

THE IDENTITY OF THE FOOTROT FUNGUS OF FLAX¹

De identiteit van de „dode harrel“-schimmel van vlas

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From comparative morphological studies and inoculation tests it is concluded that the footrot fungus of flax (current name *Ascochyta linicola* Naoum. & Vass.) can be distinguished from a ubiquitous soil-borne fungus (current name *Phoma solanicola* Prill. & Del.) only by its pathogenicity on flax and its general appearance *in vitro*. The correct name of the latter fungus proved to be *Phoma exigua* Desm. For the footrot fungus the new combination *Phoma exigua* Desm. var. *linicola* (Naoum. & Vass.) Maas is proposed. A documentation of the synonymy and literature are given for both organisms, and misapplications are discussed.

INTRODUCTION

In diagnostic mycological work at the Plant Protection Service it was noticed that the *Phoma*-like footrot fungus of flax (see e.g. KERR, 1953) shows much similarity to a ubiquitous soil-borne fungus which is often associated with disease symptoms of many plant species. This ubiquitous fungus is well known, under the name *Phoma solanicola* Prill. & Del., as the cause of the “gangrene” disease of potato, see MALCOLMSON (1958b).

By means of comparative morphological studies and pathogenicity tests the relation between the footrot fungus and the ubiquitous soil-borne fungus was investigated. The cabbage parasite *Leptosphaeria maculans* (Desm.) Ces. & de N., stat.con. *Plenodomus lingam* (Tode ex Fr.) Hoehn. was also involved in this study. ROST (1938:428) stated that this fungus may infect seedlings of flax and BREYER (1963:178) pointed out that there exists a great morphological similarity between *P. lingam* and the footrot fungus of flax. Additional inoculations were made with *Peyronellaea nicotiae* Leduc (1958), a fungus described from flax seed and most probably the same fungus which NICKLOVA (1949) connected with footrot symptoms of flax.

Finally literature and original herbarium specimens were studied to trace which *Phoma*-like fungi described from flax might be related to the footrot fungus.

MATERIALS AND METHODS

The organisms compared

The following organisms were compared: *a* five isolates of the footrot fungus: AL¹⁻⁵, received from Dr. Ir. J. VAN DER SPEK, Institute of Phytopathological Research (I.P.O.), Wageningen; *b* four isolates of the ubiquitous soil-borne fungus: PS¹⁻⁴, isolated respectively from potato, dahlia, lettuce and periwinkle; *c* an isolate of *Leptosphaeria maculans*, stat.con. *Plenodomus lingam*, isolated from cabbage and *d* an isolate of a fungus identified as *P. lingam*: BBA No. 8615, received from the “Biologische Bundesanstalt für Land- und Forstwirtschaft”, Berlin-Dahlem, which was compared by BREYER (1963) with the footrot fungus of flax.

¹ Accepted for publication 18 May, 1965.

The isolates were studied on cherry agar (300 ml juice from 500 g cherries + 1300 ml H₂O + 27.5 g agar) in petri dishes at room temperature.

Comparative pathogenicity tests

In the comparative inoculation tests all the isolates mentioned were used except for three strains (AL³⁻⁵) of the footrot fungus. In addition, a comparative inoculation test was made with a strain of *Peyronellaea nicotiae*, isolated from gherkin. In all tests the flax seed used was received from the Government's Seed Testing Station, Wageningen, where it had been found to be free from pathogenic fungi.

In the first test 50 flax seeds were submerged for about 15 minutes in a spore suspension of each isolate and were subsequently sown in steam-sterilized soil. Spore suspensions were obtained by shaking dislodged pycnidia from cultures on sterilized lupin stems in tap water. All isolates sporulated well on lupin stems. The spore concentrations in the suspensions were determined with a haemocytometer and were then brought to a fixed concentration of 5×10^7 spores/ml by dilution with water.

A second test was carried out by mixing a fragmented sporulating pure culture (one plate culture on cherry agar per pot) with the upper layer, about 2 cm, of steam-sterilized soil in 500 ml pots (\varnothing 10 cm). The inocula for this test consisted of re-isolates from the first experiment. After about one week 25 flax seeds were put into the soil infected in this way.

In a third test 20 flax seedlings about two weeks old were used for each isolate; they were dusted copiously with Carborundum powder, after which the stem bases were rubbed between thumb and forefinger. The thus slightly wounded plants were sprayed by means of a hand-atomizer with the same spore suspensions as described for the first test. The plants were then enclosed in polyethylene bags for one week.

Re-isolations were made immediately from all plants that died during the tests. At the end of each test, about three months after inoculation, all plants were judged for disease symptoms and re-isolations were also made from the plants showing symptoms.

In all tests the control plants were treated in an identical way, using tap water and sterile cherry agar.

RESULTS

Comparison of the organisms

The general appearance *in vitro* of the five isolates of the footrot fungus (Fig. 1, A-C) is characterized by slow compact growth and great uniformity. In the centre of the initially white culture a dark greenish-black colour appears, that soon spreads over the mat, leaving a narrow white margin of about 3 mm. In older cultures this white margin becomes indistinct and the entire colony turns dark. The isolates usually produce only a few pycnidia. When the pycnidia mature spores are extruded in a pinkish exudate.

The ubiquitous soil-borne fungus (Fig. 1, D-F) shows a very variable growth habit *in vitro*. The various cultural types usually appear as sectors in a pure culture of the fungus. Types with little pigment formation occur together with types of which the submerged mycelium shows a blackish-green colour.

This pigmentation, however, is seldom as strong as in the case of the footrot fungus. Little pigmentation is often associated with sparse aerial mycelium and many pycnidia (Fig. 1, D) or with much aerial mycelium and few pycnidia (Fig. 1, E)². The quantity of aerial mycelium and the number of pycnidia in pigmented types can be characterized as "intermediary" (Fig. 1, F). Cultures of these pigmented types often produce sectors corresponding to the above mentioned types with little pigment (compare HANSEN, 1938). The pycnidia have a dark tint just like those of the footrot fungus, whereas the spores are extruded in a white or pinkish slimy exudate.

Microscopic examination has proved that there are no true morphological differences between the footrot fungus and the ubiquitous soil-borne fungus. In both, the pycnidia arise in a simple meristogenous manner (KEMPTON, 1919). In a few cases closely adjacent hyphae may take part in the formation, which then becomes compound meristogenous (KEMPTON, l.c.). In both types the mature pycnidia vary in shape and size. Usually they are globular with the opening in a papilla. In pycnidial primordia structural provision for the formation of the opening can already be observed, hence one can speak here of a true ostium. The diameter of mature pycnidia varies from 75 to 200 μ . This includes compound pycnidia, arising from two or more simple pycnidia growing together. In both cases the pycnidial wall is made up of a small number of cell-layers. The outer layer consists of elongated cells with dark coloured walls, whereas the cells of the inner layer are isodiametrical with hyaline walls. The spores arise on the inner cell-layer by budding. The pycnidiospores are hyaline, globular to oblong-elliptical and sometimes a little curved. The majority are continuous, $6.0 \times 3.4 \mu$ ($4.2 - 8.5 \times 2.5 - 4.2 \mu$); a small percentage is 1- (occasionally 2-) septate, $8.5 \times 4.2 \mu$ ($7.5 - 12.0 \times 3.4 - 5.0 \mu$). The number of septate spores depends to a large extent on the growth conditions and the age of the culture.

Leptosphaeria maculans, stat.con. *Plenodomus lingam* has proved to be quite a distinct type in general appearance as well as morphologically. A description of the characters of this fungus is given by BOEREMA & VAN KESTEREN (1964).

The habit *in vitro* of the isolate BBA No. 8615 which BREYER (1963) compared with the footrot fungus agrees completely with one of the phenotypes of the ubiquitous soil-borne fungus. Morphologically this isolate shows the same characters described above for the footrot fungus and the ubiquitous soil-borne fungus.

Comparative pathogenicity tests

The results of the inoculations are given in Table 1. In all tests the highest percentage of infection and the highest number of dead plants was caused by the isolates of the footrot fungus.

In a few cases infection and dying off was caused by the ubiquitous soil-borne fungus and the isolate BBA No. 8615. In these cases symptoms were in general less serious than those of plants inoculated with the footrot fungus. In the latter case there always appeared an intense brown discoloration of the roots, the root collar and the stem bases, whereas plants infected by the common

² The photographs of the plate cultures were made with transmitted light. For this reason conglomerations of hyaline mycelium are visible as darkly coloured spots in Fig. 1, E.

soil-borne fungus and isolate BBA No. 8615 showed only a limited brown discoloration of the roots.

With *Leptosphaeria maculans*, stat.con. *Plenodomus lingam* no disease symptoms at all were obtained. Also *Peyronellaea nicotiae* caused no disease symptoms. However, at the end of the tests there was always a copious development of the fungus on the inoculated plants, when the latter were stored on humid filter-paper for a few days. Pycnidia of the fungus then appeared abundantly, especially on the naturally yellowed leaves. Also the typical dictyochlamydospores of this fungus were often observed on such leaves.

DISCUSSION AND CONCLUSIONS

It appears that the footrot fungus of flax and the ubiquitous soil-borne fungus cannot be distinguished from each other on the basis of morphology only. On artificial culture medium, however, the footrot fungus is characterized by a slower and more compact growth, a smaller variability in general appearance and a faster and more intensive dark discoloration of the centre of the culture. In this way the footrot fungus can always be clearly distinguished from the ubiquitous fungus *in vitro*. The latter fungus appears to be able to infect flax too. This corresponds well with the known fact that under certain conditions the ubiquitous fungus can cause disease symptoms on many plant species. The footrot fungus, however, shows a greater pathogenicity to flax than does the ubiquitous soil-borne fungus.

The isolate BBA No. 8615, which was compared by BREYER (1963) with the footrot fungus, has proved to be identical with the ubiquitous soil-borne fungus. So this culture has been misidentified as *Phoma lingam* at the "Biologische Bundesanstalt für Land- und Forstwirtschaft", Berlin-Dahlem. *Phoma lingam* (= *Plenodomus lingam*), the conidial state of *Leptosphaeria maculans*, produces quite a different type of pycnidium and pycnidiospores (see BOEREMA & VAN KESTEREN, 1964). The conclusion of BREYER (l.c.), that the footrot fungus shows great morphological similarity to *P. lingam* is therefore due to a misidentification. With *L. maculans*, the true *P. lingam*, neither footrot symptoms nor damping-off of flax seedlings as described by ROST (1938) could be obtained.

Peyronellaea nicotiae appears to be able to develop copiously as a saprophyte on flax. This agrees with the observations of NICKLOVA (1949), concerning the "chlamydospore-producing fungus". However, footrot symptoms, as attributed by her to this fungus, could not be obtained. In addition to this it may be noted that *P. nicotiae* is frequently isolated as a "secondary" organism from all kinds of plant species at the Plant Protection Service.

TAXONOMIC CONSEQUENCES

From their morphological characters, both the footrot fungus and the ubiquitous soil-borne fungus belong to the form-genus *Phoma* Sacc. (compare BOEREMA, 1964; BOEREMA, DORENBOSCH & LEFFRING, 1965; MALONE & MUSKETT, 1964:319).

As regards the relationship between the two fungi one must remember that we are dealing with Deuteromycetes (Imperfect fungi), an artificial classification system, designed only for practical identification purposes. From this point of view it seems reasonable to speak here of two varieties of one fungus,

because both organisms are distinct in culture and in pathogenicity, while from the purely morphological aspect they are indistinguishable.

The oldest name mentioned in connection with the footrot disease of flax is *Phoma exigua* Desm. (1849) (see e.g. DE JONGE, 1933; BREYER, 1963:182). This fungus was originally described from French buckwheat (*Polygonum tataricum* = *Fagopyrum tataricum*). On the basis of his *exsiccata*-collections, DESMAZIÈRES came to the conclusion that *P. exigua* may occur also on other crops. In this connection WESTENDORP (*in* Herb. Crypt. belge, No. 1137; Jard. Bot. Bruxelles: BR³), has identified the fungus on flax for the first time as *P. exigua*.

From an examination of the holotype of *P. exigua* on buckwheat (Pl. crypt. France, Ed. I, No. 1869; Herb. Lab. Cryptog. Mus. Paris: PC) it was clear that the pycnidia and pycnidiospores of this fungus agree completely with both varieties of the fungus here discussed. The same conclusion with regard to the footrot fungus has already been reached by KERR (1953) on the basis of studies on an isotype of *P. exigua* (Pl. crypt. France, Ed. I, No. 1869; Herb. Royal Bot. Gardens, Kew: K). In accord with DESMAZIÈRES' opinion that *P. exigua* is a "polyphagous" species, it may now be concluded that this name concerns the ubiquitous soil-borne fungus. It is noteworthy that phenotypes of this common soil-borne fungus were isolated from buckwheat in the Netherlands. *P. exigua* thus represents the oldest name yet known for the ubiquitous soil-borne fungus.

Further investigations revealed that the oldest valid name for the footrot fungus is *Ascochyta linicola* Naoum. & Vass. (1926). It thus becomes clear that the footrot fungus can now be considered as a variety of *P. exigua*, with as basionym *A. linicola*. The above mentioned facts are further documented in the synonymy of the two varieties:

PHOMA EXIGUA Desm. var. *EXIGUA*

in Ann. Sci. nat. (Bot.), Ser. 3, 11:282-283. 1849; Pl. crypt. France, Ed. 1 (Fasc. 38), No. 1869 a. 1849.

syn. e.g.: *Phoma solanicola* Prill. & Del. *in* Bull. Soc. mycol. Fr. 6:179. 1890.

? : *Phoma linicola* Bub. *in* Ann. naturh. Hofmus., Wien 28:203. 1914.

Habitat: Ubiquitous soil-borne fungus, often associated with dying plant tissue.

Misapplications:

Phoma exigua sensu Renouard, Etude culture, rouissage & teillage du Lin, Paris 132.1890; *sensu* Lepik *in* Mitt. VersSta. Phytopath. Univ. Tartu 7: 11, 14.1931; *sensu* de Jonge *in* Tijdschr. PlZiekt. 39:7-9.1933; *sensu* Johansen *in* Tidsskr. Planteavl 48:228-233.1944. = next discussed *P. exigua* var. *linicola*.

Phoma exigua sensu Rost *in* Angew. Bot. 20:427.1938; *sensu* Nicklova *in* Ochr. Rost. 22:123.1949. = ? *Peyronellaea nicotiae* Leduc.

Descriptions and illustrations:

KÖHLER *in* Angew. Bot. 10:113-139, figs. 1-9.1928 (*Phoma solanicola*); DENNIS *in* Trans. Brit. mycol. Soc. 29:11-26, fig. 1:C, G, fig. 3:2-4, 6, 7, 10, pl. 1, fig. 4.1946 (*Phoma solanicola*); MALCOLMSON *in* Trans. Brit. mycol. Soc. 41:413-418, pl. 22, figs. 1, 2.1958 (*Phoma solanicola*).

Specimens examined:

Exsiccata: DESMAZIÈRES, Pl. crypt. France, Ed. 1 (Fasc. 38), No. 1869 a (*Phoma exigua*; PC, holotype; K, isotype); DELACROIX herb. (*Phoma solanicola*; VER⁴, type); BUBAK herb. (*Phoma linicola*; BKL, type); GROVE herb. (*Phoma exigua*; K).

³ The herbaria mentioned in this paper are coded according to LANJOUW & STAFLEU (1959).

⁴ VER = Stat. centr. Path. veg. Versailles (not inserted by LANJOUW & STAFLEU, 1959).

Cultures: Isolate from potato received from MALCOLMSON (*Phoma solanicola*); isolate BBA No. 8615 examined by BREYER (1963) and received from the "Biologische Bundesanstalt" at Berlin-Dahlem (*Phoma lingam*, misapplied).

As has already been stated in the introduction, this ubiquitous fungus is well known as a wound and weak parasite of potato, under the current name of *Phoma solanicola*. For a discussion of the other names used for this fungus on potato, reference may be made to MALCOLMSON (1958a).

The type specimen of *Phoma linicola* contains a fungus indistinguishable from *P. exigua*. As *P. linicola* was not described from flax but from *Linum orientale* Boiss. (= *L. mucronatum* Bertol.) it is not likely to be the flax parasite. The further synonymy of *P. exigua* is still under investigation at the Plant Protection Service.

The fungus identified as *P. exigua* by ROST (1938) and NICKLOVA (1949) (see under "Misapplications") is supposed to produce chains of chlamydospores. *P. exigua*, however, has never been observed producing real chains of chlamydospores, whereas such chains are a typical character of *Peyronellaea nicotiae* described from flax seed by LEDUC (1958). Moreover NICKLOVA (l.c.) records that pycnidia of this "chlamydospore-producing fungus" occur often on seeds of flax. The whole description she gives of this fungus points to *P. nicotiae*.

PHOMA EXIGUA Desm. var. *LINICOLA* (Naoum. & Vass.) Maas comb. nov.

basionym: *Ascochyta linicola* Naoum. & Vass. apud NAOUMOFF in Mater. Mikol. Fitopat. Ross. 5:3.1926; in Mycology, Leningr. 1.1926 (fide DIDDENS in Tijdschr. PlZiekt. 35:251-253.1929 and KERR in Trans. Brit. mycol. Soc. 36:66-68.1953).

synonym: *Phoma linicola* Marchal & Verplancke in Bull. Soc. Bot. Belg. 59:22.1926 (fide KERR in Trans. Brit. mycol. Soc. 36:68.1953); non *Phoma linicola* Bub. in Ann. naturh. Hofmus., Wien 28:203.1914 (= *P. exigua* var. *exigua*); nec *Phoma linicola* Naoum. in Mater. Mikol. Fitopat. Ross. 5:3.1926; in Mycology, Leningr. 1.1926 (= *Macrophoma* ?).

?: *Diplodina lini* Moesz in Magyar Bot. Lapok 29:35-38.1930.

habitat: Associated with damping-off of flax seedlings and brown discoloration of roots, root collar and stem bases of flax (*Linum usitatissimum*). Good descriptions of the disease symptoms (footrot, dead stalks, dode harrel, koude brand, Ascochyta-ziekte, Stengeldürre, mortlin, etc.) are given by DIDDENS (1929), MCKAY (1947: 18-21), MUSKETT & COLHOUN (1947:39-44), KERR (1953:64) and BREYER (1963: 164-178).

Misapplications:

Phoma exigua sensu several authors on the footrot disease (see under "Misapplications" of *P. exigua* var. *exigua* = common soil-borne fungus).

Phoma herbarum sensu Ritzema Bos in Tijdschr. PlZiekt. 11:25.1905; *sensu* Kühnert, Flachs, Kultur & Verarbeitung, Berlin 62. 1920; *sensu* Kirchner, Krankheiten & Beschädigungen landw. Kulturpflanzen, Stuttgart 315-316.1923 (*P. herbarum* Westend. = ubiquitous saprophytic fungus, quite different from both varieties of *P. exigua*, see BOEREMA in Persoonia 3:9-16.1964).

Phoma lini sensu Rost in Angew. Bot. 20:427.1938; *sensu* Rüdiger in Beitr. Agrarwiss. 2:3-7.1948; *sensu* Nicklova in Ochr. Rost. 22:121-129.1949 (*P. lini* Pass. = according to the description given by SACCARDO, Syll. Fung. 10:171. 1892, quite a different fungus, occurring on *Linum tenuifolium*; type material could not be obtained).

Descriptions and illustrations:

DENNIS in Trans. Brit. mycol. Soc. 29:11-26, fig. 3:8, 9.1946 (*Ascochyta linicola*); KERR in Trans. Brit. mycol. Soc. 36:61-73, fig. 1, pl. 4: figs. 1-4, 6.1953 (*Ascochyta linicola*); BREYER in Wiss. Z. Univ. Halle 12:155-164, figs. 1, 2, 4-9.1963 (Stämme I, III and IV); see also this paper under "Comparison of the organisms".

Exsiccatum examined:

WESTENDORP, Herb. Crypt. belge, Fasc. 23, No. 1137.1857 (*Phoma exigua* Desm., misapplied; BR).

Of the many names used for the parasite of flax only the three mentioned in the synonymy should receive consideration. Only in these three instances is *Linum usitatissimum* mentioned as a host in the description. On other hosts it is impossible to ascertain whether the description relates to the footrot fungus or not.

Type material of *Ascochyta linicola* has been examined by DIDDENS (1929) and by KERR (1953). From their investigations it may be deduced, without any doubt, that this name concerns the footrot fungus. The same holds for *P. linicola* Marchal & Verplancke, of which KERR (l.c.) also has examined type material. However *P. linicola* Marchal & Verplancke is illegitimate as a later homonym of *P. linicola* Bub. (= *P. exigua* var. *exigua*), hence it cannot be used as basionym for a new combination.

The type specimens of *Diplodina lini* were lost during the second world war (communicated by Dr. SANDOR TÓTH, Mus. Nat. Hist., Dep. Bot., Budapest: BP). However, the description of *D. lini* points to this fungus being the footrot fungus.

SAMENVATTING

Om na te gaan in hoeverre de „dode harrel”-schimmel van vlas (in Nederland bekend als *Ascochyta linicola* Naoum. & Vass.) identiek is met een algemeen voorkomende zwak parasitaire grondschemmel (o.a. bekend als *Phoma solanicola* Prill. & Del.) zijn een aantal stammen van deze twee schimmels aan een vergelijkend onderzoek onderworpen, waarbij behalve de morfologische kenmerken ook de totale habitus in vitro en de pathogeniteit ten opzichte van vlas zijn onderzocht. In verband met bepaalde literatuurgegevens is ook de koolparasiet *Leptosphaeria maculans* (Desm.) Ces. & de N. (stat. con. *Plenodomus lingam* (Tode ex Fr.) Hoehn.) en de van vlaszaad beschreven maar algemeen voorkomende schimmel *Peyronellaea nicotiae* Leduc bij dit onderzoek betrokken.

TABLE 1. Results of three different inoculation tests on flax (see “Materials and Methods”). In the second test re-isolates from the first test were used as inoculum.

Resultaten van drie verschillende inoculatieproeven bij vlas.

a = percentage of completely dead plants/percentage geheel afgestorven planten

b = total percentage of infected plants/totale percentage aangetaste planten

Inoculation methods	Seed infection		Soil infection		Aerial infection	
	a	b	a	b	a	b
Isolates						
Footrot fungus / „Dode harrel”-schimmel						
AL ¹	62	67	32	64	65	90
AL ²	—	—	48	60	55	70
Ubiquitous soil-borne fungus / Algemeen voorkomende grond-schimmel						
PS ¹	4	10	0	12	0	0
PS ²	6	14	16	24	0	0
PS ³	0	0	0	0	0	0
PS ⁴	0	0	0	0	0	0
BBA No. 8615	4	6	4	4	0	0
<i>Leptosphaeria maculans</i> , stat. con. <i>Plenodomus lingam</i>	0	0	0	0	0	0
<i>Peyronellaea nicotiae</i>	0	0	0	0	0	0
Control	0	0	0	0	0	0
Isolates	a	b	a	b	a	b
Inoculatie-methoden	Zaadbesmetting		Grondbesmetting		Bovengrondse besmetting	

Het bleek, dat de „dode harrel”-schimmel alleen door zijn afwijkende uniforme groei in cultuur en door zijn veel grotere pathogeniteit ten opzichte van vlas is te onderscheiden van de algemeen voorkomende grondschemmel (fig. 1; tabel 1). Derhalve werd geconcludeerd, dat we hier het beste kunnen spreken van twee variëteiten van één schimmel, welke gezien de morfologische kenmerken thuishoort in het geslacht *Phoma* Sacc. De oudst bekende naam van de algemeen voorkomende grondschemmel bleek *Phoma exigua* Desm. te zijn. Voor de „dode harrel”-schimmel werd de nieuwe combinatie *Phoma exigua* var. *linicola* (Naoum. & Vass.) Maas geïntroduceerd. Van beide organismen is een documentatie gegeven van de synonymie, literatuurgegevens en „onjuiste toepassingen”.

De twee andere onderzochte schimmels, welke morfologisch van een geheel ander type zijn dan *Phoma exigua*, bleken niet pathogeen te zijn voor vlas (tabel 1). Voor de algemeen voorkomende *Peyronellaea nicotiae* bleek afgestorven vlas een bijzonder geschikt substraat te zijn. Het literatuurgegeven dat *Phoma lingam* (= *Plenodomus lingam*) morfologisch veel overeenkomst vertoont met de „dode harrel”-schimmel bleek op een misidentificatie te berusten en heeft in feite betrekking op de algemeen voorkomende grondschemmel.

ACKNOWLEDGEMENTS

The author is greatly indebted to Drs. G. H. BOEREMA, Head of the Mycological Section of the Netherlands Plant Protection Service, for his guidance during the work. This investigation was made possible thanks to the help of the Directors of the herbaria at Brooklyn, Brussels, Budapest, Kew, Paris and Versailles and the Director of the “Biologische Bundesanstalt für Land- und Forstwirtschaft” at Berlin-Dahlem.

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