculations were made in April and August in 1951 and September in 1953. In each of these tests five twigs were prepared for inoculation, and two for check. Many of the inoculated wounds healed over in one or two months after inoculations, but a few of them developed a die-back until the following spring.

Results of these tests are summarized in Table 2.

Table 2. Results of inoculation experiments

Isolates	Treatment	Number* ¹ of inoculation	Number* ¹ of infection	<i>Phomopsis</i> formation	<i>Diaporthe</i> formation
<i>Diaporthe</i>	Current shoot, wound incision	10	0	—	—
	Brown twig, " "	15	0	—	—
	" " burned incision	15	3	+	—
<i>Phomopsis</i>	Current shoot, wound incision	10	0	—	—
	Brown twig, " "	15	1	+	—
	" " burned incision	15	4	+	—
Check	Current shoot, wound incision	4	0	—	—
	Brown twig, " "	6	0	—	—
	" " burned incision	6	0	—	—

*¹ Total of three inoculation series

Re-isolation carried out from conidia on the die-backed lesions resulting from successful inoculations and cultures of them showed similarity to the fungus used as the inoculum.

Considered from the results of the tests mentioned above, pathogenicity of the fungus seems to be not virulent but rather weak, although the *Phomopsis* die-back is very frequently observed in the field.

The evidence obtained by the foregoing culture and inoculation experiments points to the conclusion that the *Phomopsis* is doubtlessly the imperfect stage of the *Diaporthe*.

Taxonomy of the fungus

In foreign countries, the species of *Phomopsis* inhabiting paulownia tree, so far as we have been able to trace, has not been described. In Japan HARA²⁾, however, listed *Phomopsis imperiales* SACC. et ROUM., as a fungus collected on *Paulownia tomentosa* STEUD., without any morphological notes and literature citations. The writers' efforts to find this specific name in SACCARDO's Sylloge Fungorum and others, have failed. SACCARDO et ROUM.¹²⁾ described *Phoma imperiales* on *Paulownia imperiales* SIEBOLD, with a provision that it might be a pycnidial stage of a *Diaporthe*. Judging from these facts, it is thought that HARA transferred arbitrarily the genus name of *Phoma imperiales* to *Phomopsis* by the notes of SACCARDO and ROUM. without making any mycological description.

Diaporthe on the paulownia tree has not been described so far as the writers are aware. Among the many species in WEHMYER's monograph¹⁴⁾ of the genus *Diaporthe*, *D. medusaea* NIT., *D. eres* NIT., *D. beckhausii* NIT. and *D. strumella* (FR.) FCK. seem

to be similar to the writers' fungus. According to him *Diaporthe medusaea* is a species having many synonyms and hosts such as *D. Citri* (on *Citrus*), *D. Eucalypti* (on *Eucalyptus*), *D. faginea* (on *Fagus*), *D. juglandina* (on *Juglans*), *D. ostryigena* (on *Ostrya*), *D. medusina* (on *Platanus*), *D. nodosa* (on *Syringa*), *D. crinigena* (on *Ulmus*) and others. It, however, distinctly differs from the writers' fungus in shape and size of pycnidial stage, and in its elongated necks and clustered perithecia. *Diaporthe backhausii* and *D. strumella* are different from the writers' fungus by the characteristics in the conidial stage, especially B-spores.

Diaporthe eres is also a species having many synonyms. It includes *Diaporthe fallaciosa* (on *Acer*), *D. coneglanensis* (on *Aesculus*), *D. verrucella* (on *Alnus*), *D. exasperaus* (on *Betula*), *D. sordida* (on *Corpinus*), *D. castaneti* (on *Castanea*), *D. catalpae* (on *Catalpa*), *D. conorum* (on conifers), *D. scobina* (on *Fraxinus*), *D. magnoliae* (on *Magnolia*), *D. scabra* (on *Platanus*), *D. forabilis* (on *Populus*), *D. rhois* (on *Rhus*) and others, and they are very similar to the writers' fungus in morphological characteristics except for the lack of ventral zone in the latter.

Diaporthe vaccinii SHEAR¹⁵⁾ on blueberry and cranberry fruit have smaller ascospores and pycnosporos (A- and B-spores), than the paulownia fungus.

In our country, *Diaporthe moriokaensis* SAWADA¹³⁾ on *Acer formosum*, *D. Take HARA*³⁾ on bamboo and *D. nomurai* HARA⁴⁾ causing a blight of mulberry have been known as the indigenous species. These three species are distinguished from the fungus under consideration by their larger asci and ascospores.

Other *Diaporthe* recorded in our country, namely *D. Aucubae* SACC.^{5,11)} on *Aucuba*, *D. leiphaemia* (FR.) SACC.^{5,14)} on *Quercus* and *D. umbrina* JENKINS^{5,7)} also differ distinctly from the writers' fungus.

From the fact mentioned above it is apparent that among the many species of *Diaporthe* reported hitherto *Diaporthe eres* NIT. quite agrees with the present writers' fungus. Hence, the writers have come to the conclusion that the paulownia fungus under consideration is identified as *Diaporthe eres* NIT. Relation between the *Diaporthe* and *Phomopsis* collected from the paulownia tree is as follows:

Diaporthe eres NITSCHKE

Syn.: *Phoma imperiales* SACC. et ROUM. Syll. Fung. 3: 92, 1884.

Phomopsis imperiales SACC. et ROUM. Bot. Mag. (Tokyo) 27: 67, 1913.

Hab.: On dead twigs of *Paulownia tomentosa* STEUD. (Feb. 22, 1951, Meguro, Tokyo, Japan, by, T. KOBAYASHI)

Summary

On the die-backed twigs of *Paulownia tomentosa* STEUD. a species of *Diaporthe* often occurs together with a *Phomopsis*. Genetic relation between them and identification of them were studied in this paper. They are identical with *Diaporthe eres* NIT. and *Phoma imperiales* SACC. et ROUM., respectively, and it is proved that the latter is the imperfect stage of the former.

Results of inoculation experiments showed that the fungus is only slightly pathogenic.

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Explanation of plate

Plate 1

A: *Paulownia tomentosa* STEUD. affected by a die-back

B: Die-backed twigs producing perithecia of *D. eres* ×1

C: Die-backed twigs producing pycnidia (*Phomopsis*) of *Diaporthe eres* NIT. ×1

D: Perithecia of *D. eres* ×90

E: Perithecium of *D. eres* ×150

