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The Elegans fusaria causing wilt disease of carnation. I. Taxonomy

R.P. BAAYEN[1] and W. GAMS[2]

[1] Willie Commelin Scholten Phytopathological Laboratory, Javalaan 20, 3742 CP Baarn, the Netherlands
[2] Centraalbureau voor Schimmelcultures, P.O. Box 273, 3740 AG Baarn, the Netherlands

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Abstract

The distinction of the wilt disease pathogen of carnation *Fusarium* (*oxysporum* var.) *redolens* from *F. oxysporum* (var. *oxysporum*) is considered. Previous reports that isolates of both taxa cause indistinguishable diseases in carnation are confirmed. *F.* (*oxysporum* var.) *redolens* and *F. oxysporum* were found to form one variable complex on morphological criteria. Apparently, host specialization rather than morphological variation reflects the evolutionary relationships in the *Fusarium* section *Elegans*. The distinction of *F. redolens* from *F. oxysporum* does therefore not seem justified, neither at specific nor at varietal level.

Additional keywords: Fusarium oxysporum, Fusarium oxysporum var. *redolens, Fusarium redolens, Dianthus* spp., morphology.

Introduction

The first *Fusarium* species causing wilt disease of carnation was described by Prillieux and Delacroix in 1899. This species, *Fusarium dianthi* Prill. & Del., was recognized by Wollenweber and Reinking (1935) who placed it in the section *Elegans*, subsection *Oxysporum*, together with *F. oxysporum* Schlecht. : Fr., *F. vasinfectum* Atk. and *F. redolens* Wollenw.. Snyder and Hansen (1940) reduced the entire section *Elegans* to the single species, *F. oxysporum*, of which the carnation pathogen was considered a forma, *F. oxysporum* Schlecht. : Fr. f. *dianthi* (Prill. & Del.) Snyder & Hansen. The Snyder and Hansen concept of *F. oxysporum* has become widely accepted except for the position of *F. redolens*. Gordon (1952) compared 13 isolates of *F. redolens* with 27 of *F. oxysporum* from cereal seed and on this basis revaluated the former species at varietal level as *F. oxysporum* Schlecht. : Fr. var. *redolens* (Wollenw.) Gordon. He considered var. *redolens* to be a distinct variety because of the different macroconidia, which are somewhat wider in the upper third than in the middle and resemble the conidia of *F. solani*, and the different colour of the substratum. Gerlach (1961) restored *F. redolens* as a separate species because of similar morphological criteria, and because '*F. redolens* fast 30 Jahre lang als Art bestanden und sich dieser Name weitgehend durchgesetzt hatte', although he admitted that the distinction at specific rather than varietal level was a debatable matter. The discovery of *F. redolens* strains causing wilt disease of car-

nation therefore led Gerlach and Pag (1961) to conclude that two morphologically different *Elegans* fusaria exist which cause wilt disease of carnation, even though the diseases caused by both pathogens were indistinguishable (Gerlach and Pag, 1961; Hantschke, 1961). The novel pathogen was described as *F. redolens* Wollenw. f. *dianthi* Gerlach (Gerlach and Pag, 1961), and is presently known as *F. redolens* Wollenw. f.sp. *dianthi* Gerlach (Gerlach and Nirenberg, 1982), although the combination as *forma specialis* has never been formally proposed. Likewise, the combination *F. oxysporum* Schlecht. : Fr. f.sp. *dianthi* (Prill. & Del.) Snyder & Hansen, as used since Gordon (1965), has never been formally proposed, but this is not required by the Botanical Code (Deighton et al., 1962; Voss et al., 1983). The position of *F. redolens* has remained controversial in the mycological literature. Gerlach maintained it as clearly distinct and representing a separate species (Gerlach, 1981; Gerlach and Nirenberg, 1982). Booth (1971, 1975) followed Gordon (1952) in recognizing it at varietal level. Messiaen and Cassini (1981) and Nelson et al. (1983) followed Snyder and Hansen's concept of *F. oxysporum* and did not recognize *F. redolens*. Chromosome counts (Punithalingam, 1975) and comparative esterase isoenzyme studies (Szécsi and Hornok, 1986) on these, and other, *Fusarium* taxa suggested that *F. redolens* could be a distinct species. However, both studies were carried out on only a single isolate per taxon, and therefore may not be taken as decisive evidence.

A great deal of confusion followed in the phytopathological literature on Fusarium wilt of carnation as regards the causal pathogen(s) and their nomenclature. The name *F. redolens* f.sp. *dianthi* was rarely used by authors other than Gerlach himself (rare examples are Rattink, 1983 and Margraf et al., 1986). More often, wilt was attributed to '*F. oxysporum* f.sp. *dianthi* and/or *F. oxysporum* var. *redolens*' (Garibaldi, 1978; Matthews, 1978; Jacob and Krebs, 1985). Unfortunately, the *forma specialis* designation is usually omitted for var. *redolens*, which erroneously suggests that carnation is attacked by a specialized form of *F. oxysporum* var. *oxysporum* contrary to a non-specialized form of *F. oxysporum* var. *redolens*. This error is also encountered with other crops, which are attacked by specialized forms of *F. oxysporum* and *F. redolens* (Buxton, 1955; Hepple, 1960; Ho et al., 1985a), and is probably due to the fact that formal combinations of special forms of *F.* (*oxysporum* var.) *redolens* other than f.sp. *dianthi* and f.sp. *spinaciae* have never been proposed. Usually, however, the carnation wilt pathogen was merely designated as *F. oxysporum* f.sp. *dianthi* (e.g. Pennypacker and Nelson, 1972; Garibaldi, 1983; Baayen and Elgersma, 1985; Buiatti et al., 1985; Harling and Taylor, 1985; Yuen et al., 1985), which is ambiguous as it may concern *F. oxysporum sensu lato* according to Snyder and Hansen, or *sensu stricto* following Gerlach.

Recognition of *F.* (*oxysporum* var.) *redolens* f.sp. *dianthi* Gerlach apart from *F. oxysporum* f.sp. *dianthi* (Prill. & Del.) Snyder & Hansen has considerable phytopathological consequences. It implies that pathogenic specialization on carnation has evolved independently in *F.* (*oxysporum* var.) *redolens* and in *F. oxysporum sensu stricto*. Consequently, f.sp. *dianthi* Gerlach and f.sp. *dianthi* (Prill. & Del.) Snyder & Hansen would have to be treated as two different pathogens which cause their own diseases on carnation, require separate resistance breeding programmes, etc. However, Gerlach and Pag (1961) and Hantschke (1961) have recognized that both formae speciales *dianthi* were indistinguishable in respect of their pathogenic abilities. Indeed both diseases have always been treated as one and the same, and the name *F.* (*oxysporum* var.) *redolens* f.sp. *dianthi*

has been used in the literature from the beginning as if it were just another name for *F. oxysporum* f.sp. *dianthi* (Sparnaaij and Demmink, 1977; Garibaldi, 1978; Matthews, 1978; Rattink, 1983; Jacob and Krebs, 1985; Margraf et al., 1986).

The present study was undertaken to clarify the taxonomy of the members of section *Elegans* that cause wilt disease of carnation. Thus the carnation diseases caused by *F. oxysporum* and *F. redolens* were re-examined, and both pathogens were studied morphologically using two low-nutrient media, carnation leaf agar (Fisher et al., 1982) and the synthetic medium SNA (Nirenberg, 1976). The use of these meagre substrates has recently been found to allow a good and rapid development of distinctive morphological features in *Fusarium* species (Nirenberg, 1981; Nelson et al., 1983).

Materials and methods

Isolates. Nineteen isolates labelled *F. redolens*, including seven recorded as f.sp. *dianthi*, and an arbitrary selection of 16 isolates labelled *F. oxysporum*, including 11 of f.sp. *dianthi* were examined in detail (Table 1). All wild-type isolates of *F. redolens* preserved from Gerlach's studies in Berlin (Federal Republic Germany) were examined.

Cultural and morphological characteristics of F. oxysporum and F. redolens. The stock cultures of isolates of *F. oxysporum* and *F. redolens* were grown on oatmeal agar (OA) (Gams et al., 1987). Cultural characteristics such as colony diameters (measured after seven days growth at room temperature in daylight), development of aerial mycelium, shape of the colony edge, pigmentation and odour were assessed using cultures grown on potato-dextrose agar (PDA; Difco) and OA (8.5 cm diam Petri dishes). All cultures were initiated from a flock of aerial mycelium and conidia. Colours were classified according to the Mycological Colour Chart (Rayner, 1970) for English names and the Methuen Handbook of Colour (Kornerup and Wanscher, 1963) for numerical codes. The morphology of conidia and the conidiogenous cells was examined using cultures grown on SNA (with three pieces of filter paper) and CLA. These cultures were incubated for 1-4 weeks at room temperature in daylight. The morphology of the conidia and phialides from sporodochia (when present), aerial mycelium or superficial mycelium was examined in aqueous mounts. Sixteen random macroconidia (from sporodochia or aerial mycelium), eight random microconidia and several phialides of each isolate were drawn at 2000 × magnification with a Wild M 20 microscope with a drawing tube.

Disease symptoms in carnations. Rooted cuttings of *Dianthus caryophyllus* L. cv. Sam's Pride (highly susceptible to *F. oxysporum* f.sp. *dianthi*) were obtained from Handelskwekerij Gebr. Markman B.V., Aalsmeer, planted in steam-sterilized soil in 8 cm diam pots and grown in a glasshouse for 6 weeks prior to inoculation.

Conidial suspensions of *F. oxysporum* f.sp. *dianthi* WCS 848 and *F. redolens* f.sp. *dianthi* DSM 62390 were prepared from 20-day-old Czapek Dox liquid medium (Oxoid) shake cultures by filtering through glasswool, washing once by centrifugation and diluting to c. 5×10^6 conidia ml^{-1}. Conidial suspension of *F. oxysporum* f.sp. *dianthi* WCS 847 and *F. redolens* f.sp. *dianthi* WCS 842 were prepared from 1-week-old PDA Petri dish cultures by flooding with sterile water, scraping off the mycelium, filtering the resulting suspension through glasswool and adjusting it to c. 5×10^6 conidia ml^{-1}. Stem inoculations of six carnations per isolate with 2×20 µl conidial suspension per

Table 1. List of *F. oxysporum* and *F. redolens* isolates used and their origin. CBS = culture collection of the Centraalbureau voor Schimmelcultures, Baarn; DSM = Deutsche Sammlung von Mikroorganismen, Göttingen/Braunschweig (1974 catalogue); A.G. = culture collection of prof. A. Garibaldi, Turin; WCS = culture collection of the Willie Commelin Scholten Phytopathological Laboratory, Baarn.

Fusarium oxysporum Schlecht.: Fr.
f.sp. *cattleyae* Foster -- CBS 742.79, ex *Phalaenopsis* sp., W. Gerlach
f.sp. *chrysanthemi* Littrell et al. -- CBS 127.81, ex *Chrysanthemum* sp., USA
f.sp. *cyclaminis* Gerlach -- WCS 845, ex *Cyclamen* sp., H. Rattink
f.sp. *dianthi* (Prill. & Del.) Snyder & Hansen race 1 Garibaldi -- WCS 827 (= A.G. 1), ex *Dianthus* sp., A. Garibaldi; WCS 829 (= A.G. F101), ex *Dianthus* sp., A. Garibaldi
f.sp. *dianthi* race 2 Garibaldi -- WCS 816, ex *Dianthus caryophyllus*, H. Rattink; WCS 830, ex *Dianthus caryophyllus*, H. Rattink; WCS 834 (= A.G. 75), ex *Dianthus* sp., A. Garibaldi; WCS 847, ex *Dianthus caryophyllus*, R.P. Baayen; WCS 848, ex *Dianthus caryophyllus*, R.P. Baayen
f.sp. *dianthi* race 4 Garibaldi -- WCS 837 (= A.G. 261), ex *Dianthus* sp., A. Garibaldi; WCS 838 (= A.G. 310), ex *Dianthus* sp., A. Garibaldi; WCS 839 (= A.G. F79), ex *Dianthus* sp., A. Garibaldi
f.sp. *dianthi* race 8 Garibaldi -- WCS 840, ex *Dianthus* sp., A. Garibaldi
f.sp. *narcissi* (Cooke & Massee) Snyder & Hansen -- CBS 196.65, ex *Narcissus* sp., W. Gerlach
f.sp. *opuntiarum* Pettinari -- CBS 743.79, ex *Zygocactus* sp., W. Gerlach

Fusarium oxysporum Schlecht.: Fr.
var. *redolens* (Wollenw.) Gordon -- CBS 128.73, ex *Lycopersicon esculentum*, CMI

Fusarium redolens Wollenw.
f.sp. *dianthi* Gerlach -- CBS 248.61 (originally = DSM 62390, type isolate of f.sp. *dianthi*), ex *Dianthus caryophyllus*, D. Hantschke, det. W. Gerlach; CBS 366.87, ex *Dianthus* sp., J.W. Veenbaas-Rijks; DSM 62390 (= CBS 360.87), ex *Dianthus caryophyllus*, D. Hantschke, det. W. Gerlach, type isolate of f.sp. *dianthi*, newly received culture from the Institut für Mikrobiologie, Berlin-Dahlem; DSM 62391 (= CBS 361.87), ex *Dianthus caryophyllus*, D. Hantschke, det. W. Gerlach; DSM 62392 (= CBS 362.87), ex *Dianthus caryophyllus*, D. Hantschke, det. W. Gerlach; DSM 62393 (= CBS 363.87), ex *Dianthus barbatus*, D. Hantschke, det. W. Gerlach; WCS 842, ex *Dianthus caryophyllus*, H. Rattink

Fusarium redolens Wollenw., unspecified isolates.
CBS 180.29, ex *Pisum* sp., H.W. Wollenweber; DSM 62378 (= CBS 364.87), ex *Dianthus caryophyllus*, W. Gerlach; DSM 62379 (= CBS 365.87), ex *Dianthus caryophyllus*, W. Gerlach; DSM 62380, ex *Asparagus* sp., W. Gerlach; DSM 62383, ex *Helleborus* sp., W. Gerlach; DSM 62384, ex *Fragaria* sp., W. Gerlach; DSM 62385, ex *Convallaria majalis*, W. Gerlach; DSM 62386, ex *Fritillaria* sp., W. Sauthoff, det. W. Gerlach; DSM 64524, ex *Solanum tuberosum*, E. Langerfeld, det. H. Nirenberg; DSM 64613, ex *Pisum* sp., H. Nirenberg; WCS 846, H. Rattink

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plant were carried out as described by Baayen and Elgersma (1985). Development of disease symptoms was studied during 6 weeks.

Virulence of F. redolens f.sp. dianthi to cultivars differential for races 1, 2 and 4 of F. oxysporum f.sp. dianthi. Rooted cuttings of the cultivars Novada, Elsy, Pallas, Lena and Early Sam and of the selections Carrier 929 and IVT 62093-G were planted in steam-sterilised soil in 8 cm diam pots and grown in the glasshouse for 2 weeks prior to inoculation.

A conidial suspension of *F. redolens* f.sp. *dianthi* DSM 62392 was prepared from an 8-day-old shake culture as described above. Eight carnations per cultivar (in the case of 'Early Sam', four carnations) were root-inoculated by pouring 5 ml conidial suspension per plant on the soil after the roots had been damaged by thrice pushing a blade into the soil. Development of disease symptoms was studied during 6 weeks. Wilt was indexed at least twice a week using the method described by Baayen and De Maat (1987).

Results

Cultural characteristics. All isolates grew 5.0-7.5 cm diam in 7 days on PDA, and 5.5-8.0 cm diam on OA. The isolates differed considerably in growth rate, but no consistent differences in growth rate were found between the taxa. There was considerable variation in respect of the development of aerial mycelium which varied from sparse to abundant. In some isolates, the aerial mycelium developed in vague or well-defined concentric zones. The colony margins were regular and sharp to irregular and fimbriate, with the fringes growing on the surface of, or also down into the agar. The pigmentation of the cultures varied from saffron, salmon and buff to rose, red, vinaceous and purple shades (Table 2). All isolates produced varying amount of a soft to sharp, sweet odour reminiscent of apples. The odour usually was stronger on PDA than on OA, where it often was somewhat musty.

Two main types of pigmentation were observed (Table 2). Most isolates of *F. oxysporum* and a few of *F. redolens* developed various shades of livid-red to livid-purple or rarely sepia in the colony centre on PDA. On OA the pigmentation was usually paler. These isolates varied in growth rate and production of aerial mycelium, had a regular

Table 2. Pigmentation produced by isolates originally labelled as *F. oxysporum* (°) and *F. redolens* (ʳ) on PDA after one week in the centre of the colonies.

salmon, saffron to slightly orange (Methuen codes 5-6A_{4-5})	DSM 62378, 62379, 62380, 62383, 62385, 62386, 62390, 62391, 62392, 62393, 64524, 64613 (all ʳ)
salmon (5-6A_{3-4}, 6B_{3-4})	CBS 180.29ʳ; DSM 62384ʳ; WCS 837°, 846ʳ
buff (5A_{2-3}, 6-7A_2, 4B_{3-4})	CBS 196.65°
buff to rosy buff (5-7A_{2-3}, 7B_3)	WCS 840°
flesh and rosy vinaceous to greyish rose (8-10A_3, 8-13B_{3-4}, 8-9C_{3-4})	CBS 128.73ʳ; WCS 830°
coral, livid red, vinaceous to livid vinaceous (10B_{5-6}, 10C_{5-7}, 9-12D_{4-7}, 10-12E_{5-6})	CBS 248.61ʳ, 366.87ʳ, 742.79°; WCS 816°, 827°, 847°, 848°
dark vinaceous, livid purple, dark livid to dark purple (13D_5, 11-13E_7, 13F_{7-8})	CBS 127.81, 743.89; WCS 829, 834, 838, 845 (all °)
sepia (10F_8)	WCS 842ʳ

and sharp colony margin and, if slightly fimbriate at all, never had the fringes growing down into the agar. The majority of isolates of *F. redolens* were salmon to saffron to slightly orange in the colony centre on PDA, and buff to salmon on OA. These isolates were more uniform in colony characteristics, with powdery aerial mycelium, typically extending to the colony margin. The margin itself mostly was irregularly fimbriate on PDA, with the fringes not only growing on the surface of, but also down into the agar. The isolates CBS 180.29 and WCS 846 of *F. redolens*, and CBS 196.65 and WCS 837 of *F. oxysporum* were similarly but less intensely pigmented, produced less aerial mycelium, and had a sharp margin. There was a number of isolates with intermediate pigmentation, representing a continuous series: salmon, saffron to slightly orange – buff to salmon – rosy-buff to buff – greyish rose, rosy-vinaceous and flesh – (livid-)vinaceous, livid-red and coral – dark vinaceous, dark livid, dark and livid-purple (see also Table 2).

Macroconidia (Figs 1-3). Cream, peach or orange sporodochia developed after c. two weeks in most isolates received as *F. redolens* (except CBS 180.29, CBS 248.61 and CBS 366.87), but rarely in those received as *F. oxysporum* (only in CBS 742.79, CBS 743.79 and WCS 845). Macroconidia were studied when possible from sporodochia (2-4 weeks old cultures), otherwise from aerial mycelium or, in case of absence, from mycelium on the agar surface. A few isolates did not produce macroconidia at all (CBS 127.81, WCS 816, WCS 830, WCS 837).

Shape and size of the macroconidia generally were uniform within a culture. Macroconidia from SNA and CLA cultures of one isolate generally were similarly shaped but sometimes differed slightly in size but without a consistent trend (Figs 1, 2). Shape and size of the macroconidia varied considerably within the two groups of isolates originally distinguished. The variation among isolates from carnation (Fig. 1) equalled the variation among the isolates from other crops (Fig. 2). Typical *F. oxysporum* macroconidia (Fig. 1b, p; Fig. 2b, d) were straight to slightly curved towards both ends, relatively narrow (c. 3.0-4.5 μm), widest in the middle, equally and gradually tapering towards both ends, and provided with a narrowly pedicellate basal cell and an elongate, non-hooked apical cell. Typical *F. redolens* macroconidia (Fig. 1e, j, k; Fig. 2k, n) were falcate to moderately curved, c 4.5-6.3 μm wide, widest in the upper third, and provided with a bluntly rounded or broadly pedicellate basal cell, and a thick, non-hooked and blunt-tipped (Fig. 1j; Fig. 2n) or hooked and pointed (Fig. 1e, k; Fig. 2k) apical cell. Many intermediate forms occurred. The macroconidia of isolates from carnation are arranged in Fig. 1 so as to show various transition series from typical *F. redolens* (left) to *F. oxysporum* (right). Transitional forms were also encountered among the isolates of *F. oxysporum* and *F. redolens* from other plants (compare Figs 2a and 2f, and 2b and 2g, for example).

Some of the isolates received as either *F. oxysporum* or *F. redolens*, rather were found to correspond to the other species in macroconidial shape. WCS 848 (from carnation; Fig. 1n), originally labelled *F. oxysporum*, was similar to *F. redolens*, while CBS 180.29 (from pea; Fig. 2f), WCS 842 (from carnation; Fig. 1i) and WCS 846 (Fig. 2g), originally labelled *F. redolens*, resembled *F. oxysporum*. The case of CBS 180.29 is remarkable: this isolate was identified as *F. redolens* by Wollenweber himself, and therefore is likely to have changed during cultivation. *F. oxysporum* var. *redolens* CBS 128.73 (originally from CMI, IMI 141101) also produced macroconidia corresponding of the *F. oxysporum*

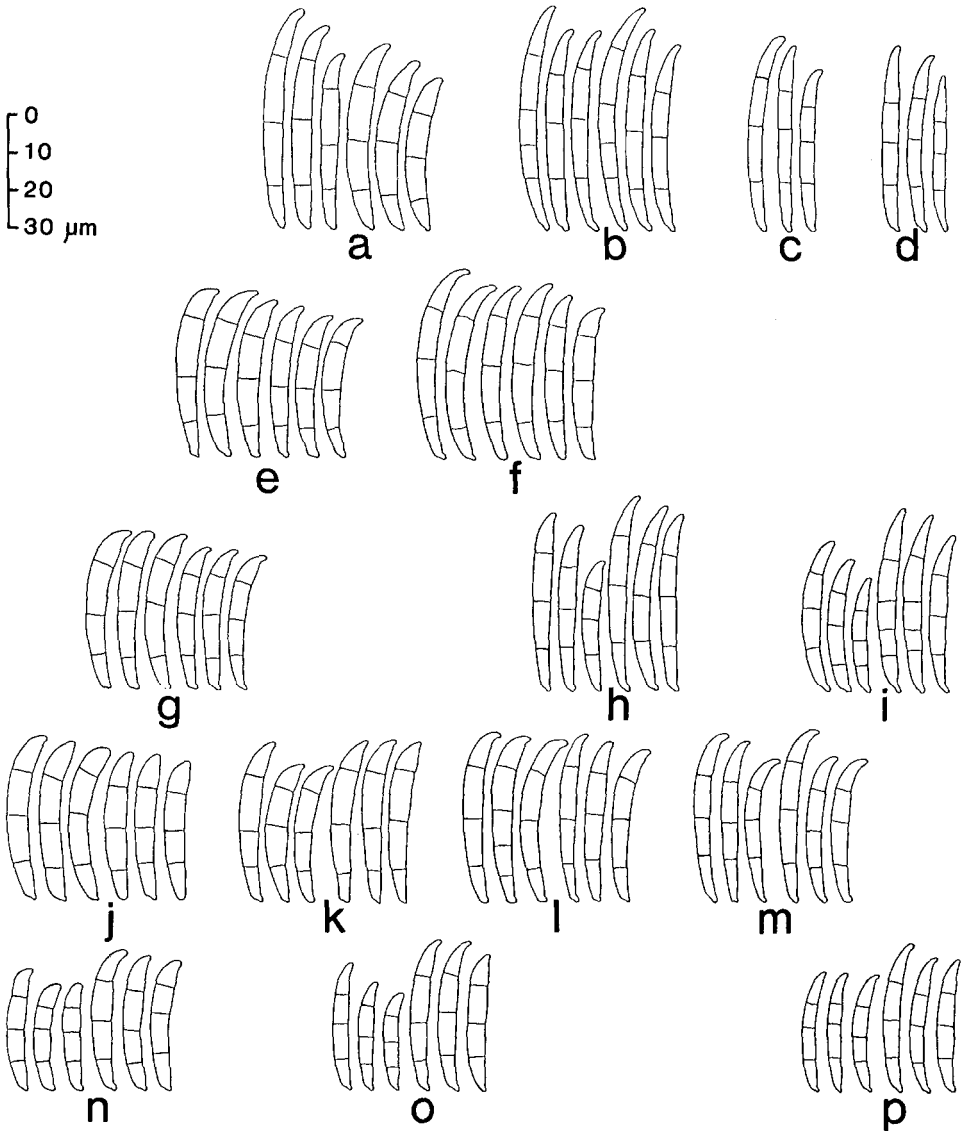

Fig. 1. Drawings of macroconidia of isolates of *F. oxysporum* (b-d, h, m, n, p) and *F. redolens* (a, e-g, i-l, o) from carnation (× 500) arranged according to their shape. Of the six representative macroconidia illustrated for each isolate, the three at the left originate from SNA and the three at the right from CLA cultures. a. CBS 248.61; b. WCS 829; c. WCS 847 (conidia from CLA culture only); d. WCS 827 (conidia from CLA culture only); e. DSM 62390; f. DSM 62379; g. DSM 62392; h. WCS 839; i. WCS 842; j. DSM 62393; k. DSM 62391; l. DSM 62378; m. WCS 834; n. WCS 848; o. CBS 366.87; p. WCS 840. Figs e-g, i (right three conidia) and j-l show sporodochial conidia; Figs a-d, h, i (left three conidia) and m-p conidia from aerial mycelium.

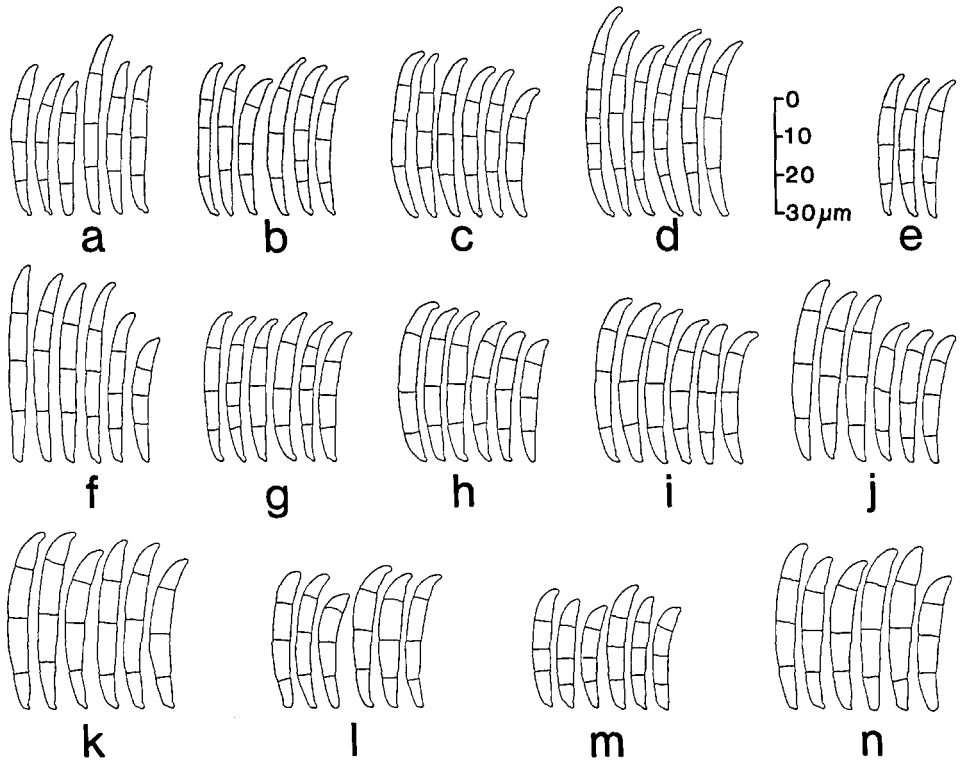

Fig. 2. Drawings of macroconidia of isolates of *F. oxysporum* (a-d), *F. oxysporum* var. *redolens* (e) and *F. redolens* (f-n) from other plants than carnation (× 500). Of the six macroconidia illustrated for each strain, the three at the left originate from SNA and the three at the right from CLA cultures. a. CBS 742.79; b. WCS 845; c. CBS 196.65; d. CBS 743.79; e. CBS 128.73; f. CBS 180.29; g. WCS 846; h. DSM 62383; i. DSM 62385; j. DSM 62380; k. DSM 64613; l. DSM 64524; m. DSM 62384; n. DSM 62386. Figs a (left three conidia), b (right three conidia), d (right three conidia) e, g-l and n show sporodochial conidia; Figs a (right three conidia), b (left three conidia), c, d (left three conidia), f and m conidia from aerial mycelium.

type (Fig. 2e). CBS 248.61, a subculture of the same isolate as DSM 62390 (the type isolate of *F. redolens* f.sp. *dianthi*), now deviates completely from the original strain in cultural characteristics (see above), but its macroconidia are quite similar to those of DSM 62390 and evidently correspond with *F. redolens* rather than *F. oxysporum* (Fig. 1). On SNA, CBS 248.61 produced conidia of the *F. oxysporum* type (Fig. 3b) although slightly wider; on CLA, macroconidia were of the *F. redolens* type but widest in the middle instead of in the upper third. In the DSM culture which is probably closer to the original strain, larger (on SNA) or smaller (on CLA), wide, more or less falcate macroconidia were seen (Fig. 3a).

Microconidia (Fig. 4). Shape and size of 1-celled microconidia (2-celled ones were not studied) from SNA and CLA cultures of the same isolate were similar for all isolates examined. Within cultures, the microconidia were uniformly shaped but varied in size.

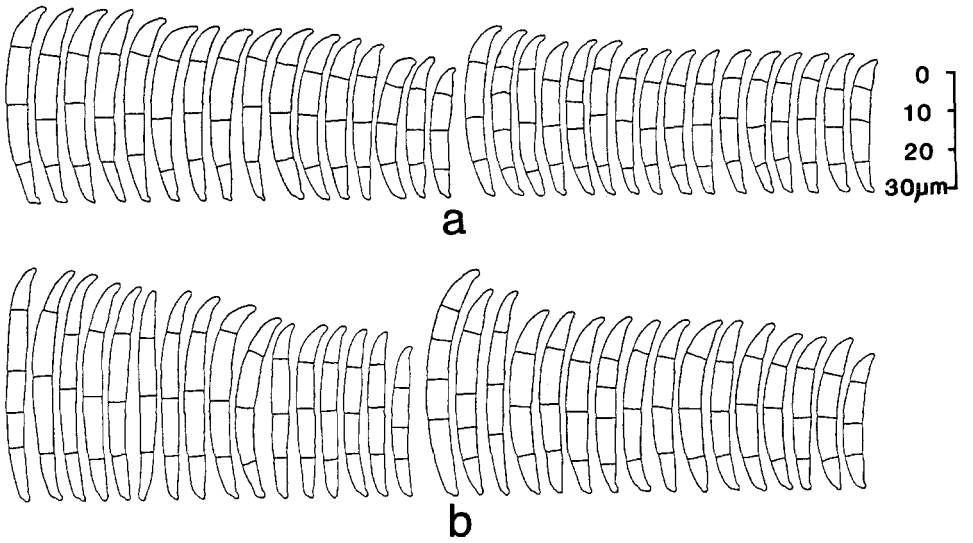

Fig. 3. Drawings of macroconidia (× 500) of two subcultures of the type strain of *F. redolens* f.sp. *dianthi*, DSM 62390 (a) and CBS 248.61 (b). Of the macroconidia shown for each strain, the sixteen at the left originate from a SNA and the sixteen at the right from a CLA culture.

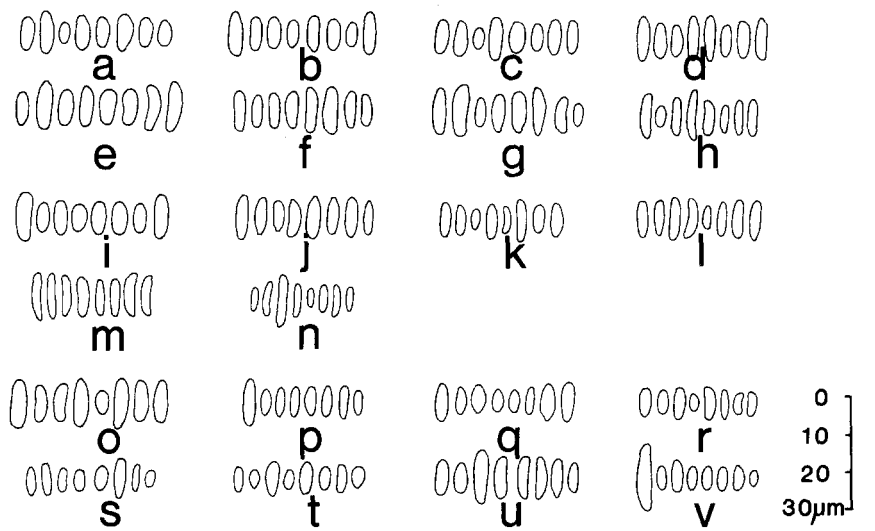

Fig. 4. Drawings of microconidia (× 500) from SNA cultures of strains of *F. oxysporum* (i-n, s-v), *F. oxysporum* var. *redolens* (r) and *F. redolens* (a-h, o-q) from carnation (a-n) and from other plants (o-v). a. DSM 62393; b. DSM 62392; c. DSM 62390; d. CBS 248.61; e. DSM 62378; f. DSM 62379; g. CBS 366.87; h. WCS 842; i. WCS 848; j. WCS 839; k. WCS 840; l. WCS 834; m. WCS 827; n. WCS 837; o. DSM 62384; p. CBS 180.29; q. WCS 846; r. CBS 128.73; s. CBS 743.79; t. CBS 742.79; u. WCS 845; v. CBS 127.81.

Microconidial shape varied among the isolates from narrowly cylindrical to broadly oval, and from straight to curved or reniform (Fig. 4). The microconidia usually were not distinctly pedicellate. Their size varied within the range 5-13 × 1.6-5 μm. Microconidia of isolates of *F. oxysporum* were particularly variable in shape and size (Fig. 4i, n, s, u). Microconidia of isolates of *F. redolens* usually were slightly larger and broadly oval (Fig. 4a, e), although smaller and narrower types occurred as well (Fig. 4f, p, q).

Phialides (Fig. 5). Shape and size of the phialides (Fig. 5) were quite variable within cultures, ranging from short and narrowly subcylindric to broadly obclavate, up to long and (sub)cylindric to subulate (Fig. 5c, f, h). Small phialides frequently lacked the basal septum (Fig. 5c), large ones sometimes had an additional septum halfway along their length (Fig. 5a, h). SNA and CLA cultures of the same isolate yielded similar phialides.

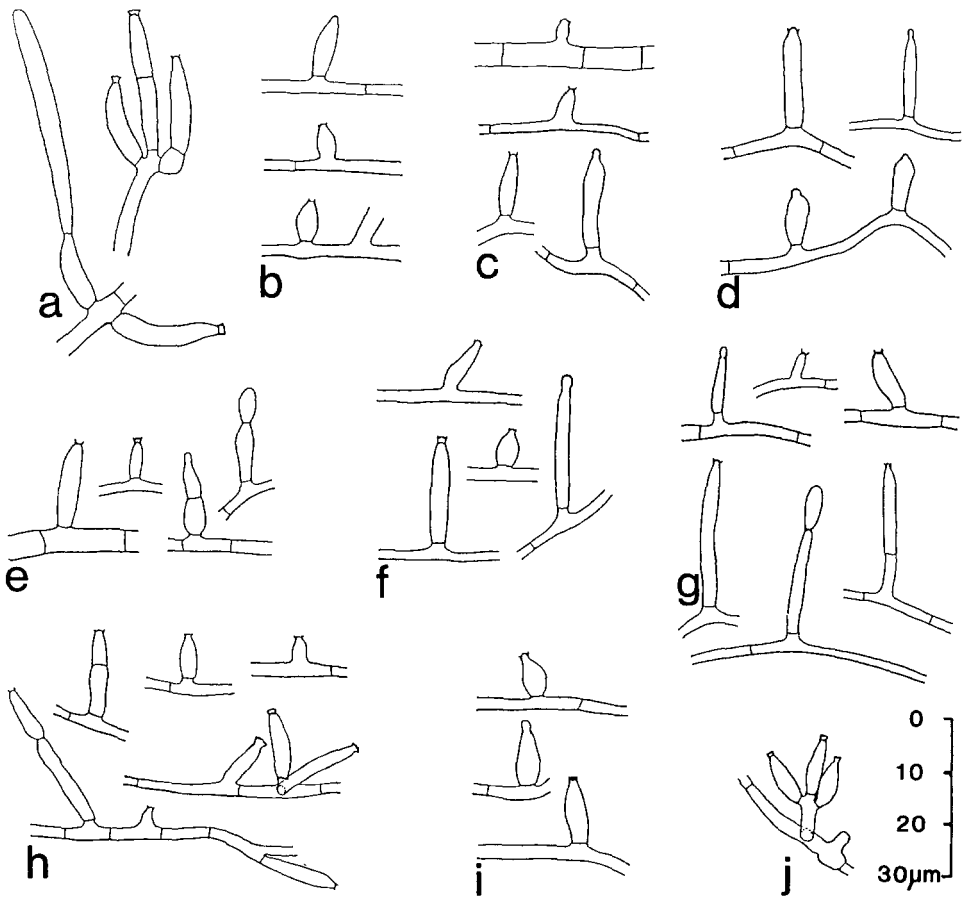

Fig. 5. Drawings of phialides (× 700) from SNA and CLA cultures of *F. oxysporum* (a-f) and *F. redolens* (g-j) from carnation (a-d, h-j) and from other plants (e-g). a. WCS 827; b. WCS 829; c. WCS 834; d. WCS 840; e. CBS 742.79; f. CBS 743.79; g. CBS 180.29; h. DSM 62378, 62390, 62391 and 62392; i. CBS 248.61; j. CBS 366.87.

Some isolates produced mainly short, obclavate phialides (Fig. 5b, i) and others mainly long, (sub)cylindric ones (Fig. 5f, g). Consistent differences in phialide morphology between isolates of *F. oxysporum* and *F. redolens* were not observed.

Inoculations. *F. oxysporum* WCS 842 and WCS 847 (vinaceous pigmentation, narrow conidia), WCS 848 (vinaceous pigmentation, wide conidia) and *F. redolens* DSM 62390 (salmon pigmentation, wide conidia) all provoked similar disease symptoms in stem-inoculated 'Sam's Pride' carnations. Withering and sometimes yellowing of both the leaves and the stem surface slowly spread upwards from the inoculation site on one or two sides of the stem, while the vascular tissues on the affected side underwent degradation and often became brown-edged. The degradation repeatedly resulted in hollow-stemmed and quickly dying plants. In some plants, stunting of shoots occurred as well. The inoculated organisms were reisolated from the diseased plants.

F. redolens f.sp. *dianthi* DSM 62392 provoked similar disease symptoms in root-inoculated plants of 'Early Sam', 'Lena' and 'IVT 62093-G' (in order of decreasing susceptibility), and the inoculated organism was recovered from diseased plants of these cultivars. 'Pallas', 'Elsy', 'Carrier 929' and 'Novada' did not develop any disease symptoms. The relative resistance levels of the cultivars to DSM 62392 are compared in Table 3 with the known resistance levels of these cultivars to races 1, 2 and 4 of *F. oxysporum* f.sp. *dianthi* (Demmink et al., 1987; Demmink, unpublished). Using this differential set of cultivars, DSM 62392 clearly corresponded in virulence with race 2 of *F. oxysporum* f.sp. *dianthi*.

Table 3. Levels of resistance of seven carnation cultivars to *F. redolens* f.sp. *dianthi* DSM 62392, and known resistance levels of these cultivars to races 1, 2 and 4 of *F. oxysporum* f.sp. *dianthi* (+: resistant, −: susceptible).

Cultivars	Pathogens			
	F. redolens f.sp. *dianthi*	*F. oxysporum* f.sp. *dianthi*		
	DSM 62392	race 1	race 2	race 4
Novada	+ +	+ +	+ +	+ +
Carrier 929	+ +	?	+ +	?
Elsy	+ +	− −	+	+ +
Pallas	+ +	+ +	+	− −
IVT 62093-G	±	?	±	?
Lena	−	+ +	− −	−
Early Sam	− −	− −	− −	− −

Discussion

The present results confirm that *F. oxysporum* f.sp. *dianthi* and *F. redolens* f.sp. *dianthi* cause identical disease symptoms on carnation as previously reported by Hantschke (1961) and Gerlach and Pag (1961). These symptoms, particularly the brown-edged vascular tissue suffering heavy degradation, are characteristic for Fusarium wilt of car-

nation as caused by races 2 and 4 of *F. oxysporum* f.sp. *dianthi* (race 1 causes different symptoms; Baayen et al., 1988) and easily distinguish the disease from Phialophora wilt of carnation and from Fusarium wilt diseases of other crops. Both taxa of *Fusarium* also share the strict specialization on *Dianthus* spp. and related genera of the Caryophyllaceae (Gerlach and Pag, 1961). Isolate DSM 62392 of *F. redolens* f.sp. *dianthi* also corresponded in virulence with the common race 2 of *F. oxysporum* f.sp. *dianthi*. From the phytopathological point of view, *F. redolens* f.sp. *dianthi* indeed appears to be identical to *F. oxysporum* f.sp. *dianthi*.

The case of carnation is not unique. On pea, from which *F. redolens* was originally described (Wollenweber, 1913), *F.* (*oxysporum* var.) *redolens* causes a wilt disease indistinguishable from that caused by *F. oxysporum* f.sp. *pisi* (Buxton, 1955; Gerlach and Pag, 1961). The same holds for Fusarium wilt of oil palm (Ho et al., 1985a, 1985b), chrysanthemum and gerbera (H. Rattink, Research Station for Floriculture, Aalsmeer, personal communication). Detailed studies on *F. oxysporum* and *F. redolens* from other crops, which would probably reveal similar cases, are lacking, presumably because *F. redolens* is rarely encountered. In general, however, the pathogenic potential of *F. redolens* seems to correspond with that of *F. oxysporum* (Booth, 1975). Both species contain pathogenic (often specialized) forms causing vascular wilts, and forms causing damping-off and cortical rots of roots and bulbs (Gerlach and Pag, 1961; Booth, 1971).

Comparison of colony pigmentation and conidium morphology in first instance suggested the presence of two distinct groups among the isolates, which roughly corresponded with *F. oxysporum* and *F. redolens* in the concept of Gerlach. The distinction was not clear-cut, however. Firstly, a continuous variation occurred between both groups in respect of pigmentation and conidium morphology. Secondly, pigmentation and conidium morphology were contradictory in some isolates: CBS 248.61 and WCS 848 produced red pigments but wide conidia, and CBS 180.29, CBS 196.65 and WCS 846 produced salmon pigments but narrow conidia. Thirdly, the differences in pigmentation and conidium morphology between the two groups were not stable.

Transitional forms between *F. oxysporum* and *F. redolens* as presently described were previously mentioned (without any documentation) by Messiaen and Cassini (1968, 1981), and for strains from carnation by Arthur and Matthews (1980). Their occurrence already becomes apparent when one studies the many species, varieties and formae recognized by Wollenweber (1913, 1916-1930-1935, 1931, 1943) and Wollenweber and Reinking (1935). Within section *Elegans*, Wollenweber characterized subsection *Oxysporum* by comparatively wide macroconidia (3.7-5.0 μm, compared with 3.0-4.0 μm in subsections *Constrictum* and *Orthocera*). Within this subsection, *F. oxysporum* var. *gladioli*, *F. oxysporum* var. *aurantiacum* and *F. dianthi* were reported to have wider (3-5.5 μm) macroconidia than usual (3-4.7 μm), and *F. redolens* the widest ones (3-6.5 μm). Transitions in shape were described as well. *F. oxysporum* var. *aurantiacum* was reported to have the usual spindle-shaped macroconidia widest in the middle, but not only *F. redolens* but also *F. dianthi* were reported to have hooked to falcate macroconidia widest in the upper third (Wollenweber and Reinking, 1935; Wollenweber, 1943).

Pigmentation does not seem to be a reliable character for distinguishing both species either. Isolate CBS 248.61 of *F. redolens* f.sp. *dianthi* produced red instead of salmon pigments. Similarly, *F. oxysporum* f.sp. *narcissi* CBS 196.65 (identification by Gerlach) produced salmon instead of red pigments. According to Gerlach and Nirenberg (1982),

the pigmentation of *F. oxysporum* is quite variable, ranging from pale beige, salmon, rose to intense purple, vinaceous and dark bluish violet. The pigmentation of *F. redolens* was described by Wollenweber as pale ochre, flesh, rose-violet or lilac (Wollenweber, 1931; Wollenweber and Reinking, 1935), by Booth (1971) as pale to reddish brown, and by Gerlach and Nirenberg (1982) as pale beige, incarnadine to ochre, finally reddish-brown, but never distinctly red, vinaceous or bluish. Reddish violet pigments were produced by *F. redolens* on rice agar, however (Gerlach, 1961; Hantschke, 1961).

On the whole, the isolates received from Berlin, where they have been preserved in soil tubes since the first isolation, appeared to be in optimal condition and to match the original morphology of *F. redolens* better than the CBS cultures. But isolates of *F. redolens* tend to change to the *F. oxysporum* type. The type isolate of *F. redolens* f.sp. *dianthi*, DSM 62390, produced salmon to saffron pigments and wide, falcate macroconidia, while the same isolate, CBS 248.61, produced red instead of salmon pigments and differed in other cultural characteristics as well, but still produced wide macroconidia on CLA. The Wollenweber isolate (CBS 180.29) of *F. redolens*, which now produced relatively narrow conidia, is likely to have changed as well. Degeneration of *F. redolens* isolates to *F. oxysporum* types has also been observed several times at the CBS (E.J. Hermanides-Nijhof, personal communication). Already Wollenweber (1931) mentioned that '*Oxysporum*-Fusarien gelegentlich zurückschlagen zu asporodochialen Formen und dann manchen Fusarien der Subsectio *Orthocera* ähneln'. Isolates CBS 366.87 and WCS 842 which were received as *F. redolens* but morphologically rather corresponded to *F. oxysporum* may be altered forms as well.

The taxonomic study thus corroborates rather than contradicts the conclusion from the phytopathological data that *F. redolens* and *F. oxysporum* are conspecific. Further evidence of the genetic identity of *F. redolens* and *F. oxysporum*-like descendants is provided by the vegetative compatibility patterns among *Elegans* fusaria (R.P. Baayen, 1988). All available data therefore indicate that the evolutionary relationships in section *Elegans* are reflected by the formae speciales rather than by the morphological types '*oxysporum*' and '*redolens*'. The distiction of *F. redolens* or *F. oxysporum* var. *redolens* from *F. oxysporum* is therefore not justified. As a consequence, Snyder and Hansen's concept of *F. oxysporum* is upheld, and the carnation wilt pathogen is designated unambiguously as *F. oxysporum* Schlecht. : Fr. emend. Snyder & Hansen f.sp. *dianthi* (Prill. & Del.) Snyder & Hansen.

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Samenvatting

De Elegans-fusaria die verwelkingsziekte veroorzaken bij anjer. I. Taxonomie

Het onderscheid tussen *Fusarium* (*oxysporum* var.) *redolens* en *F.* (*oxysporum* var.) *oxysporum* als verwekkers van verwelkingsziekte bij anjer wordt ter discussie gesteld.

Fytopathologisch onderzoek bevestigde vermeldingen in de literatuur dat voor anjer pathogene isolaten van beide soorten ziekten veroorzaken die niet te onderscheiden zijn; dit is ook bekend voor andere gewassen. Op morfologische gronden bleken *F. (oxysporum* var.) *redolens* en *F. oxysporum* één variabel complex te vormen. Kennelijk geeft de pathogene specialisatie in *Fusarium* sectie *Elegans* de evolutionaire verwantschappen beter weer dan de morfologische variatie. Het onderscheiden van *F. redolens* naast *F. oxysporum* is daarom noch als soort, noch als variëteit gerechtvaardigd.

References

Arthur, A.E. & Matthews, P., 1980. Wilt resistance on the way. Grower 93: 20-31.

Baayen, R.P., 1988. Fusarium wilt of carnation. Disease development, resistance mechanisms of the host and taxonomy of the pathogen. Ph.D. thesis, Utrecht University, Utrecht, 165 pp.

Baayen, R.P. & Elgersma, D.M., 1985. Colonization and histopathology of susceptible and resistant carnation cultivars infected with *Fusarium oxysporum* f.sp. *dianthi*. Netherlands Journal of Plant Pathology 91: 119-135.

Baayen, R.P., Elgersma, D.M., Demmink, J.F. & Sparnaaij, L.D., 1988. Differences in pathogenesis observed among susceptible interactions of carnation with four races of *Fusarium oxysporum* f.sp. *dianthi*. Netherlands Journal of Plant Pathology 94: 81-94.

Baayen, R.P., & Maat, A.L. de, 1987. Passive transport of microconidia of *Fusarium oxysporum* f.sp. *dianthi* in carnation after root inoculation. Netherlands Journal of Plant Pathology 93: 3-13.

Booth, C., 1971. The genus *Fusarium*. Commonwealth Mycological Institute, Kew, England, 237 pp.

Booth, C., 1975. The present status of *Fusarium* taxonomy. Annual Review of Phytopathology 13: 83-93.

Buiatti, M., Scala, A., Bettini, P., Nascari, G., Morpurgo, R., Bogani, P., Pellegrini, G., Gimelli, F. & Venturo, R., 1985. Correlations between in vivo resistance to *Fusarium* and in vitro response to fungal elicitors and toxic substances in carnation. Theoretical and Applied Genetics 70: 42-47.

Buxton, E.W., 1955. *Fusarium* diseases of peas. Transactions of the British Mycological Society 38: 309-316.

Deighton, F.C., Stevenson, J.A., & Cummins, G.B., 1962. Formae speciales and the code. Taxon 11: 70-71.

Demmink, J.F., Sparnaaij, L.D. & Baayen, R.P., 1987. Interactions between races of *Fusarium oxysporum* f.sp. *dianthi* and cultivars of carnation. Acta Horticulturae 216: 125-129.

Fisher, N.L., Burgess, L.W., Toussoun, T.A. & Nelson, P.E., 1982. Carnation leaves as a substrate and for preserving cultures of *Fusarium* species. Phytopathology 72: 151-153.

Gams, W., Van der Aa, H.A., Van der Plaats-Niterink, A.J., Samson, R.A. & Stalpers, J.A., 1987. CBS Course of Mycology. Third edition. Centraalbureau voor Schimmelcultures, Baarn/Delft, 136 pp.

Garibaldi, A., 1978. Fungal and bacterial diseases of carnation and gerbera. Proceedings of the Eucarpia meeting on Carnation and Gerbera, Alassio 1978: 69-88.

Garibaldi, A., 1983. Resistenza di cultivar di garofano nei confronti di otto patotipi di *Fusarium oxysporum* f.sp. *dianthi* (Prill. et Del.) Snyd et Hans. Rivista della Ortoflorofrutticoltura Italiana 67: 261-270.

Gerlach, W., 1961. *Fusarium redolens* Wr., seine Morphologie und systematische Stellung. Ein Beitrag zur Kenntnis der *Elegans*-Fusarien. Phytopathologische Zeitschrift 42: 150-160.

Gerlach, W., 1981. The present concept of *Fusarium* classification. In: Nelson, P.E., Toussoun, T.A. & Cook, R.J. (Eds), *Fusarium*: diseases, biology and taxonomy. Pennsylvania State University Press, University Park and London, p. 413-426.

Gerlach, W. & Nirenberg, H., 1982. The genus *Fusarium* – a pictorial Atlas. Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft, Berlin-Dahlem 209: 1-406.
Gerlach, W. & Pag, H., 1961. *Fusarium redolens* Wr., seine phytopathologische Bedeutung und eine an *Dianthus*-Arten gefäßparasitäre Form (*F. redolens* Wr. f. *dianthi* Gerlach). Phytopathologische Zeitschrift 42: 349-361.
Gordon, W.L., 1952. The occurrence of *Fusarium* species in Canada. II. Prevalence and taxonomy of *Fusarium* species in cereal seed. Canadian Journal of Botany 30: 209-251.
Gordon, W.L., 1965. Pathogenic strains of *Fusarium oxysporum*. Canadian Journal of Botany 43: 1309-1318.
Hantschke, D., 1961. Untersuchungen über Welkekrankheiten der Edelnelke in Deutschland und ihre Erreger. Phytopathologische Zeitschrift 43: 113-168.
Harling, R. & Taylor, G.S., 1985. A light microscope study of resistant and susceptible carnations infected with *Fusarium oxysporum* f.sp. *dianthi*. Canadian Journal of Botany 63: 638-646.
Hepple, S., 1960. Infection of peas by wilt disease fungi. Nature, London 185: 333-334.
Ho, Y.W., Varghese, G. & Taylor, G.S., 1985a. *Fusarium oxysporum* var. *redolens* from Africa as a cause of vascular wilt disease of oil palm. Phytopathologische Zeitschrift 113: 373-376.
Ho, Y.W., Varghese, G. & Taylor, G.S., 1985b. Histopathology of oil palm seedlings infected by pathogenic *Fusarium oxysporum* isolates from Africa. Phytopathologische Zeitschrift 114: 312-324.
Jacob, M. & Krebs, B., 1985. Auftreten und Bekämpfung der Fusariumwelke bei Edelnelken. Nachrichtenblatt für den Pflanzenschutz in der DDR 39: 16-19.
Kornerup, A. & Wanscher, J.H., 1963. Methuen Handbook of Colour. Third edition. Eyre Methuen, London, 252 pp.
Margraf, K., Hoffmann, L. & Kühn, H., 1986. Die Gefäßfusariosen als dominierender Depressionsfaktor in der Edelnelkenproduktion. Nachrichtenblatt für den Pflanzenschutz in der DDR 40: 219-223.
Matthews, P., 1978. Variation in English isolates of *Fusarium oxysporum* f.sp. *dianthi*. Proceedings of the Eucarpia meeting on Carnation and Gerbera, Alassio 1978: 115-126.
Messiaen, C.M. & Cassini, R., 1968. Recherches sur les fusarioses. IV. La systématique des *Fusarium*. Annales des Épiphyties 19: 387-454.
Messiaen, C.M. & Cassini, R., 1981. Taxonomy of *Fusarium*. In: Nelson, P.E., Toussoun, T.A. & Cook, R.J. (Eds), *Fusarium*: diseases, biology and taxonomy. Pennsylvania State University Press, University Park and London, p. 427-445.
Nelson, P.E., Toussoun, T.A. & Marasas, W.F.O., 1983. *Fusarium* species. An illustrated manual for identification. Pennsylvania State University Press, University Park and London, 193 pp.
Nirenberg, H.I., 1976. Untersuchungen über die morphologische und biologische Differenzierung in der *Fusarium*-sektion *Liseola*. Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft, Berlin-Dahlem 169: 1-117.
Nirenberg, H.I., 1981. A simplified method for identifying *Fusarium* spp. occurring on wheat. Canadian Journal of Botany 59: 1599-1609.
Pennypacker, B.W. & Nelson, P.E., 1972. Histopathology of carnation infected with *Fusarium oxysporum* f.sp. *dianthi*. Phytopathology 62: 1318-1326.
Prillieux, E. & Delacroix, G., 1899. La maladie des oeillets à Antibes. Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences 129: 744-745.
Punithalingam, E., 1975. Cytology of some *Fusarium* species. Nova Hedwigia 26: 275-303.
Rattink, H., 1983. Spread and control of Fusarium wilt in carnations on artificial substrates. Acta Horticulturae 141: 103-108.
Rayner, R.W., 1970. A mycological colour chart. Commonwealth Mycological Institute, Kew, and British Mycological Society, U.K., 34 pp.
Snyder, W.C. & Hansen, H.N., 1940. The species concept in *Fusarium*. American Journal of Botany 27: 64-67.

Sparnaaij, L.D. & Demmink, J.F., 1977. Progress towards *Fusarium* resistance in carnations. Acta Horticulturae 71: 107-113.
Szécsi, Á. & Hornok, L., 1986. Genetic distance in fungus genus *Fusarium* measured by comparative computer analysis of isoelectrofocusing esterase profiles. Acta Phytopathologica et Entomologica Hungarica 21: 215-230.
Voss, E.G., Burdet, H.M., Chaloner, W.G., Demoulin, V., Hiepko, P., McNeill, J., Meikle, R.D., Nicolson, D.H., Rollins, R.C. & Silva, P.C., 1983. International Code of Botanical Nomenclature. Bohn, Scheltema & Holkema, Utrecht / Dr W. Junk, The Hague, 472 pp.
Wollenweber, H.W., 1913. Studies on the *Fusarium* problem. Phytopathology 3: 24-50.
Wollenweber, H.W., 1916, 1930, 1935. Fusaria autographice delineata. Berlin, 1200 plates.
Wollenweber, H.W., 1931. *Fusarium*-Monographie. I. Fungi parasitici et saprophytici. Zeitschrift für Parasitenkunde 3: 269-516.
Wollenweber, H.W., 1943. *Fusarium*-Monographie. II. Fungi parasitici et saprophytici. Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene, Abteilung II, 106: 104-135, 171-202.
Wollenweber, H.W. & Reinking, O.A., 1935. Die Fusarien, ihre Beschreibung, Schadwirkung und Bekämpfung. Paul Parey, Berlin, 355 pp.
Yuen, G.Y., Schroth, M.N. & McCain, A.H., 1985. Reduction of Fusarium wilt of carnation with suppressive soils and antagonistic bacteria. Plant Disease 69: 1071-1075.

Book review

I. Vegh, 1987. Champignons des arbres et arbustes d'ornement. Premier inventaire des champignons identifiés en France. INRA, Paris. 122 pp. ISBN-2-85340-811-6. Price: FF. 155.00.

This book consists of two parts. The first, which occupies half the volume, consists of a list of pathogenic fungi found in France on trees and shrubs. The list is based on data collected during the last 30 years by the diagnostic section of the INRA Station de Pathologie Végétale in Versailles and is supplemented with data from the literature. The Latin names of the anamorph and, if known, of the teleomorph are followed by the French common name. The fungi are listed by their host plant. No descriptions are given of the fungi, or of the symptoms they cause. Unfortunately, scant attention has been paid to the nomenclature, which is often out of date. As the author states in his introduction, it is a first provisional list: no attempt has been made to be comprehensive. The second part of the volume consists of 247 colour plates of disease symptoms. Nearly all of them are excellent and clearly depict the characteristic disease symptoms. Both the contents and the format of this booklet (a ring-bound paperback) qualify it as a guide intended for use in the field. The excellent illustrations of disease symptoms make it useful to anybody intended in the pathology of trees and shrubs. As there is little text, readers who are not familiar with French should not experience many problems.

M. de Kam