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Fusarium oxysporum f.sp. cucurbitacearum n.f. embracing all formae speciales of F. oxysporum attacking Cucurbitaceous crops

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Abstract

Isolates of *Fusarium oxysporum* from wilted muskmelons, watermelons, cucumbers and from the muskmelon rootstock *Benincasa hispida* were screened for pathogenicity on seedlings and adult plants of these crops and related species. In seedling tests the isolates were not typically species-specific, contrary to what might be expected as an implication of their characterization as forma specialis. They often attacked species of several genera of plants, but not beyond the family of the *Cucurbitaceae*. In the adult stage, plants were much more exclusively attacked by their corresponding formae speciales, but essential exceptions occurred. Isolates from cucumber were highly pathogenic to muskmelons, in the adult stage even causing more wilt of the latter than of cucumber.

Comparing the results of these experiments with data from the literature, it is argued that the proposed f.sp. *cucurbitacearum*, embracing all formae speciales which specialize on plants within the family of the *Cucurbitaceae*, would best fit in with the present state of knowledge. A proposition is given for equivalence of old and new classifications of isolates.

Additional keywords: race, muskmelon, watermelon, cucumber, *Cucurbitaceae*, screening for resistance.

Introduction

In many agricultural crops wilt caused by *Fusarium oxysporum* is well known. Generally the pathogen is specialized on one host species; cross infection is exceptional. The different isolates are recognized as 'formae speciales'. The number of formae speciales (ff.sp.) described is steadily increasing (Gordon, 1965: 66 ff.sp.; Armstrong and Armstrong, 1968: 69 ff.sp.; Booth, 1971: 72 ff.sp.; Armstrong and Armstrong, 1981: 77 ff.sp.). With some crops, races are distinguished within the formae speciales, e.g. *F. oxysporum* f.sp. *pisi* race 5, f.sp. *lycopersici* race 2, f.sp. *melonis* race 1.2.

Exceptions to the rule of a high host specificity do exist. Armstrong and Armstrong (1968) grouped *F. oxysporum* isolates causing wilt in crops like cabbage, radish and stock in one f.sp. *conglutinans*, since cross infections, and thus host overlap occurred. Generally race 1 of f.sp. *conglutinans* attacks different types of cabbage, race 2 radish, race 3 and 4 stock, whereas race 5 attacks cabbage at relatively low temperatures (Ramirez-Villupadua et al., 1985; P.W. Bosland, pers. comm.). The exact delimitations of the various races of f.sp. *conglutinans* are not sharp and one crop variety may suffer from attack by two or more different races. Contrary to f.sp. *conglutinans* for which the occurrence on species belonging to the family of the *Cruciferae* is the unifying principle, Armstrong and Armstrong (1978) considered ff.sp. *melonis*, *cucumerinum*, and *niveum*, causing wilt of muskmelon, cucumber and watermelon respectively, as sufficiently specific to the host species. Therefore no f.sp. *cucurbitacearum* has been adopted to embrace the formae speciales mentioned and to which the more recently described ones, ff.sp. *luffae* (Kawai et al., 1958), *lagenariae* (Matuo and Yamamoto, 1967), *momordicae* (Sun and Huang, 1983), and *benincasae* (Gerlagh and Ester, 1985) could have been added. However, cross infectivity in the seedling stage is well known (Reid, 1958; Palti and Joffe, 1971; Martyn and McLaughlin, 1983b; Martyn, 1985; McMillan, 1986). But one of the arguments used in favour of separate formae speciales is the increased specificity of the formae speciales mentioned when experiments are executed with older plants than those normally used in seedling tests (Owen, 1956; Fletcher and Kingham, 1966).

Having been confronted with new isolates from wilted horticultural crops like muskmelons and cucumbers, we assessed their pathogenicity to a wider range of cucurbitaceous species and cultivars of some of the commercial representatives, in comparison with established formae speciales. On a more limited scale we compared the results of seedling tests with adult-plant screening. The results of this research and data from the literature were considered in order to decide whether the different formae speciales should be maintained or grouped into one new forma specialis covering all isolates of *Fusarium oxysporum* attacking members of the family of the *Cucurbitaceae*.

Materials and methods

Isolates. For resistance breeding purposes a number of isolates of *F. oxysporum* were available at the Research Institute for Plant Protection (IPO). These are referred to under a-g in Table 1. From wilted plants some more *F. oxysporum* isolates were obtained in recent years, as indicated in Table 1 under h-p.

Inoculation and disease assessment. Unless otherwise stated, the applied inoculation procedure consisted in dipping the roots of seedlings of about two weeks old, with the first true leaf just starting to expand, in a culture suspension of *F. oxysporum*, which contained about 1.5×10^6 conidia/ml. This culture suspension was obtained by growing the pathogen for about ten days at 22 °C in a liquid Czapek-Dox medium. After inoculation, the seedlings were planted in flat trays with potting soil. They were incubated in a glasshouse at 24/22 °C (day/night temperature). During the first day the trays were covered with a plastic lid to facilitate plant establishment. Next day the lid was partially opened. Two days after inoculation the cover was completely eliminated. In winter artificial light was used to supplement day length and to increase photosynthesis.

About two weeks after inoculation the plants were scored for susceptibility and resistance. In most experiments five plants per cultivar or species were used. The reaction was scored as susceptible (S) when at least three of them showed wilting. These plants were dead one week later. The plants were scored resistant (R) when they did not show wilting or strong growth retardation. The categories 'moderately resistant' or 'moderately susceptible' (MR and MS) were used to indicate an intermediate reac-

Table 1. Different formae speciales and isolates of *F. oxysporum* used in the experiments.

Isolate number	Forma specialis	Plant source	Origin
a	*melonis* race 0*	muskmelon	IPO
b	*melonis* race 1*	muskmelon	IPO
c	*melonis* race 2*	muskmelon	IPO
d	*melonis* race 1.2*	muskmelon	G. Risser, INRA, France
e	*cucumerinum*	cucumber	IPO
f	*niveum* race 1**	watermelon	D. Netzer, Volcani Center, Israel
g	*niveum* race 2**	watermelon	D. Netzer, Volcani Center, Israel
h	*benincasae*	*Benincasa hispida*	IPO, 1983, see Gerlagh and Ester (1985)
i	*benincasae*	*B. hispida*	Belgium, 1985, isolation at IPO
j	*benincasae*	*B. hispida*	Netherlands, 1985, isolation at IPO
k	*cucumerinum****	cucumber 'Corona'	Plant Protection Service, Wageningen, PD 85/453A
l	*cucumerinum****	cucumber 'Lucinde'	Plant Protection Service, Wageningen, PD 85/453B
m	*cucumerinum****	cucumber	Plant Protection Service, Wageningen, PD 85/453C
n	*cucumerinum****	cucumber	Plant Protection Service, Wageningen, PD 86/466-1
o	*cucumerinum****	cucumber	Plant Protection Service, Wageningen, PD 86/466-2
p	*cucumerinum****	cucumber	Plant Protection Service, Wageningen, PD 86/466-3

* Race identification according to Risser et al., 1976.
** cf. Netzer, 1976. Race 1 is an isolate from the USA with higher virulence than race 0; race 2 is the very virulent one existing a.o. in Israel and Greece.
*** Tentative identification, based on species from which the isolate was obtained.

tion, either quantitatively or qualitatively. MS and S taken together were also noted as compatible (C), R as incompatible (I), whereas MR was considered as incompatible (and noted ~ I). In many different experiments cultivars and species have been screened several times for resistance to the isolates enumerated.

In one large experiment 'adult' plants have been examined. They were grown in pots with 3 litres of potting soil. At 7 weeks after sowing the roots of the plants were damaged with a knife, and inoculum (50 ml of culture suspension with about 1.5×10^6 conidia/ml) was added to the soil. Wilting was scored from 2 weeks from inoculation on. Eight weeks after inoculation the experiment was terminated. From non-wilted plants browning of roots and of vessels and medullary tissue of the hypocotyl was scored, and an effort was undertaken to isolate *Fusarium oxysporum* from the stem between the fifth and sixth nodes. To test the isolation method, *F. oxysporum* was also isolated from some wilted plants. Stem pieces of about 2 cm length were superficially sterilised by dipping in 96% ethanol. A small piece of tissue from its centre was cut into very fine pieces. Fifteen pieces of each plant were plated on agar. With wilted plants this resulted in 15 colonies of *F. oxysporum*.

Table 2. Species of cucurbitaceous crops screened for resistance to different isolates of *F. oxysporum*.

Species	Common name	Comment
Benincasa hispida (Thunb.) Cogn.	wax gourd	rootstock for muskmelon; seed obtained from several companies
Citrullus vulgaris Eckl. & Zeyh.	watermelon	various cvs tested; many sources of seed
Cucumis melo L.	muskmelon	various cvs tested; many sources of seed
Cucumis metuliferus Naud.	African horned cucumber; jelly melon	seed obtained from IVT, Wageningen
Cucumis sativus L.	cucumber	various cvs tested; many sources of seed
Cucurbita ficifolia Bouche	fig leaf gourd	rootstock for cucumber; seed obtained from several companies
Cucurbita pepo L.	squash, courgette	rootstock RS 841; many different cvs of zucchini (courgette) and calabashes from different sources
Luffa cylindrica (L.) M.J. Roem	sponge gourd	seed from IVT
Momordica charantia L.	bitter gourd	seed from IVT and Agricultural University Wageningen
Sicyos angulatus L.	bur cucumber	rootstock KJ 100 (from Sluis & Groot); wild material (from IVT)

Among the genera mentioned in this table *Benincasa* and *Citrullus* belong to one subtribe, *Luffa* is in a different subtribe within the same tribe (Jeffrey, 1980). All other genera are in different tribes.

Test plants. For the different experiments plants were chosen from the species mentioned in Table 2. In a special experiment wild material belonging to the genus *Cucumis* was screened for its reaction with different isolates of *F. oxysporum*. In this case only five plants per combination were available in only one experiment. The seeds were obtained from S. Zijlstra, Institute for Horticultural Plant Breeding (IVT). The data are indicated in Table 5.

Results

Seedling tests. With the different races of f.sp. *melonis* and seedlings of cvs of melon the expected race-specific results were obtained, corresponding to the known gene-for-gene system (Risser et al., 1976) (data not shown). The races of f.sp. *melonis* even reacted differentially with cvs of watermelon. The order of increasing virulence (from 0 to 1.2) did not necessarily mean increased virulence towards cvs of watermelon. Thus 'Fairfax' was susceptible to the races 0 and 1, but resistant to 2 and 1.2 (Table 3).

The other species, apart from cucumbers and courgettes, were not represented by a sufficient number of cvs to permit an analysis on gene-for-gene basis as for muskmelons and watermelons. Furthermore, arguments to distinguish races of f.sp. *cucumerinum* are as yet rare (cf. Armstrong et al., 1978), and for courgette there is not even a forma specialis of its own. The results of screening are summarized in Table 4.

Especially *C. pepo* plants were rarely very susceptible, but might show some wilting. This reaction was rather variable between different experiments, as were other cases of intermediate resistance. Nevertheless it was sufficiently clear that many isolates were pathogenic on seedlings of other species or even genera than the one from which they had been isolated. It was also clear that different isolates from the same wilted crop, and even from one crop in the same glasshouse, sometimes were not identical (e.g. n/o and p on *C. pepo*; cf. Leary and Wilbur, 1976).

The experiments with the wild *Cucumis* species further demonstrated the lack of specificity of the pathogen in seedling tests (Table 5).

In general the two representatives of one species behaved similarly. *F. oxysporum* f.sp. *melonis* (a, b, c, d) attacked *C. melo*, but especially the races 2 (c) and 1.2 (d) also showed pathogenicity towards *C. africanus* and *C. zeyheri*. Isolate 1 from cucumber

Table 3. Interaction of seedlings of cvs of watermelon with races of *F. oxysporum* f.sp. *melonis* and f.sp. *niveum*.

Cultivar	f.sp. *melonis*				f.sp. *niveum*	
	0	1	2	1.2	1	2
Sugar Baby	S	S	MS	S	S	S
Panonia	S	S	S	S	S	S
Fairfax	S	S	R	R	MS	S
Congo	R	R	R	R	MR	S

R = resistant; S = susceptible; MR = moderately resistant; MS = moderately susceptible.

Table 4. Interactions in the seedling stage of different species of cucurbitaceous crops with isolates of ff.sp. of *F. oxysporum*.

Host species	Isolates												
	f.sp. *melonis*				f.sp. *cucumerinum*					f.sp. *niveum*		f.sp. *benincasae*	
	0	1	2	1.2									
	a	b	c	d	e	k	l/m	n/o	p	f	g	h	i/j
Citrullus vulgaris	C	C	C	C	C	C	C	C	C	C	C	C	C
Cucumis melo	C	C	C	C	C	C	C	C	C	I	I	I	I
sativus	I	I	I	I	C	C	C	C	C	I	I	I	I
metuliferus	I	I	I	C	I	–	–	–	–	–	I	I	–
Cucurbita pepo													
RS 841	I	I	I	I	I	I	I	–	–	I	I	I	I
other courgettes	C	C	C	C	I	I	I	C	I	I	C	C	I
Cucurbita ficifolia	I	I	I	I	I	C	C	C	C	–	I	I	I
Benincasa hispida	I	I	I	I	I	I	C	–	–	I	I	C	C
Sicyos angulatus	I	I	I	I	–	I	C	–	–	I	I	I	I
Luffa cylindrica	I	I	I	I	I	–	–	–	–	I	~I	I	–
Momordica charantia	I	I	I	I	–	I	–	–	–	–	–	I	–

Isolates a – p: see Table 1.
C = compatible; susceptible interaction of the pathogen with at least one cultivar or line of the species mentioned.
I = incompatible.
~I = incompatible, though minor symptoms have been observed on rare occasions (corresponding to moderately resistant).
– = not tested.

was much more aggressive than e (f.sp. *cucumerinum*), but the resistant reaction of *C. melo* no. 1793 revealed that isolate 1 was not merely more aggressive, but that also a differential interaction pattern was present. *F. oxysporum* f.sp. *niveum*, race 2 (g) proved to be pathogenic on *C. zeyheri* (4×) and one of the *C. sativus* representatives only. The lack of pathogenicity of f.sp. *benincasae* (h, i, j) towards *Cucumis* spp. is apparent (cf. Table 4).

Screening of adult plants. The overlap in host range was greatly reduced when adult plants were screened for resistance (Table 6). With adult plants only one species wilted with each forma specialis. This species was the expected host in the case of f.sp. *melonis*, f.sp. *niveum*, and f.sp. *benincasae*. However f.sp. *cucumerinum* isolate e did not wilt any species. Isolate 1 from cucumber did not wilt cucumber, but did wilt melon, though not 100% of the plants.

An effort was made to isolate *F. oxysporum* from non-wilted plants, and browning of the interior part of the hypocotyl was assessed (Table 6). Muskmelon reacted to all isolates except f.sp. *niveum* 2 with wilting or browning of at least some plants. Cucumber inoculated with isolate 1 resisted wilting, but the vascular system showed

Table 5. Reaction of different wild collections of *Cucumis* spp., inoculated with ff.sp. and isolates of *F. oxysporum* in seedling tests.

Species	Genebank no. and origin	Isolate								
		f.sp. *melonis*				f.sp. *cucumerinum*		f.sp. *niveum* 2	f.sp. *benincasae*	
		0	1	2	1.2					
		a	b	c	d	e	l	g	h	i/j
Cucumis, subgenus *Melo*										
C. africanus L.	1788, USA	I	I	C	C	I	C	I	I	I
	2302, S-Africa	C	I	C	C	I	C	I	I	I
C. anguria var. *anguria* L.	0307, Brasil	I	I	I	I	I	C	I	I	I
	2152, Ethiopia	C	I	I	~I	I	C	I	I	I
C. anguria var. *longipes* A. Meeuse	1735, S-Africa	I	I	I	I	I	C	I	I	I
C. melo L.	1793, Iran	C	C	C	C	C	I	I	I	I
	1817[], USSR	C	C	C	C	C	C	I	I	I
C. melo var. *agrestis* Naud.	1816, India	C	C	C	C	C	C	~I	I	I
C. metuliferus Naud.	1802, S-Africa	I	I	I	C	I	C	I	~I	I
	1985, USA	~I	I	~I	C	I	C	I	I	I
C. zeyheri Sond. (2×)	1750, S-Africa	C	I	C	C	C	C	I	I	I
	1773[], Turkey	I	–	–	C	–	–	–	–	–
C. zeyheri Sond. (4×)	1053, S-Africa	C	~I	C	C	C	C	C	I	I
	1807[], S-Africa	I	I	C	C	I	C	C	I	I
Cucumis, subgenus *Cucumis*										
C. sativus L.	0632, Turkey	I	I	I	I	C	C	C	I	I
	1745, India	I	I	I	I	C	C	I	I	I
C. sativus var. *hardwickii* Alef.	0777, India	I	I	I	I	C	C	I	I	I
	1963, S-Africa	I	I	I	I	C	C	I	I	I

Isolates a - l: see Table 1.
C = compatible; susceptible reaction.
I = incompatible; resistant reaction.
~I = incompatible, though some minor symptoms were visible in a very few plants.
– = not tested.
[] = only two plants per treatment.

browning beyond the hypocotyl in four out of five plants. From courgette the pathogen could be isolated in some cases. This is the only species that harboured the fungus without showing symptoms.

Discussion

Reactions of seedlings versus adult plants. Screening for resistance of cultivars of melons, watermelons or cucumbers is usually done with seedlings, both by sowing in infested soil or by root-dipping of young plants (Owen, 1956; Palmer and Williams, 1981; Martyn and McLaughlin, 1983b; McMillan, 1986). Some authors explicitly indicate that this is the best stage. Thus Latin and Snell (1986) claimed to obtain best correspondence with field observations when using 11-day-old seedlings (first true leaf

Table 6. Reaction of adult plants to inoculation with different isolates of *F. oxysporum*.

Species/cultivar	Isolate				
	f.sp. *melonis*	f.sp. *cucumerinum*		f.sp. *niveum*	f.sp. *benincasae*
	1.2 (d)	e[1]	1	2 (g)	h
Citrullus vulgaris 'Sugar Baby'	R	R	R	S	R
'Congo'	R	R	R	S	1B[2]
Cucumis melo 'Carmeline'	S	2B	3S/2B[3]	R	2B
Cucumis sativus 'Corona'	R	R	4B	R	R
Cucumis metuliferus	R	R	R	R	R
Cucurbita ficifolia	R	R	R	R	R
Cucurbita pepo 'Greyzini'	R	1B	1F[2]	3F	R
Benincasa hispida	R	R	R	R	S

Isolates d - l: see Table 1.
R = resistant, no wilting; S = all plants susceptible, wilted (not scored for browning or presence of *Fusarium*).

[1] The concentration of the inoculum was 10^5 conidia/ml only.

[2] In the absence of wilting, the number of plants with vascular browning of the hypocotyl and beyond (B), and the number from which *F. oxysporum* could be isolated (5th - 6th node) (F), on a total of five plants examined, are indicated.

[3] Three plants had wilted; the two remaining plants showed vascular browning.

expanding). With 6-day-old seedlings (cotyledon stage) varieties not yet show their resistance to the full extent, and thus the difference in resistance is not well assessed. Armstrong and Armstrong (1975) used somewhat older seedlings to prevent damping-off and to assess adult plant resistance. Apart from scientific considerations, a seedling test is in any case most amenable for breeders, since the method gives quick responses, and the space requested is limited.

The cross infections which have been obtained in the present experiments are abundantly confirmed in the literature (Owen, 1956; Reid, 1958; Martyn and McLaughlin, 1983a; McMillan, 1986). In these experiments pathogenicity of isolates of *F. oxysporum* from *Cucurbitaceae* is highly unspecific to the species when tested in the seedling stage. However this lack of specificity does not pass a certain borderline. I.e. cucurbitaceous crops are only attacked by isolates from plants within the same family, and such isolates do not induce wilting of plants beyond this family (Armstrong and Armstrong, 1978).

These results correspond to the findings of Bouhot (1981). He obtained changes in host spectrum when submitting conidia to mutagenic treatment. Starting with conidia of ff.sp. *niveum* and *cucumerinum*, and screening on three hosts (watermelon, cucumber and muskmelon), he obtained in one organism most of the possible combinations from complete loss of pathogenicity to acquisition of pathogenicity to the two complementary hosts, besides the original one, just like obtaining the possible combinations of virulence genes in f.sp. *melonis* starting from different races of this forma specialis. He did not succeed in acquiring pathogenicity to (one of) these hosts when starting with a saprophytic *F. oxysporum* or with f.sp. *gladioli*. Thus a unifying principle occurs in these formae speciales specialized on cucurbitaceous hosts.

Differences in susceptibility between host species are to be noticed. In our experiments watermelons were attacked in seedling stage by a large spectrum of formae speciales and isolates, and muskmelons by isolates of ff.sp. *melonis* and *cucumerinum*. Cucumbers, which belong to the same genus as muskmelons, were only attacked by f.sp. *cucumerinum* or isolates from cucumber (which have tentatively been given the identification 'f.sp. *cucumerinum*'; see Table 1). No other isolates than the specific formae speciales are known to attack *Luffa*, *Benincasa* (with the exception of isolates l and m from cucumber), *Lagenaria* or *Momordica*. And their formae speciales, with few exceptions (Armstrong and Armstrong, 1978) do not attack other crops (Matuo and Yamamoto, 1967; Kanehira and Shinohara, 1980; Sun and Huang, 1983). More specialized research in regions where these crops are grown on a large scale and with intensive crop rotations might change the picture. According to Bruehl (1976) formae speciales might have developed in *F. oxysporum* to exploit different hosts as special ecological niches ('radiate' evolution). Combinations of virulence factors will offer advantages when the different crops can be found in rotations on the same sites.

Adult plants develop higher resistance to the pathogen (Fletcher and Kingham, 1966; Armstrong and Armstrong, 1975). This starts already very early (Owen, 1956). With plants of four weeks of age the specificity of the formae speciales is quite good. Nevertheless we found an isolate from cucumber to cause wilting of muskmelon in the adult (seven-week-old at inoculation) plant stage, whereas cucumber did not wilt. However there was vascular browning beyond the hypocotyl in these non-wilting cucumber plants. We consider this browning as a token of compatibility (Kanehira and Shinohara, 1980; cf. Pelcz, 1984a). On the other hand Armstrong and Armstrong (1975; 1978) and Zink et al. (1983) considered browning not to be a reliable criterion. In Crucifers, however, Armstrong and Armstrong (1966) supposed root discoloration at low temperatures to be equivalent to wilting at high temperatures. We conclude that both cucumber and muskmelon are susceptible, but if only wilting was taken into consideration, this would identify the pathogen as f.sp. *melonis*. Melon is not the original host however. Armstrong and Armstrong (1978) maintained that the formae speciales are highly specific to the primary host, which should usually be the one from which the pathogen has been isolated. But they also claimed an isolate obtained from cucumbers from Israel to belong to f.sp. *melonis*, and even four isolates from melons from Germany were rebaptized f.sp. *cucumerinum*. Moreover they recognized the existence of 'numerous papers' with 'contradictions in host range'. Notwithstanding a clear increase in specificity with increasing age of plants, the generalized use of seedling tests, and the exceptions found, even with adult plants, suggest that the recognition of one comprehensive forma specialis for the family of the *Cucurbitaceae* is much more consistent with the observed facts. The situation seems quite similar to the one described for f.sp. *conglutinans* with Crucifers.

We fully support the opinions of Bouhot (1981) and McMillan (1986) in this respect. It would certainly not be logical to include our isolate l – and most probably the same applies to e, k, m, n, o and p – in f.sp. *melonis*. These isolates from cucumber share with others, mentioned in the literature from all over the world, their capacity to cause wilt of melons (McKeen, 1951; Kosswig, 1955; Owen, 1956; Takada, 1982; McMillan, 1986) and often also of watermelons (Gerlagh and Ester, 1985) or even of courgettes

(Palti and Joffe, 1971). This contrasts to the absence of wilting of cucumber in the seedling test with isolates from muskmelons (Armstrong et al., 1978; Kanehira and Shinohara, 1980). Exceptions to the latter are the four isolates from Germany mentioned by Armstrong and Armstrong (1978), and to a limited extent an isolate used by Owen (1956). McMillan (1986) showed isolates from the Bahamas to be highly unspecific, whereas those from Florida were specific to their original host. But his Table 1 nevertheless indicates isolates from cucumber from Florida to wilt both cucumber and melons.

Horizontal versus vertical pathogenicity. Specificity greatly depends on whether the resistance is absolute or partial. Partial resistance is largely dependent on environmental conditions such as inoculation method, inoculum potential, temperature or light during incubation (Reid, 1958; Armstrong and Armstrong, 1978; Pelcz, 1984b). Root damage by nematodes or increasing inoculum concentration by a factor 10 or 100 shift moderately resistant cultivars to plain susceptibility (Douglas, 1970; Martyn and McLaughlin, 1983b; Caperton et al., 1986; Latin and Snell, 1986). Under these conditions absolute resistance does not decrease in effect (Douglas, 1970; Caperton et al., 1986).

It is interesting to speculate on the type of resistance found e.g. in *C. pepo*. The rootstock RS 841 is a representative of this species. It has a capacity for vigorous growth. In a single experiment even RS 841 however was killed by *F. oxysporum*. Thus it seems possible that the resistance of *C. pepo* is highly dependent on heavy growth and rapid reaction to the pathogen. Much of the difference between authors may as well depend on differing degrees of root damage, influencing the plant's capacity to resume active growth. Thus Armstrong et al. (1978) inoculated very young plants by root cutting without uprooting, and Latin and Snell's (1986) 'pipette method' is in principle comparable. The latter system leads to much less wilting than the root-dipping method with plants of the same age. Descriptions of the disease development of *Fusarium* wilt indicate the importance of rapid development of tyloses and quick replacement of blocked vessels by new ones (Kuniyasu and Takeuchi, 1983; Mahjoub et al., 1984; Sen and Palodhi, 1984). Cross protection, which is claimed by several authors to occur against formae speciales of *F. oxysporum* in cucurbitaceous crops (Risser and Rode, 1973; Molot et al., 1979; Martyn, 1985), is supposed to be due to establishing a preparedness to the pathogen. The defence reactions in a cross-protected plant are more rapid than without such a protection. This can be considered as equivalent to an increase in partial resistance. Vascular browning without wilting, as found with adult cucumbers (Table 6) might be indicative of a high degree of partial resistance. The ease with which isolates from cucumber generally wilt muskmelons (in seedling and often also in the adult stage), and the scarcity of the reciprocal phenomenon might be explained by assuming an increasing level of 'horizontal' resistance from muskmelons to cucumbers. Inversely, f.sp. *melonis* would then have a rather low 'horizontal' pathogenicity (Robinson, 1976), and f.sp. *cucumerinum* would have a high degree of horizontal pathogenicity. In test conditions f.sp. *cucumerinum* would then be able to provoke wilt of muskmelons more easily than of cucumbers. The cucumber isolate of Fletcher and Kingham (1966) was able to wilt young, but not old melons. It is tempting to use data from other research (Owen, 1956; Fletcher and Kingham, 1966; Martyn and McLaughlin, 1983a; McMillan, 1986) to range more crops according to increasing horizontal resistance. The order might then be: muskmelon, watermelon < cucumber < courgette. The selection pressure by the pathogen, and corresponding breeding activities, have resulted in the present situation, in which races are very easily distinguished for melons, but less so for watermelon and cucumber, though even with the latter crop absolute resistance has been described (Armstrong et al., 1978; Palmer and Williams, 1981). No forma specialis has been described for courgette. Populations with a high degree of horizontal pathogenicity, needed to wilt cucumber, even seem to survive with difficulty, since problems of cucumber wilt occur only in some years, and the disease may be exceptional in other years or even disappear spontaneously (Kosswig, 1955; H.A. van Kesteren, pers. comm.).

Loss of pathogenicity after prolonged culture on artificial media is described to occur more readily towards secondary than towards primary hosts (Armstrong and Armstrong, 1975). This could be explained as primarily a decrease in horizontal pathogenicity. In our experiments the fresh isolates from cucumber (k-p) were more virulent than the old isolate of f.sp. *cucumerinum* (e). They even showed a wider host range (Table 4). Specific virulence, as e.g. to varieties of muskmelon, is remarkably stable (Bouhot, 1981).

It thus seems possible that within the proposed f.sp. *cucurbitacearum* races exist with varying degrees of horizontal pathogenicity, besides races with well-defined vertical pathogenicity, such as the races of f.sp. *melonis*. Combinations of both types of pathogenicity in the pathogen and of both types of resistance in the host complicate the analysis. A more detailed elucidation of these questions will demand much more research.

Proposed classification

It has been shown that specificity of isolates is limited in the seedling stage, so that cross infectivity regularly occurs. Especially the isolates from cucumber and muskmelon, both *Cucumis* species, play a key role, with their lack of symmetry in the cross infectivity. But cross infectivity also occurs with plants of other genera, even belonging to other tribes. With adult plants the specificity is 'better', but still the remarkable compatibility of isolates from cucumber with muskmelon as the host, is prevalent.

A seedling test is normally used to determine to which forma specialis a pathogenic isolate of *F. oxysporum* belongs. Clearly the different isolates of *F. oxysporum* from *Cucurbitaceae* have common characteristics which unite them as a group and distinguish them from isolates from other plants. This is a strong argument to combine the different formae speciales known to be pathogens of members of the *Cucurbitaceae*. Furthermore, an easy and unambiguous identification of a forma specialis is necessary, whereas identification of races always demands much more elaborate screening. Therefore we propose to erect a f.sp. *cucurbitacearum* (see Discussion), which is defined by the possibility to infect and cause wilting of seedlings and/or adult plants of one or more of the species belonging to the *Cucurbitaceae*. Exact race identification within this forma specialis is more complicated. For some of the formae speciales known up till now, a detailed analysis has been published. Races 0, 1, 2 and 1.2 of f.sp. *melonis* are well defined in relation to corresponding resistance genes. But in other cases data are lacking. To accomodate for different races of unequal degree of exactness of identification, we propose a new system of notation, which should exclude confusion. If

Table 7. Proposed equivalence of races of *F. oxysporum* f.sp. *cucurbitacearum* with older identifications.

Old identification	New Identification
F. oxysporum...	*F. oxysporum* f.sp. *cucurbitacearum...*
f.sp. *melonis*	race me
f.sp. *melonis* race 0	race me 0
f.sp. *melonis* race 1	race me 1
f.sp. *melonis* race 2	race me 2
f.sp. *melonis* race 1.2	race me 1.2
f.sp. *niveum*	race ni
f.sp. *niveum* race 0	race ni 0
f.sp. *niveum* race 1	race ni 1
f.sp. *niveum* race 2	race ni 2
f.sp. *cucumerinum*	race cu
f.sp. *luffae*	race lu
f.sp. *lagenariae*	race la
f.sp. *momordicae*	race mo
f.sp. *benincasae*	race be

a certain crop is considered to be the principal host, the race is indicated with the first two letters of the present forma specialis name, thus "race me" replaces the old "f.sp. *melonis*". Numbers might follow this race indication whenever (sub)races are known, whether arbitrarily numbered or matching known resistance genes, e.g. "race me 2". Table 7 shows the resulting classification. Fundamental research in the future might add refinement to this classification.

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Samenvatting

Fusarium oxysporum f.sp. cucurbitacearum n.f., een samenvoeging van alle voor Cucurbitaceae pathogene formae speciales van F. oxysporum

Isolaten van *Fusarium oxysporum* uit verwelkte meloenen, watermeloenen, komkommers en uit de meloene-onderstam *Benincasa hispida* werden getoetst op pathogeniteit voor zaailingen en volwassen planten van deze gewassen en verwante soorten. In zaailingtoetsen waren de isolaten weinig soort-specifiek, in tegenstelling tot wat mocht worden afgeleid uit hun karakterisering als forma specialis. Zij tastten vaak soorten uit verschillende geslachten aan, maar niet buiten de grenzen van de familie der *Cucurbitaceae*. In het volwassen stadium waren de interacties veel specifieker en werden planten slechts aangetast door de bijbehorende formae speciales. Enkele essentiële uitzonderingen kwamen echter voor. Isolaten van komkommer waren zeer pathogeen voor meloen. In het volwassen stadium veroorzaakten zij zelfs sterkere verwelking van meloen dan van komkommer.

Vergelijking van de resultaten van deze proeven met gegevens uit de literatuur leidt tot de conclusie dat de voorgestelde f.sp. *cucurbitacearum*, die alle formae speciales met specialisatie op *Cucurbitaceae* omvat, het best overeenkomt met de huidige stand van kennis. Een voorstel wordt gedaan ter vervanging van de oude classificatie van isolaten door corresponderende nieuwe aanduidingen.

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Book review

D. Spaar, H. Kleinhempel & R. Fritzsche, 1986. Diagnose von Krankheiten und Beschädigungen an Kulturpflanzen – Gemüse. VEB Deutscher Landwirtschaftsverlag, Berlin. For non-socialist countries: Springer-Verlag, Berlin/Heidelberg/New York/Tokyo. 406 pp. ISBN 3-540 13314-3/0-387 13314-3. Price DM 140.

The book is original in many aspects. The language is German, which limits its domain to a market of a little over 100 million people in Central Europe. The audience is defined as plant protection specialists in scientific, practical and teaching positions and students at different levels. The preface announces the book as one in a series on diseases and damage of different crops, but no indication is given of other crops to be covered. The appearance of a first volume in the series, on methods to be used for identification, is however mentioned.