TIJDSCHRIFT OVER PLANTEZIEKTEN

Onder redactie van Dr. J. A. VON ARX; Mej. H. L. G. DE BRUYN; Mevr. Ir. M. POST-BAKKER; Prof. Dr. J. P. H. VAN DER WANT en Dr. H. H. EVENHUIS (secretaris)

Redactie-adres:

Instituut voor Plantenziektenkundig Onderzoek, Binnenhaven 4a, Wageningen

Drukkers-Uitgevers: H. Veenman & Zonen N.V. - Wageningen

67e JAARGANG (1961)

AN UNDERGROUND ATTACK OF THE RUST UROMYCES COLCHICI ON COLCHICUM IN THE NETHERLANDS¹

Met een samenvatting: Een in Nederland waargenomen ondergrondse aantasting door de roest Uromyces colchici bij Colchicum

BY

G. H. BOEREMA

Plantenziektenkundige Dienst, Wageningen

Introduction

Colchium rust in the Netherlands was first brought to our attention in 1955 by a representative of the Plant Quarantine Division, United States Department of Agriculture. The finding was made by Mr. N. G. SANTACROCE, an official of that Division, who has been working in The Netherlands by cooperative agreement on the pre-shipment clearance of flower bulbs. The first Colchicum found to be infected by him was the Colchicum hybrid "Violet Queen". The rust was found on the dry, outer tunic of the corm.

Since that time this disease has been intercepted several times on the same hybrid. Indications are that the disease has become widespread in the hybrid "Violet Queen". The disease has also been discovered on growing plants in the field.

Mr. N. G. Santacroce (unpublished) reports that this rust has also been found on the dry tunics of *Colchicum bornmuelleri* Freyn and the *Colchicum* hybrids "Autumn Queen" and "The Giant".

By careful examination of the material it appears that this curious rust, ocurring for the most part on the subterranean parts of *Colchicum* in The Netherlands, is identical with *Uromyces colchici* Massee. This species is reputed to be of great rarity; it has been found only on two other occasions in England.

HISTORY OF THE ABOVE-GROUND ATTACK OF UROMYCES COLCHICI

The Fungus

Uromyces colchici was first described by MASSEE in 1892: "Sporeclusters

¹ Accepted for publication 1 Nov., 1960.

numerous, large, elliptical, sometimes, circinating blackish-brown, occurring on both surfaces of the leaf; teleutospores broadly elliptical or subglobose, apex slightly prominent, and pierced by a single germspore, epispore about 24 μ thick, smooth, bright-brown, 28–38 \times 21–28 μ ; pedicel colourless, persistent, uniformly attenuated towards the base, 70–80 \times 5–6 μ . On Colchicum spectabilis, Kew Gardens."

This description has been copied into the textbooks of Cooke (1906) and Grove (1913). Grove (1913) investigated the original material of Massee and corrected the description of the teleutospores as follows:

"Spores subglobose to ovate, rounded above, with a broad flat hyaline papilla, smooth, pale-brown, $28\text{--}40 \times 20\text{--}28\,\mu$; epispore $3\text{--}3\frac{1}{2}\,\mu$ thick; pedicels hyaline, rather long, but very deciduous."

The type material of *U. colchici* is deposited at the Herbaria of the New York Botanical Garden, and of the Royal Botanical Gardens at Kew where three leaf-fragments with teleutosori remain. From our investigation of the latter, it is established that Grove's (1913) description of the teleutospores of *U. colchici* (fig. 1) is the most accurate. It must be noted, however, that the spores are not smooth, but instead are covered with regularly arranged small warts. This is clearly seen when one examines the teleutospores dry or in an air-bubble (fig. 1C).

WILSON & BISBY (1954) also investigated the material at the Kew Herbarium and concluded that U. colchici bore great resemblance to Uromyces gageae Beck. A great deal of controversy exists concerning the identity of *U. gageae*. Some authors believe that this rust is the same as *Uromyces ornithogali* Lév. (e.g. Guyot, 1951). Others infer that U. gageae and U. ornithogali are not identical at all (e.g. Hylander, Jørstad & Nannfeldt (1953) who indicate U. ornithogali with the synonym Uromyces acutatus Fuck. Nevertheless, it is absolutely certain that U. colchici is not identical to the known rusts occurring on Gagea spp. and Ornithogalum spp. The teleutospores of U. colchici are very characteristic and differ from those of *U. gageae* and *U. ornithogali*. For instance, the teleutospore of U. colchici has an obviously broad and flat papilla (vide fig. 1 and Grove, 1913). The spores of the species U. gageae as well as those of U. ornithogali have papillae which are narrow and long. Furthermore, the epispore of *U. colchici* is considerably thicker than that of either *U. gageae* or *U.* ornithogali. It is by this characteristic papilla that U. colchici can be distinctly distinguished from all other Uromyces species described on bulbous and rhizomatous plant species in the families Amaryllidaceae, Iridaceae and Liliaceae.

From the observations of MASSEE (1892, 1899) it may be said that U. colchici

 $^{^{1}}$ The background of this controversy was a dispute as to whether there are or are not present little warts on the teleutospores. In $U.\,gageae$ the teleutospores are supposed to be smooth and decidedly verruculose in the case of $U.\,ornithogali$. In our investigations of $U.\,gageae$ and $U.\,ornithogali$ from material obtained from the herbaria at Kew, Leyden and Groningen it would appear that there is actually a question of two types. In some of the exsiccates examined, the dark-brown teleutospores showed conspicuously clear warts, while most of the exsiccates, among which was the original material of Beck, the teleutospores which were coloured palebrown were quite smooth. However, from a casual examination, it is found that the spores of latter type (pale-brown) are also covered with little warts! This can be seen more clearly when the spores are observed dry or in an air-bubble.

is a rust which does not change of host-plant (autoecious), forming teleutospores solely, which must hibernate before germination (micro-type)¹.

The above-ground symptoms as observed by MASSEE

Massee reported the extremely large elliptical teleutosori ($5-8 \times 3-5$ mm) on both sides of *Colchicum*-leaves (compare fig. 2A).

The sorus on the leaf-fragment from the herbarium at Kew which we examined measured 7×3.5 mm (fig. 2B). These sporeclusters remain covered a long time by the epidermis, and are often found to be circinating on the leaf-blade (fig. 2A). Massee found them more commonly on the lowest leaf (first formed leaf). The sori appear to develop first on the leaf-sheath and later occurring on the leaf-blade as well. On the higher (later developed) leaves only some sporadically scattered teleutosori were found, always developing much later, which suggests an upward extension of the mycelium (Massee, 1892).

Host plants and localities of the above-ground infection

The host-plant mentioned in the original description of Massee in 1892 as Colchicum spectabilis has not been described elsewhere. The specific identification of this host plant, apparently, appears to be a mistake, because later on MASSEE (1899, 1915), COOKE (1906), and GROVE (1913) continually write about Colchicum speciosum Stev. It is from this latter species, which has its origin in Asia Minor and the Caucasus, that many Colchicum hybrids (Boom & Ruys, 1950) have been derived. For two years, MASSEE (1892) found the rust exclusively on this species of *Colchicum*, which was evidently so susceptible that all plants on the plot were infected with the rust. In the third year, MASSEE (1899, 1915) observed that the rust had infected the adjacent plants of Colchicum autumnalis L. and "Colchicum bavaricum". The latter species has never been described as such; however, Wilson & Bisby (1954) have concluded that C. bavaricum is a synonym of C. variegatum L. which also comes from Asia Minor. Moore (1959) has adopted this interpretation. Following the observations of MASSEE, U. colchici was found once more in Yorkshire, England (Mason & Grainger, 1937) on an unidentified species of Colchicum.

GUYOT (1951) points out that UNGER (1833) mentioned the presence of an *Uredo* sp. on *Colchicum autumnale* L. in Austria. This might have been the same rust as *U. colchici*, since formerly many species of *Uromyces* were listed as *Uredo* (compare GÄUMANN, 1959²). Unfortunately UNGER did not give a description, consequently the relationship of this fungus cannot be established.

Besides the reports mentioned above, we know of no other observations on the occurrence of this fungus on the above-ground parts of *Colchicum*. Therefore the remark of GÄUMANN (1959) "Verbreitungsgebiet sporadisch durch ganz Europa" (occurring sporadically in all Europe) is only hypothetical.

¹ During the German expedition to the Himalaya in 1937, a rust with an aecidium stage was found on the leaves of *Colchicum aureum* Bak., which was described by ULBRICHT as *Aecidium colchici – aurei* Ulbr. (See Moore, 1949 as well). In France, a rust with an uredial stage very similar to an aecidium had been found on *Colchicum autumnale* L., which was described as *Uredo colchici – autumnalis* Guyot & Massenot (Guyor, 1958).

It is, however, certain that these stages of rusts do not belong to the life-cycle of *Uromyces colchici* Massee.

² Unger (1833) did not use the binomen *Uredo colchici* as Gäumann (1959) erroneously concluded from Guyot (1951).

DESCRIPTION OF THE UNDERGROUND ATTACK

Hostplants

The Colchicum hybrid "Violet Queen" produces pretty, dark-purple flowers with a white base. Corms of this variety have been found infected with Uromyces colchici since 1955 in the Netherlands. The parental origin of this hybrid, already distinguished as "first class" in 1927 (Anonymus, 1956) can no longer be traced. Undoubtedly, however, it appears to be an offspring of the rose-purple flowering C. speciosum Stev. (Boom & Ruys, 1950), the species on which U. colchici was originally found. This is also true of the Colchicum hybrids "Autumn Queen" and "The Giant" which are also reported as being attacked by U. colchici. Both hybrids have been in cultivation for a long time (Anonymus, 1956). Colchicum bornmuelleri Freyn has also been observed infected by this rust. Both C. bornmuelleri and C. speciosum came originally from Asia Minor.

Symptoms of the disease

The teleutosori of *U. colchici* were found on the corm-tunic of the above-named *Colchicums*. This tunic is the well developed sheath of the lowest leaf. In most cases, the teleutosori were found exclusively on the innerside of the tunic (compare fig. 3). In some cases, however, teleutosori were observed on the outer side of the tunic and located at the same position on the tunic as the inner teleutosori.

Infections of the tunic are usually confined to one side of the corm. Usually, this was a "side" of the characteristic bilateral symmetrical corm (compare figs. 3A, 5, 6). In a few cases, the infection was not quite so obviously one-sided and the teleutosori were also found on the flattened, extended side of the corm (fig. 3C).

From the specimens examined, teleutosori were also found on the upper part of the corm-tunic, that is on that part of the tunic which encloses the (old) stem. Coincidentally, it is found that sometimes on the growing plant, spots of the rust can be seen on the blanched part of the sheath of the lowest leaf. Tunic (outer covering of corm) infections are naturally visible only after the corms have been dug from the soil. Teleutosori have never been observed on the green parts of the leaf-sheats nor on the leaf-blades of the growing plants in The Netherlands. Sometimes, *Colchicum* plants having infected corms, showed conspicuous yellow spots on the leaf-blade of the lowest leaf. All other above-ground parts of the plant and the fleshy part of the corm showed no signs of the disease. It would appear, therefore, that infection remains restricted to the tunic (including leaf-sheath).

Teleutosori can be observed most clearly immediately after digging, before the tunic becomes dry and brown. It is at this time, when the tunic is still light coloured, that there is the greatest contrast with the dark-brown sporeclusters. When teleutosori are formed on the inner side only, the outer symptoms of the tunic will show as somewhat swollen, brown spots (fig. 3A, B). By carefully separating the infected part of the tunic from the flesh, there is observed an excellent view of the sporeclusters formed on the inner side of the tunic (fig. 3D, left). In doing so, spores of the rust usually remain adhering to the white flesh of the corm giving the appearance of a brownish-black powder (fig. 3D, right). When the teleutospores become mature, the tunic becomes broken or torn in the center of the infected spot (fig. 3C, D).

It is remarkable, that the teleutosori, which are at first covered by the epidermis (fig. 4), are often arranged in concentric rings (fig. 3D). In most cases, it could be established that infection had developed along the vertically running main veins (fig. 3B, 4).

The dimensions of the teleutosori are 1–3 mm by 1–8 mm, but often there is no definate separation between sori. The teleutospores were completely identical in detail to those examined from material of MASSEE of the Kew-Herbarium (fig. 1).

It was noted that when the tunic becomes brown and dead which is usually at the time of late harvest or later, the teleutosori become less prominent. The tunic then has nearly the same colour as the granular masses of teleutospores (fig. 5A). As a result of the development of the teleutosori on the inner side of the tunic, it becomes lossened from the flesh at these spots. As result of this separation, rather large segments of the infected tunic remain in the ground during corm harvesting (figs. 5B, 6). The brownish-black powdery spores on the white cormflesh are rather conspicuous at this time (fig. 6).

In so far as the infected tunic has not yet come off, characteristic, dark-brown, concentric rings may often be seen in diseased spots (fig. 5B).

In experiments with diseased corms, completely healthy flowers developed in the field with no evidence of infection. All leaves were also quite healthy. The newly-formed corms were in most cases again infected. In a few cases, the newly formed corms, produced by planting diseased corm material, showed no signs of infection.

DISCUSSION

The phenomena of the underground attack

We are confronted here with a curious fact that a rust has been found on the underground tunic of *Colchicum* hybrids and the species *Colchicum bornmuelleri* in The Netherlands, which in the last century had been found incidentally on the leaves of *Colchicum speciosum* and other *Colchicum* species.

This infection may be characterized as being "an underground infection", as the disease develops on that part of the plant which is in the soil, although, some of the teleutosori may develop on the part of the tunic which encloses the stem above the soil level.

This unusual rust attacking the subterranean parts of a plant, is not the only case known, for a quite similar rust attacking the underground parts of the plant has been regularly found on *Crocus* hybrids in The Netherlands since 1956 (BOEREMA, 1959). In the latter case we are concerned with the rust, *Uromyces croci* Pass., a species found regularly on the leaves of different species of *Crocus* in South and South-East Europe, dating back to 1826. A major difference between the underground infections of *Crocus* and *Colchicum* is, that in the case of *Crocus* the fungus attacks the tunic and the fleshy part of the corm, while in *Colchicum* only the tunic is affected. Consequently *U. croci* causes more damage on the whole than *U. colchici* on affected corms.

From the facts established here, there follows the assumption that we are dealing with two rusts which by adaptation have become able to attack the underground parts of *Colchicum* and *Crocus* in The Netherlands. This adaptation is probably on account of the application of special cultivation methods of *Colchicum* and *Crocus* which have been in effect for many decennia. The possibili-

ties for the above-ground life-cycle of these rusts are, in effect, practically reduced to zero by the combination of the practice of harvesting the corms of these plants every year and multi-annual crop rotation. In other words, these rusts can only maintain themselves by adaptation to the underground parts of these plants. Therefore, in these underground infections one could probably speak of genetically "adapted" strains. Naturally, this hypothesis will still need to be proven.

The corm-tunic of *Colchicum*, as has been already stated above when discussing symptoms of the disease, is no more than the well developed leaf-sheath of the lowest leaf. Consequently, the lowest leaf and the tunic are homologous. Since Massee (1892, 1899) observed the infection on the leaf-sheath and leafblade of the lowest leaf, it can be said that there is very little difference between the above-ground infection found by him and the underground infection occurring in The Netherlands. Anatomically, the tunic on Colchicum does not differ greatly from an ordinary leaf. The only real difference is that the tunic lacks chlorophyll. If this is really a question of genetical adaptation in the case of the underground infection, the presence or absence of chlorophyll is perhaps also essential for the respective strains found above-ground and underground. Significantly it is typical in the case of the disease observed in The Netherlands that, whenever teleutosori are found on the above-ground parts, they are found only in the leaf-sheath that is devoid of chlorophyll. In this connection, further investigations referring to the small, yellow spots which are sometimes found on the leaf-blade of the lowest leaf in underground infections may give indications. With the infection of leaves by rust-fungi, chlorophyll is generally only important as an indirect provider of a nutrient-source for the fungus (compare Hors-FALL & DIMOND, 1959).

A striking feature of the underground infection is that the teleutosori are for the most part found on the inner side of the tunic. While MASSEE found the teleutosori on both sides of the leaves, they were apparently found especially on the outer side of the leaf-sheath (fig. 2). Also, in the case of the underground infection of *Crocus* by *Uromyces croci*, the teleutosori are developed mainly on the inner side of the tunic. These are possible logical consequences in the deviating way of life concerning underground infections, because the formation and development of the new plant parts, to become infected by the teleutospores, are produced on the inner side of the old tunic.

The infection cycle of the above-ground and underground attack

From the figures produced by MASSEE (1899, 1915) and COOKE (1906) on leaf infection (compare fig. 2A), it would appear that in above-ground infection the teleutosori were formed in many cases on the veins of the leaf. This was often found to be true in the case of underground infections also (fig. 3A, B). By means of microtome sections (fig. 4), it was further established that the mycelium of the rust in underground infection grows rank in the cells of the vascular bundles (intracellular) and that it communicates from there with the teleutosori formed under the epidermis via whole mycelium strands between the big parenchyma cells of the tunic (intercellular). It seems plausible, therefore, that the extension of the infection, in both cases, has taken place via the veins especially. This is in accordance with MASSEE's observation that the above-ground infection nearly always begins on the leaf-sheath and gradually becomes extended over the leaf-

blade. Therefore, it may be explained that in underground attack observed id The Netherlands, where infection generally occurs underground, the teleutosori will also develop eventually on the above-ground part of the tunic, that is, on the white part of the sheath of the lowest leaf. The formation of teleutosori on the higher, green leaf parts is then possibly prevented by the presence of chlorophyll (see above).

In addition, in view of the concentric arrangement of the teleutosori commonly found in the above-ground infection reported by MASSEE (1899, 1915) (cf. fig. 2), and in the underground infections (fig. 3D), there is also question of a concentrical extension of the mycelium. In the case of the underground infection, this concentrical extension is exceedingly conspicuous on account of the dark-brown, concentric rings in the dead, dry tissue (fig. 5B).

From Massee's descriptions, it may be derived that in the case of above-ground attacks, secondary infections did not occur in the same season. Consequently, all teleutosori on the plants had developed in the above-mentioned systemic way from a primary infection in the spring. This is further explained by the absence of other spore-stages and by the fact that Massee (1899) established that teleutospores can germinate only after hibernating (autoecious-microcycle).

GROVE (1913) describes the life-cycle of the above-ground infection as follows:

"The teleutospores remain on the dead leaves and germinate in the following spring, so that if *Colchicum* is again planted in the same ground or allowed to remain there, it is liable to contract the disease year after year".

Concerning the underground infection on *Colchicum*, the same principle may be assumed to hold. The new infections probably take place in spring by basidiospores from the germinating teleutospores coming from the old, diseased tunics. In this way, the new corm and the small split-corms formed within the old tunics can become infected. In addition, the anatomy of the underground parts of *Colchicum* is such that this infection may take place on both "sides" and on the flattened part of the newly-formed corms. At these places, the old tunic is directly bounded by the membranous tunic of the new corms, while the bulging and rounded part of the new corms is "protected" by the corm-flesh of the old one. This may explain why teleutosori are especially found on one "side" only of the new corm, although occasionally they are found on the flattened side also.

When healthy corms are planted in a soil in which diseased tunic fragments are present, the new corms may become infected by the germinating spores in spring. Infection of newly-formed corms may take place naturally by the spread of spores in the sori which are sometimes found at ground level.

That sometimes newly-formed corms had not become infected when produced from diseased planting material, may be explained by a period of storage, unfavourable to spore conservations.

AMPLIFIED DESCRIPTION OF UROMYCES COLCHICI

Uromyces colchici Massee 1892 (Grevillea 21,6) char. ampl. Autoecious – microcycle.

Two different types of attack:

A. Leaf infection (Massee, 1892, 1899, 1915, Grove, 1913)

Teleutosori distributed on the leaf-sheath and on both sides of the leaf-blade, most abundant on the lowest leaf and always commencing at the base of the sheath; sori on the sheath, large, elliptical, $5-8\times 3-5$ mm, often confluent; on the leaf-blade as a rule smaller and often arranged in circular groups; in both cases for a long time covered by the epidermis which cracks at length, subpulverulent, brown.

B. Tunic infection

Teleutosori on the inner side and incidentically on the outside of the cormtunic; sometimes also on the connecting part of the leaf-sheath of the lowest leaf which does not contain chlorophyll; sori on the tunic most often on one side of the typically two-sided symmetrical corm, but sometimes on the flattened and elongated side of the corm; varying greatly in dimensions, $1-8 \times 1-4$ mm, often arranged in concentric rings without distinct borders between the sori, at first covered by the epidermis, which later becomes broken.

Teleutospores subglobose to ovoid, round above, with a broad flat hyaline papilla, regularly covered with small warts, palebrown, 28–40 \times 20–28 μ ; epispore 3–3½ μ thick; pedicels hyaline, uniformly attenuated toward the base, 70–80 \times 5–6 μ , very deciduous.

Leaf infection found on *Colchicum speciosum* Stev. (= *C. spectabilis* Auct.), *Colchicum autumnale* L. and *Colchicum bavaricum* Auct. (= *C. variegatum* L.?), Kew Gardens, England (Massee 1892, 1899, 1915; Wilson & Bisby, 1954) and on *Colchicum* spec., Yorkshire (Mason & Grainger, 1937).

Tunic infections found on the *Colchicum* hybrids "Violet Queen", "Autumn Queen", "The Giant" and *Colchicum bornmuelleri* Freyn, bulb fields in The Netherlands.

Herbarium material with the tunic infection has been deposited in the "Rijksherbarium", Leyden, The Netherlands and The Herbarium of the Royal Botanic Gardens, Kew, England.

SUMMARY

- 1. Underground infection of *Colchicum* by the rust *Uromyces colchici* Massee has been regularly observed in The Netherlands since 1955.
- 2. A review of the literature is given. The disease is reputed as being one of extreme rarity. Symptoms of the diseased corms are extensively described here.
- 3. In the discussion, an analysis and comparison has been made between the underground corm infection found in The Netherlands and the above-ground infection observed earlier.
- 4. Finally an amplified description of *Uromyces colchici* is given.

SAMENVATTING

Sinds 1955 wordt bij de in Nederland gekweekte *Colchicum*-hybride "Violet Queen" regelmatig een roestaantasting van de knolrok geconstateerd. Incidenteel werd deze als "ondergronds" te karakteriseren aantasting ook vastgesteld bij *Colchicum bornmuelleri* Freyn en de *Colchicum* hybriden "Autumn Queen" en "The Giant".

De betreffende roest bleek identiek te zijn met *Uromyces colchici* Massee (1892). Deze niet-waardplantwisselende roest, die uitsluitend teleutosporen vormt (fig. 1), staat als zeer zeldzaam te boek. Bovengrondse bladaantastingen

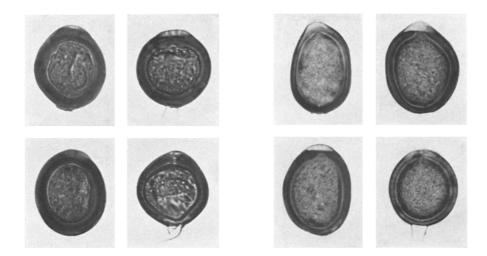


Fig. 1A Fig. 1B

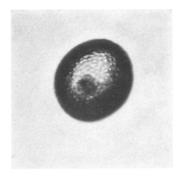


Fig. 1C

- Fig. 1. Teleutospores of *Uromyces colchici* Massee. Magnification \times 640.
 - A. Optical section. Spores from the leaf of Colchicum speciosum Stev. Material of MASSEE, 1892. Herbarium Royal Botanic Gardens Kew.
 - B. Optical Section. Spores from the corm-tunic of the *Colchicum* hybrid "Violet Queen" 1959.
 - C. Lateral view in air-bubble. Spore from the leaf of *Colchicum speciosum* Stev. Material of Massee, 1892. Herbarium Royal Botanic Gardens Kew.

Teleutosporen van Uromyces colchici Massee. Vergroting 640 ×.

- A. Optische doorsnede. Sporen van blad van Colchicum speciosum Stev. Materiaal van Massee, 1892. Herbarium Royal Botanic Gardens Kew.
- B. Optische doorsnede. Sporen van knolrok van Colchicum-hybride "Violet Queen" 1959.
- C. Zijaanzicht in luchtbel. Spore van blad van Colchicum speciosum Stev. Materiaal van Massee, 1892. Herbarium Royal Botanic Gardens Kew.

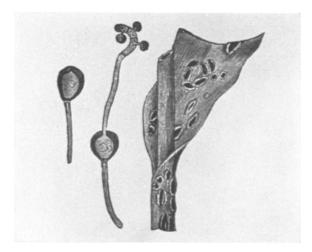


Fig. 85. — *Uromyces colchici*. 1, portion of a diseased *Colchicum* leaf; 2, teleutospores, one of which has germinated and produced a promycelium bearing three secondary spores. Fig. 1 reduced, Fig. 2 mag.

Fig. 2A



Fig. 2B

- Fig. 2A. A reproduction from Massee: Diseases of cultivated plants and trees (1915).

 Tekening van het door Massee waargenomen bovengrondse ziektebeeld van Uromyces colchici Massee, gecombineerd met een afbeelding van twee teleutosporen, waarvan één is gekiemd. Reproduktie uit: "Diseases of cultivated plants and trees", Massee, 1915.
 - B. Photograph of a teleutosorus of *Uromyces colchici* Massee on a leaf fragment of *Colchicum speciosum* Stev. Magnification × 6.5. Material of Massee, 1892. Herbarium Royal Botanic Gardens Kew.

Foto van een teleutosorus van Uromyces colchici Massee op een bladfragment van Colchicum speciosum Stev. Vergroting 6,5 ×. Materiaal van Massee, 1892. Herbarium Royal Botanic Gardens Kew.



Fig. 3A

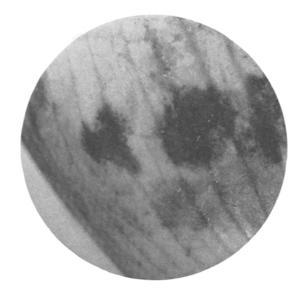


Fig. 3B



Fig. 3C



Fig. 3D

- Fig. 3. Early dug plants of the *Colchicum* hybrid "Violet Queen" attacked by *Uromyces colchici* Massee.
 - A. Early stage: The slightly protuding brown spots indicate the places where teleutosori have developed on the inner-side of the tunic.
 - B. Detail of these brown spots: Position on the veins is clearly visible.
 - C. Advanced stage: Cracked tunic in the area in which teleutosori are formed.
 - D. Left: Exposed inner side of the diseased tunic showing mass of teleutosori in concentric rings.
 Right: Imprint of diseased rust spot on the white-corm-flesh made by loosened, darkbrown teleutospores.

Vroeg gerooide planten van de Colchicum-hybride "Violet Queen", aangetast door Uromyces colchici Massee.

- A. Vroeg stadium: De plaatsen, waar aan de binnenzijde van de rok teleutosori zijn gevormd, zijn te herkennen als iets verheven, bruine vlekjes.
- B. Detail van deze bruine vlekjes: Het is goed te zien dat ze zich op de nerven bevinden.
- C. Later stadium: De rok is in het centrum van de aantasting opengescheurd.
- D. Links: Aan de binnenzijde van de los geprepareerde rok zijn de in concentrische ringen gerangschikte teleutosori zeer opvallend.

Rechts: De losgelaten teleutosporen vormen een afdruk van de aantasting op het witte knolvlees.

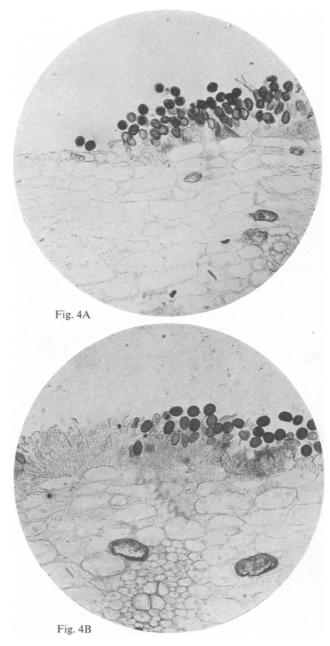


Fig. 4. Transverse microtome sections of the tunic showing parts of a teleutosorus of *Uromyces colchici* Massee. Magnification × 130.

Photograph A: Part of the remaining epidermis at left. On both photographs the mycelium is visible among the large parenchymacells (intercellular) and in the cells of the vascular bundle (intracellular) of the photograph B.

Dwarse microtoom-coupes van een door Uromyces colchici Massee aangetaste knolrok. Vergroting $130 \times$. De epidermis is alleen op foto A nog te zien (links); boven de teleutosori is deze niet meer aanwezig. Op beide foto's ziet men tussen de grote parenchymatische cellen het mycelium van de roest (intercellulair), terwijl op foto B te zien is dat dit mycelium ook woekert in de cellen van de vaatbundel (intracellulair).

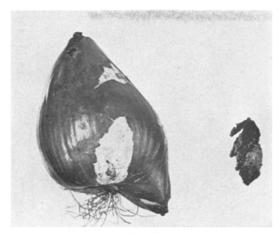


Fig. 5A

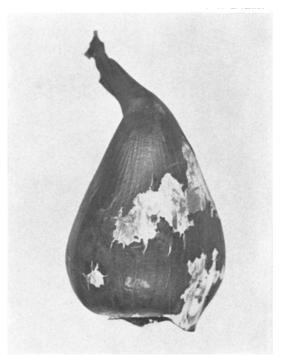


Fig. 5B

- Fig. 5. Mature corms of the *Colchicum* hybrid "Violet Queen" infected by *Uromyces colchici* Massee.
 - A. A piece of the infected tunic removed to show the ripened teleutosori from the inner side.
 - B. Still visible dark-brown concentric rings in the diseased tunic.

Afgerijpte knollen van de Colchicum-hybride "Violet Queen", aangetast door Uromyces colchici Massee.

- A. Een deel van de aangetaste rok is verwijderd om de rijpe teleutosori aan de binnenzijde te laten zien.
- B. Op het nog aanwezige, zieke rokweefsel ziet men donkere, concentrische ringen.

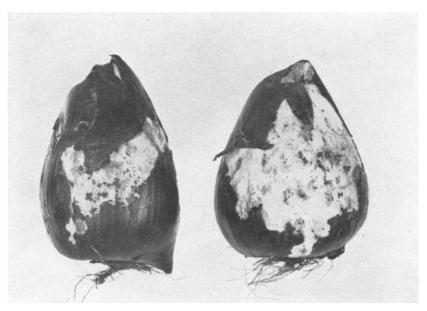


Fig. 6. Old corms of the *Colchicum* hybrid "Violet Queen" with partly removed diseased tunics.

Afgerijpte knollen van de Colchicum-hybride "Violet Queen", waarvan het zieke rokgedeelte grotendeels heeft losgelaten.

door *U. colchici* (fig. 2) zijn nl. slechts op twee plaatsen in Engeland geconstateerd, en wel in Kew (MASSEE, 1892, 1899 en 1915) en in Yorkshire (MASON & GRAINGER, 1937). De mogelijkheid van ondergronds optreden van deze roest was niet bekend.

Na een uitvoerige bespreking van de literatuurgegevens over *U. colchici* als veroorzaker van bovengrondse aantastingen, wordt de in Nederland waargenomen ondergrondse aantasting beschreven.

Bij de bovengenoemde *Colchicum*-hybriden, respectievelijk species, werden de teleutosori van *U. colchici* gevonden aan de binnenzijde en incidenteel ook aan de buitenzijde van de knolrok. Dit is uiteraard alleen vast te stellen na het rooien van de planten. Soms werden ook teleutosori gevonden op het stengelomvattende deel van de rok dat aansluit op de groene bladschede van het onderste blad. Hierdoor kan men soms in het veld even boven de grond aantastingsplekken waarnemen. Op de groene delen van de planten werden echter nooit sori gevonden; wel werden soms op de bladschijf van het onderste blad typische gele vlekjes waargenomen.

De aantasting is bijzonder opvallend als men de knollen vroeg rooit en het rokweefsel dus nog niet bruin verkleurd is (fig. 3). Later, als de rok bruin verkleurd en afgestorven is, is de roestaantasting de oorzaak dat het rokweefsel ter plaatse gaat scheuren en bij het rooien gedeeltelijk loslaat (fig. 5 en 6). Op het witte knolvlees blijft dan meestal als een bruinzwart poeder een aantal sporen achter (fig. 5 en 6). Een kenmerk van de aantasting in dit stadium is ook het optreden van vele donkerbruine, concentrische ringen in het afgestorven aangetaste rokweefsel (fig. 5B). Opvallend is, dat de rok vaak slechts aan één bepaalde zijde van de knol is aangetast. Meestal is dit een "zijkant" van de tweezijdig symmetrische knol (fig. 3A, 5, 6); soms worden de sori echter voornamelijk gevonden op het rokgedeelte aan de afgeplatte, verlengde zijde van de knol (fig. 3C).

In de discussie wordt er op gewezen, dat sinds 1956 een overeenkomstige ondergrondse roestaantasting bij *Crocus* wordt geconstateerd, veroorzaakt door *Uromyces croci* Pass. (Boerema, 1959). De mogelijkheid wordt overwogen, dat er bij deze twee in Nederland uitsluitend ondergronds optredende roesten sprake is van een adaptatie aan de cultuurmethode die bij deze planten op de kwekerijen reeds vele decennia wordt toegepast. Doordat de knollen op deze kwekerijen elk jaar weer uit de grond worden gehaald, is de bovengrondse levenscyclus van deze roesten zo goed als onmogelijk geworden, speciaal ook daar men hierbij steeds een ruime vruchtwisseling toepast. Met andere woorden deze roesten kunnen zich op de kwekerijen alleen handhaven als ze zich aanpassen aan de ondergrondse delen, wat dus blijkbaar nu is gebeurd. Deze hypothese houdt dus in dat hier mogelijk sprake is van erfelijk geadapteerde, fysiologische rassen van *U. colchici* en *U. croci*.

Verder worden in de discussie de gegevens over de levenscyclus van de bovengrondse aantasting door U. colchici vergeleken met de eigen waarnemingen over de biologie van de ondergrondse aantasting.

Bij de ondergrondse aantasting zullen de nieuwe infecties waarschijnlijk ontstaan door de basidiosporen van de in het voorjaar kiemende teleutosporen. Op deze wijze kan bij ziek plantmateriaal de vliezige rok van de binnen de oude knolrok gevormde, nieuwe knollen worden aangetast. Bij gezond plantmateriaal kan de infectie eventueel door in de grond aanwezige, oude, aangetaste rokfragmenten plaatsvinden.

Het feit dat de rok vaak slechts aan een "zijkant" van de knol is aangetast, bleek samen te hangen met de anatomie van *Colchicum*. De beide "zijkanten" en de afgeplatte, verlengde zijde van de nieuw gevormde knollen staan nl. in direct contact met de oude knolrok, terwijl de bolle zijde van de nieuwe knollen "beschermd" wordt door het knolvlees van het oude. Hierdoor is de kans van een infectie aan een zijkant van de nieuwe knollen het grootst.

Uitbreiding van de aantasting vindt waarschijnlijk plaats via de nerven (vgl. fig. 4), waardoor tenslotte ook teleutosori op het witte deel van de bladschede van het onderste blad kunnen ontstaan. Wat de oorzaak is dat er op de hoger gelegen, groene, dus chlorofyl bevattende delen geen teleutosori gevormd worden, moet nog nader worden onderzocht. Daar waar zich sori ontwikkelen, heeft ook een concentrische uitbreiding van het mycelium plaats, wat blijkt uit de meestal in concentrische ringen gerangschikte sori (fig. 3D) en de donkerbruine, concentrische ringen in het afgestorven rokweefsel (fig. 5B).

De publikatie wordt afgesloten met een aanvullende beschrijving van *Uromyces colchici*.

ACKNOWLEDGEMENTS

The author is very grateful to the Directions of the Herbaria at Kew, Leyden and Groningen for the excellent cooperation during this research.

My special thanks and appreciation are expressed to Mr. N. G. Santacroce for the contributions made by him on the underground appearance of *Uromyces colchici*, and for reviewing the English text.

From those who assisted in the preparation of this manuscript for publication, I wish to mention Mr. R. Surjotono especially, who carried out the preliminary investigations.

REFERENCES

Anonymus, – 1956. Variëteitsnamen-register van Hyacinthen, Bol-Iris en andere diverse bijgoedgewassen. Kon. alg. Ver. Bloemb. Cult. Haarlem.

BOEREMA, G. H., - 1959. Uromyces croci Pass. bij Krokus-soorten. Versl. en Meded. Plantenz.-k. Dienst, Wageningen 133:130-135.

BOOM, B. K. & J. D. RUYS, - 1950. Flora der gekweekte kruidachtige gewassen, Wageningen: 316.

COOKE, M. C., - 1906. Fungoid pests of cultivated plants: 277. (Reprinted from J. Roy. hort. Soc. 1902, 27: 400.)

GÄUMANN, E., – 1959. Die Rostpilze Mitteleuropas mit besonderer Berücksichtigung der Schweiz, Bern: 285–286.

GROVE, W. B., - 1913. The British Rust Fungi (Uredinales). Cambridge.

GUYOT, A. L., - 1951. Les Urédinées II. Encycl. mycolog. 15: 24-25; 46-55.

Guyot, A. L., -1958. Les Urédinées. Corrections, Additions et Observations V in Uredineana V. Encycl. mycolog. 31: 713-760.

HORSFALL, J. G. & A. E. DIMOND, - 1959. Plant Pathology. New York, London: 307.

HYLANDER, M., I. JORSTAD & J. A. NANNFELDT, – 1953. Enumerato Uredinearum Scandinavicarum. Opera Botanica 1: 1–102.

MASON, F. A. & I. GRAINGER, -1937. A catalogue of Yorkshire Fungi. Yorkshire.

MASSEE, G., - 1892. Uromyces (Micruromyces) colchici, Mass. Grevillea 21:6.

MASSEE, G., - 1899. A Text-book of Plant Diseases. London: 227.

MASSEE, G., -1915. Diseases of cultivated plants and trees. London: 292.

MOORE, W. C., - 1949. Diseases of bulbs. Bull. Min. Agric. London: 117: 57.

MOORE, W. C., - 1959. British parasitic fungi. Cambridge: 402.

Ulbrich, E., – 1937. Die von der deutschen Himalaya-Expedition 1937 gesammelten Pilze. Notizbl. bot. Gart., Berlin-Dahlem 122, 14:150.

UNGER, F., - 1833. Die Exantheme der Pflanzen. Wien: 186-187.

WILSON, M. & G. R. BISBY, - 1954. List of British Uredinales. Trans. Brit. mycol. Soc. 37:78.