REVIEW

Fusarium Species, their Taxonomy, Variability and Significance in Plant Pathology

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Abstract

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Fusarium Link (1809) is an anamorph genus with worldwide distribution and a remarkable degree of biodiversity. Its species are common in soil and have been found on a very wide range of vascular plants. Some specialized species are parasitic on other fungi and or insects. In the system of fungi the genus *Fusarium* is classified in the class Hyphomycetes which belongs to the *Deuteromycotina*. Teleomorphs have been placed in the genera *Nectria* and *Gibberella*, order *Hypocreales* (*Ascomycetes*). The taxonomy of the genus *Fusarium* is not settled and the number of species and sections varies. A few recent classification systems of this genus exist. *Fusarium* spp. have mostly been studied in the context of their ability to cause diseases of many economically important crop plants. Some species produce mycotoxins and other metabolites that can be harmful to humans and livestock. There is a wide variability in pathogenicity, and in many *Fusarium* spp. various *formae speciales* (*f.sp.*) and physiological races are known. In this paper a description of the 14 most important soil and plant pathogenic *Fusarium* spp. is provided.

Keywords: *Fusarium* spp.; biodiversity; taxonomy and classification; morphology; *in vitro* growth characters; geographical distribution; ecology; toxins and other metabolites; pathogenicity; *formae speciales* and races

GENERAL PART

Taxonomy and classification systems of *Fusarium* spp.

The genus *Fusarium* exhibits a remarkable degree of biodiversity of morphological, physiological and ecological attributes. An ideal taxonomic system should reflect the genetic relatedness of taxa. It should also recognise, at an appropriate level, taxa which are distinguished by practical and significant aspects of their pathogenicity, mycotoxicology or ecology (BURGESS *et al.* 1997). The anamorph genus *Fusarium* Link (1809) has attracted more attention of various scientists than any other group of fungi. The generic name *Fusarium* was used for the first time by LINK (1809). The genus type is considered to be *Fusarium sambucinum* Fuckel (GERLACH & NIRENBERG 1982).

The history of *Fusarium* systematics has shown marked swings between excessively narrow species concepts and those which are so broad that practical information on pathogenicity and toxigenicity has been lost. Recent studies of biodiversity in *Fusarium* are based on the examination of large populations of isolates in which traditional morphological criteria are integrated with detailed data on pathogenic specialisation, toxin production and ecology, and more recently with information derived from molecular taxonomic studies (BURGESS *et al.* 1997).

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During the first decades of taxonomic research, many scientists contributed to describe over 1000 species, varieties and forms of *Fusarium*. APPEL and WOLLENWEBER (1910) and WOLLENWEBER (1913) published a series of important studies. On their basis the modern concept of the genus *Fusarium* was created (WOLLENWEBER & REINKING 1935). The authors reduced over 1100 species of *Fusarium* to 65 species and 22 forms and varietes. A much simpler system with only nine species was published by SNYDER and HANSEN (1940). Although this system was very popular, especially in the U.S.A., it is now considered as unsatisfactory.

Later classification systems were developed by MESSIAEN and CASSINI (1968, 1981), GERLACH and NIRENBERG (1982), NELSON *et al.* (1983), and one of the most used systems by BOOTH (1971) is based on descriptions of 12 sections, 44 species and 7 varietes of *Fusarium* spp. Recently, BRAYFORD (1993) considered 12 sections with 52 species and 4 varietes (Table 1). These classifications and phylogenetic relationships are verified by molecular genetical criteria (e.g. LOGRIECO *et al.* 1997).

Taxonomically, the genus *Fusarium* is classified in the class *Hyphomycetes*, belonging to the *Deuteromycotina*. Teleomorphs of *Fusarium* spp. have been placed in several ascomycete genera such as *Hypomyces* (Fr.) Tul., *Calonectria* de Not. and *Micronectriella* Höhnel, but currently they are regarded as a part of *Nectria* (Fr.) Fr. or the closely related genus *Gibberella* Sacc., order Hypocreales (SEIFERT 1996).

Morphology

The genus *Fusarium* is characterized usually by fast growing, pale or bright-coloured colonies with a felty aerial mycelium and diffuse or sporodochial sporulation. *Fusarium* spp. produce fusiform, curved, multiseptate macroconidia with a pointed apical cell and pointed basal cell that has the appearance of a foot. In some species smaller, 0–1 septate microconidia are formed. Thick-walled chlamydospores may be present, however, depending on the species (BOOTH 1971).

Most of the *Fusarium* spp. isolated from nature produce their macroconidia on sporodochia. These sporodo-

Table 1. List of sections and species of *Fusarium* spp. – according to BRAYFORD (1993)

Section	Anamorph (*Fusarium*)	Teleomorph (*Gibberella, Nectria*)
Elegans	***F. oxysporum*** Schlecht.[1)]	unknown
	F. udum Butler	*G. indica* Rai et Upadhyay
	F. xylarioides Steyaert	*G. xylarioides* Heim et Saccas
Liseola	*F. annulatum* Bugnicourt	unknown
	F. beomiforme Nelson, Toussoun et Burgess	unknown
	F. dlamini Marasas, Nelson et Toussoun	unknown
	F. moniliforme Sheld	*G. fujikuroi* v. *moniliformis* (Wineland) Kuhlman
	F. moniliforme v. *intermedium* Neish et Leggett	*G. fujikuroi* v. *intermedia* Kuhlman
	F. moniliforme v. *subglutinans* Wollenw.	*G. fujikuroi* v. *subglutinans* Edwards et Reinking
	F. napiforme Marasas, Nelson et Rabie	unknown
	F. nygamai Burgess et Trimboli	*Gibberella* sp.
	F. succisae (Schröter) Sacc.	unknown
Sporotrichiella	***F. poae*** (Peck) Wollenw.	unknown
	F. tricinctum (Corda) Sacc.	*G. tricincta* El-Gholl, McRitchie, Schoulties et Ridings
Arthrosporiella	***F. avenaceum*** (Fr.) Sacc.	*G. avenacea* R. J. Cook
	F. camptoceras Wollenw. et Reinking	unknown
	F. chlamydosporum Wollenw. et Reinking	unknown
	F. pallidoroseum (Cooke) Sacc.	unknown
	F. polyphialidicum Marasas, Nelson, Toussoun et Van Wyk	unknown
	F. sporotrichioides Sherb.	unknown
Gibbosum	***F. acuminatum*** Ellis et Everhart	*G. acuminata* Wollenw.
	F. compactum (Wollenw.) Gordon	unknown
	F. equiseti (Corda) Sacc.	*G. intricans* Wollenw.
	F. longipes Wollenw. et Reinking	unknown

Table 1 to be continued

Section	Anamorph (*Fusarium*)	Teleomorph (*Gibberella, Nectria*)
Discolor	*F. buharicum* Jacz.	unknown
	F. crookwellense Burgess, Nelson et Toussoun	unknown
	F. culmorum (W. G. Sm.) Sacc.	unknown
	F. flocciferum Corda	unknown
	F. graminearum Schwabe	*G. zeae* (Schw.) Petch
	F. heterosporum Nees	*G. gordonii* C. Booth
	F. sambucinum Fuckel	*G. pulicaris* (Fr.) Sacc.
	F. tumidum Sherb.	*G. tumida* Broadhurst et Johnston
Lateritium	***F. lateritium*** Nees	*G. baccata* (Wallr.) Sacc.
	F. lateritium v. *buxi* C. Booth	*G. buxi* (Fuckel) Wint.
	F. stilboides Wollenw.	*G. stilboides* Gordon ex C. Booth
Martiella	*F. bugnicourtii* Brayford	unknown
	F. coeruleum Lib. ex Sacc	unknown
Ventricosum	*F. illudens* C. Booth	*N. illudens* Berk.
	F. solani (Martius) Sacc.	*N. haematococca* Berk. et Br.
	F. staphleae Samuels et Rogerson	*N. atrofusca* (Schw.)Ell. et Everh.
	F. ventricosum Appel et Wollenw.	*N. ventricosa* C. Booth
Spicarioides	*F. decemcellulare* Brick	*N. rigidiuscula* Berk. et Br.
Episphaeria [2)]	*F. aquaeductuum* Lagerh.	*N. purtonii* (Grev.) Berk.
	F. aquaeductuum v. *medium* Wollenw.	*N. episphaeria* (Tode:Fr.) Fr.
	F. buxicola Sacc.	*N. desmazierii* Becc. et De Not.
	F. ciliatum Link	unknown; possibly *N. decora* (Wallr.) Fuckel, fide Samuels et Nirenberg
	F. epistroma (Höhn) C. Booth	*N. magnusiana* Rehm ex Sacc.
	F. expansum Schlecht.	*N. stilbosporae* Tul.
	F. melanochlorum (Casp.) Sacc.	*N. flavoviridis* (Fuckel)Wollenw.
	F. merismoides Corda	unknown
	F. sphaeriae Fuckel	*N. leptosphaeriae* Niessl
Coccophillum[3)]	*F. coccidicola* Henn.	*N. diploa* Berk. et Curt.
	F. coccophilum (Desm.) Wollenw. et Reinking	*N. flammea* (Tul.) Dingley
	F. larvarum Fuckel	*N. aurantiicola* Berk. et Br.
	F. tasmanicum (MacAlpine) Rossman	*N. coccidophaga* (Petch) Rossman
Setofusarium	*F. setosum* Nirenberg et Samuels	*N. setofusariae* Samuels et Nirenberg

[1)] *Fusarium* spp. (in bold) described in this paper
[2)] Section includes spp. known as parasites of pyrenomycetous ascomycetes or as saprophytes living on plant debris in soil or water
[3)] Section includes spp. parasitising on scale insects

chial types often mutate in culture, especially on rich media. Mutations may occur rarely in nature. The mutants mostly show a loss of pathogenicity, and the ability to produce toxins may be reduced or lost (NELSON *et al.* 1983). Two major types of mutants arise from the sporodochial type: 1) the pionnotal type, and 2) the mycelial type. The pionnotal type produces little or no aerial mycelium, masses of macroconidia on the surface of the colony and more intense pigmentation of colonies than the sporodochial colonies. The characteristics of the mycelial type are the production of abundant aerial mycelium, the production of very few or no macroconidia and frequent lack of sporodochia and pigmentation in culture (NELSON *et al.* 1994).

Geographical Distribution and Occurrence

Representatives of the genus *Fusarium* occur in a wide range of ecological niches in most regions of the world (BURGESS *et al.* 1997) and are widely spread from Arctic tundra and Subantarctic regions (LORI *et al.* 1999) to tropical rain forests (BRAYFORD 1993). Some species tend to occur predominantly in tropical and subtropical regions (*F. oxysporum* f. sp. *cubense*), some appear to be restricted to cold climatic and alpine zones e.g. *F. sambucinum* (BURGESS *et al.* 1988), whereas others have a cosmopolitan distribution (e.g. *F. oxysporum*). The latter species have a high degree of variability in their physiological and pathogenic characteristics (Table 2) and morphology in culture. This variability has presumably enabled them to occupy diverse ecological niches in many geographical areas (BURGESS 1981; BURGESS *et al.* 1988). Other species which are less variable, such as species exhibiting a high degree of host specificity (for example those that occur on scale insects), tend to be less widely distributed (SEIFERT 1996).

Fusarium spp. are common in soil and associated with roots of living plants, or they persist as chlamydospores or hyphae in plant residues and organic matter (GORDON 1960). Several species produce airborne conidia and are common colonisers of stems, leaves and floral parts of plants. Some species occur in freshwater, and several species are parasites on other fungi (*Pyrenomycetes*) or on scale insects (BURGESS 1981). PRICE (1984) divided the *Fusarium* spp. into four main groups: 1) plant pathogens (including mycoparasites), 2) insect pathogens, 3) saprophytes, and 4) soil inhabitants. A few species bridge the gap between the various groups, attacking both plants and insects or are able to live actively away from their host.

Production of Toxins and other Metabolites

Many *Fusarium* spp. are regarded as "field fungi" rather than "storage fungi" since they do not grow at reduced moisture (SMITH *et al.* 1984). *Fusarium* spp. are a common part of the fungal mycoflora of seed (MAUDE 1995; NEERGAARD 1977). Some species may be seed-borne pathogens and/or can produce a variety of toxic metabolites (DRYSDALE 1982; SNIJDERS 1990). A list of these metabolites is summarized in Table 3. The majority of *Fusarium* metabolites belong to the trichothecene group

Table 2. List of soil *Fusarium* species and their host specificity – according to BRAYFORD (1993)

A) Number of *formae speciales* described within *Fusarium* spp.

Section	Species	Number of formae speciales
Elegans	*F. oxysporum*	96
Martiella	*F. solani*	19

B) Number of races described within *formae speciales* of *Fusarium*

Fusarium spp.	Forma specialis	Number of races
F. oxysporum	*batatas*	2
	callistephi	2
	conglutinans	2
	cubense	4
	cucumerinum	3
	dianthi	3
	lupini	3
	lycopersici	3
	matthioli	2
	melonis	4
	niveum	3
	perniciosum	2
	phaseoli	2
	pisi	4
	tracheiphilum	3
	vasinfectum	6
F. solani	*cucurbitae*	2
	radicicola	2

Table 3. Survey of *Fusarium* spp., their toxins and other metabolites

Fusarium spp.	Toxins and other metabolites	References
F. acuminatum	Trichothecenes	WING *et al.* (1991, 1993)
	Zearalenon	BOSCH & MIROCHA (1992)
F. avenaceum	Antibiotic Y	GOLINSKI *et al.* (1986)
	Acetamidobutenolid and Enniatin B	HERSHENHORN *et al.* (1992)
	Fusarin C	GOLINSKI & CHELKOWSKI (1992)
	Chlamydosporol	SHIER & ABBAS (1992)
	Moniliformin	SHARMAN *et al.* (1991)
	Zearalenon	ZHU & ZHANG (1991)
	Trichothecenes	LAUREN *et al.* (1992)
F. crookwellense	Apotrichothecenes	GREENHALGH *et al.* (1989)
	Fusarin C	GOLINSKI & CHELKOWSKI (1992)
	Trichothecenes	LAUREN *et al.* (1992)
	Zearalenon	GOLINSKI & CHELKOWSKI (1992)
F. culmorum	Chlamydosporol	ABBAS *et al.* (1992)
	Fusarin C	GOLINSKI & CHELKOWSKI (1992)
	Moniliformin	SCOTT *et al.* (1987)
	Trichothecenes	MARASAS *et al.* (1984)
	Zearalenon	MARASAS *et al.* (1984)
F. equiseti	Trichothecenes	MARASAS *et al.* (1984)
	Zearalenol	BOTTALICO *et al.* (1985)
	Zearalenon	BOTTALICO *et al.* (1985)
F. graminearum	Fusarin C	THRANE (1988)
	Trichothecenes (type A)	LOGRIECO *et al.* (1993)
	Trichothecenes (type B)	ICHINOE *et al.* (1983)
	Zearalenon	WINDELS *et al.* (1989)
F. moniliforme	Fumonisins	LESLIE *et al.* (1992)
	Fusarins	JACKSON & LANSER (1993)
	Macrofusin	LAURENT *et al.* (1989)
	Micromonilin	LAURENT *et al.* (1989)
	Moniliformin	MARASAS *et al.* (1984)
	Trichothecenes	LI *et al.* (1990)
	Zearalenon	MARASAS *et al.* (1984)
F. oxysporum	Moniliformin	CHELKOWSKI *et al.* (1990)
	Sambutoxin	KIM & LEE (1994)
	Wortmannin	ABBAS *et al.* (1991)
	Zearalenon	RICHARDSON *et al.* (1985)
F. pallidoroseum	Anhydrofusarubin	HASHMI & THRANE (1990)
	Bostrycoidin	HASHMI & THRANE (1990)
	Chlamydosporol	SHIER & ABBAS (1992)
	Equisetin	HASHMI & THRANE (1990)
	Fusarubin	HASHMI & THRANE (1990)
	Moniliformin	HASHMI & THRANE (1990)
	Pyrones	ALTOMARE *et al.* (1997)
	Zearalenon	ZHU & ZHANG (1991)

Table 3 to be continued

Fusarium spp.	Toxins and other metabolites	References
F. poae	Enniatin	BURMEISTER & PLATTNER (1987)
	Fusarin C	GOLINSKI & CHELKOWSKI (1992)
	Moniliformin	CHELKOWSKI *et al.* (1990)
F. solani	Trichothecenes	UENO (1977)
F. sporotrichioides	Fusarin C	THRANE (1988)
	Moniliformin	SCOTT *et al.* (1987)
	Trichothecenes	LOGRIECO *et al.* (1990)
F. tricinctum	Chlamydosporol	SOLFRIZZO & VISCONTI (1991)
	Enniatin	BURMEISTER & PLATTNER (1987)
	Fusarin C	GOLINSKI & CHELKOWSKI (1992)
	Moniliformin	CHELKOWSKI *et al.* (1990)
	Visoltricin	VISCONTI & SOLFRIZZO (1994)

of sesquiterpenes (GOLINSKI *et al.* 1997; MOSS 1984). Fusariotoxins can be very harmful to humans and livestock (NELSON *et al.* 1994).

Significance of *Fusarium* spp. in Plant Pathology and Variation in Pathogenicity

Fusarium spp. have mostly been studied in relation to their ability to cause diseases of many economically important plants. A broad range of disease symptom expression is known: seedling blights; root rots; basal rot of bulbs; stem, leaf and head blights of cereals; postharvest storage rots; cankers of woody hosts; vascular wilts (NELSON *et al.* 1981).

Species of the genus *Fusarium* can be primary pathogens of plants or can negatively affect host plants together with other pathogenic fungi or nematodes. However, they can also be common secondary pathogens of plant tissue that has been stressed by abiotic or biotic factors (BRAYFORD 1993). When *Fusarium* spp. act as primary pathogens they can express various degrees of host specificity. Pathogen specificity on the species level has been classified into *formae speciales* (*f.sp.*), and in some cases into physiological races (Table 2), on the basis of the reaction of differential genotypes of the host plant (AMSTRONG & AMSTRONG 1968). For example, more than 120 different *formae speciales* have been described for *F. oxysporum* (HAWKSWORTH *et al.* 1995). It is not possible to reliably differentiate between *formae speciales* or between pathogenic and saprophytic strains by means of morphology. Tests through inoculation of the host plants are currently required to identify *formae speciales* and races, although the recent development of *in vitro* and molecular identification techniques has made some progress (CORRELL 1991; BAAYEN & WAALWIJK 1997; WOO *et al.* 1998).

A further aspect indicating differentiation within some *Fusarium* spp. are their sexual relationships. It is known that some isolates are homothallic, while others are heterothallic; however, some appear to be only anamorphic. In terms of genetics, these mating groups could be interpreted as distinct biological species, but it is difficult to distinguish between mating groups by using morphological criteria (MATUO & SNYDER 1973). Mating groups have been described e.g. within the broadly defined morphological species *F. solani* sensu SNYDER and HANSEN (1941).

SPECIAL PART

Description of the Most Important Soil and Plant Pathogenic *Fusarium* Species

The following alphabetical list includes the most common *Fusarium* spp. – modified and improved according to BOOTH (1971) and BRAYFORD (1993) (Table 1) – with their main characteristics and significance in soil biology and plant pathology.

Fusarium acuminatum Ellis et Everhart (Fig. 1)

Colonies on PSA (Potato Sucrose Agar) with floccose aerial mycelium and with pink pigment darkening to honey or light brown, reverse livid red to dark vinaceous. Growth rate on PSA is 80–100 mm/10 days (diam.). Macroconidia, mainly 3–5 septate, 25–60 × 2–5.5 µm, arise from cylindrical conidiogenous cells. On SNA (Synthetic Nutrient Agar) the shape of macroconidia is falcate/lunate, widest near the middle and tapering evenly to a pointed apical cell and distinctly pedicellate basal cell. Microconidia normally absent. Chlamydospores present singly, in chains or clusters. Recently, *F. acuminatum* has been split into two taxonomic groups, formally described

as *F. acuminatum* Ell. & Ev. subsp. *acuminatum* Burgess & al. and *F. acuminatum* subsp. *armeniacum* Forbes, Windels et Burges according to their morphological, cultural and ecological characteristics, and toxigenic variability (ALTOMARE *et al.* 1995; BURGESS *et al.* 1997). There is evidence about a close phylogenetic relationship between *F. acuminatum* subsp. *armeniacum* and *F. sporotrichioides* based on comparisons of partial ribosomal RNA sequences (LOGRIECO *et al.* 1992).

The species *F. acuminatum* is widely distributed on a wide range of hosts, mostly as a saprobe and as a secondary invader (ALTOMARE *et al.* 1995). The fungus lives in association with roots of diverse herbaceous and woody hosts (LORI *et al.* 1999). It causes root and crown rots and occurs as part of disease complexes with other fungi and nematodes. It can cause postharvest rotting of fruit. In addition to root and foot rot of cereals, it can cause a symptomless infection of cereal roots (HILL *et al.* 1987). *F. acuminatum* is a common component of cereal seed and producer of toxins of the group enniatins (VISCONTI *et al.* 1992).

Fusarium avenaceum (Fr.) Sacc. (Fig. 2)
syn.: *F. diversisporum* Sherb., *F. anguioides* Sherb.

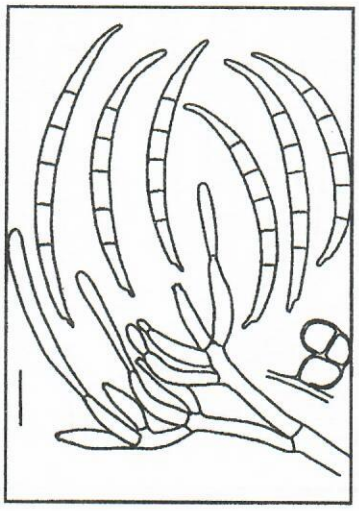
Colonies on PSA with floccose aerial mycelium, white at first, darkening to pink or livid vinaceous; dark vinaceous near the centre. Growth rate on PSA is 40–70 mm per 10 days (diam.). On SNA the formation of two types of macroconidia is known: 1) macroconidia (3–5 septate, 40–100 × 2–5 µm, filiform, thin-walled, curved, with pointed apex and pedicellate basal cell) forming orange, slimy sporodochia on the agar surface; 2) macroconidia (1–3 septate, 15–50 × 3–5 µm, fusiform, with pointed apex and conical basal cell lacking pedicella) arising from polyblastic cells in aerial mycelium. Microconidia normally absent, but sparse ovoid microconidia are produced by young colonies of some strains. Chlamydospores absent.

This species is widely distributed, but more common in temperate regions. The fungus has a wide host range and is known as either a primary pathogen or component of disease complexes on seedlings and mature plants of diverse crops (AL-HAMDANY 1998; LITTERICK & MCQUILKEN 1998), including cereals (KLAASEN & MARASAS 1998; NARKIEWICZ-JODKO & GIL 1997; REMLEIN-STAROSTA 1997) and Fusarium head blight (FHB) of barley (SALAS *et al.* 1999). It is also a pathogen of woody plants, causing seedling blight, stem cankers and is associated with dieback (OLESKEVICH *et al.* 1998).

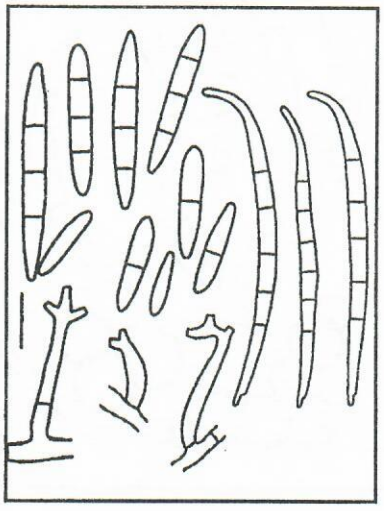
Fusarium crookwellense Burgess, Nelson et Toussoun (Fig. 3)

Colonies on PSA with floccose aerial mycelium, initially white, darkening to honey and greyish rose to dark vinaceous. Growth rate on PSA is 50–75 mm/4 days (diam.). On SNA sporulation abundant in slimy sporodochia, conidiogenous cells cylindrical/swollen. Macroconidia 5–7 septate, 30–55 × 4–5 µm, appearing thick walled, falcate, swollen in the middle, apical cell tapering to a point, foot cell with distinctly protruding pedicel. Microconidia absent. Globose chlamydospores present in mature colonies.

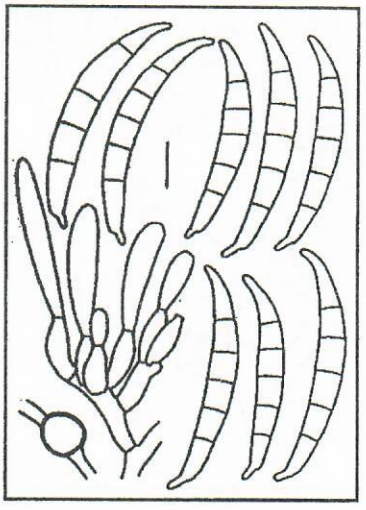
The fungus has a wide geographical distribution but is more common in temperate climates. It forms part of stalk, foot and root rot complexes on cereals, including wheat and maize (SAYER & LAUREN 1991), and grass/clover pastures where it produces zearalenone (TOWERS & SPROSEN 1995).



1. *F. acuminatum*



2. *F. avenaceum*



3. *F. crookwellense*

Fig. 1–3. Morphology of conidia and conidiophores of *Fusarium* spp. – according to BRAYFORD (1993); scale bar = 10 µm

Fusarium culmorum (W. G. Sm.) Sacc. (Fig. 4)

Colonies on PSA with floccose aerial mycelium, pink at first, darkening to livid red and honey colour to dark vinaceous. Growth rate on PSA is 50-80 mm/4 days (diam.). On SNA sporulation abundant in sporodochia. Cylindrical/swollen conidiogenous cells (monophialides) borne in clusters on irregularly branching conidiophores. Macroconidia mostly 3–5 septate, 30–50 × 5–9 µm, appearing short and fat, thick walled, with curved dorsal surface and straight ventral surface, pointed apical cell and wedge-shaped basal cell without a distinctly protruding pedicel. Microconidia absent, sometimes sparsely occurring in old cultures. Chlamydospores mostly intercalary, single or in short chains.

This species is typical for regions with a cool climate. It causes root and foot rot, headblight, ear blight (scab) and seedling disease of cereals (KLAASEN & MARASAS 1998; NARKIEWICZ-JODKO & GIL 1997; PARRY *et al.* 1995). *F. culmorum* is not restricted only to *Gramineae*, but may cause disease on a wide range of other host plants (NELSON *et al.* 1981).

The most important toxins produced by *F. culmorum* are summarized in Table 3. The major trichothecene metabolite is 3-acetyldeoxynivalenol (ZAMIR & FARAH 2000). During storage, the mycotoxin (DON and ZEN toxins) content of infected wheat seed increases under warm and humid conditions (HOMDORK *et al.* 2000a). It is possible to reduce or prevent DON contained in infected wheat seed by applying in the developing crop the systemic fungicide tebuconazole (as Folicur) (HOMDORK *et al.* 2000b).

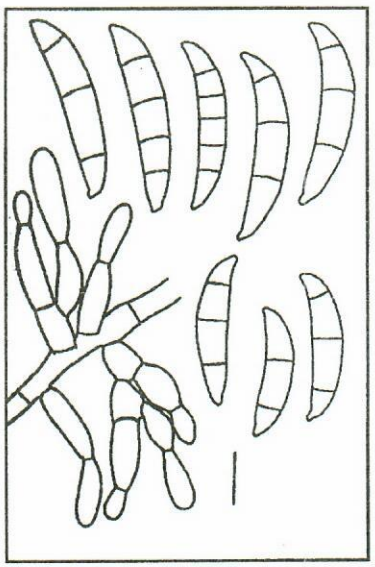
Fusarium equiseti (Corda) Sacc. (Fig. 5)

Colonies on PSA with abundant, floccose aerial mycelium, pink, in some strains darkening to hazel. Growth rate on PSA is 80–100 mm/10 days (diam.). On SNA macroconidia formed in orange sporodochia and small, slimy droplets. Conidiogenous cells borne in clusters on irregularly branching conidiophores with a single conidiogenous locus. Macroconidia 3–7 septate, 20–80 × 3–6 µm, curved, swollen in the middle, with pointed elongated apical cell and distinctly pedicellate foot cell. Microconidia absent, but sometimes 0–1 septate spores may be present in young cultures. Thick-walled chlamydospores forming abundantly.

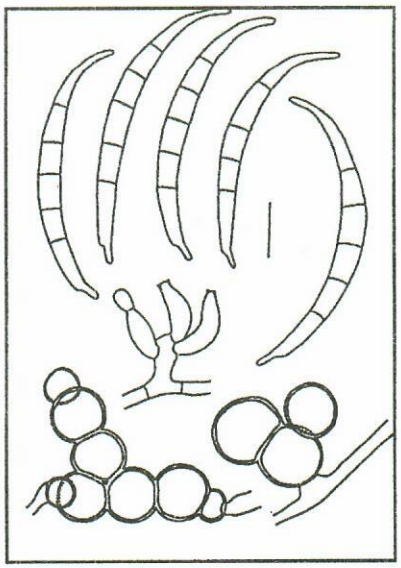
This fungus is widely distributed mainly in soils of a warm climate (ADLER & LEW 1995), but is also found in temperate areas (WOLCAN *et al.* 1993). It occurs in soil and in association with roots of many plants. *F. equiseti* may be a primary cause of disease such as root/foot/rhizome rot, stem rot, postharvest fruit and vegetable rot, or be part of disease complexes with other pathogens (LORI *et al.* 1999).

Fusarium graminearum Schwabe (Fig. 6)

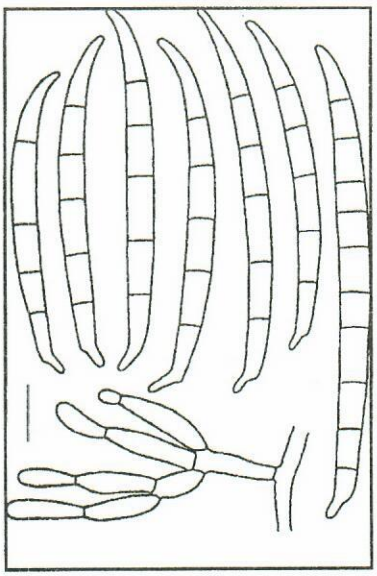
Colonies on PSA with floccose aerial mycelium, white, darkening to greyish rose to dark vinaceous. Growth rate is 40–70 mm/4 days (diam.). On SNA macroconidia are usually present on the agar surface. Sporulation also occurring from conidiogenous cells in the aerial mycelium. Conidiogenous cells cylindrical/swollen, scattered singly or borne apically on irregularly branching conidiophores. Macroconidia mostly 5–6 septate, 45–65 × 3–5.5 µm, fal-



4. *F. culmorum*



5. *F. equiseti*



6. *F. graminearum*

Fig. 4–6. Morphology of conidia and conidiophores of *Fusarium* spp. – according to BRAYFORD (1993); scale bar = 10 µm

cate or straight, with slighty curved dorsal surface, slightly swollen in the middle, with distinctly protruding pedicel on the foot cell, the apical cell tapering to a fine point. Microconidia absent. Chlamydospores sparse or absent.

This fungus is common in warm climate regions (MEHROTRA *et al.* 1998) but also occurs in temperate regions (WINDELS 2000). It is one of the economically most important species in the genus. *F. graminearum* is best known as a pathogen of cereals, causing seedling blights, root, foot, crown and stem rot, kernel and head blight (DILLMACKY & JONES 2000; REMLEIN-STAROSTA 1997; SALAS *et al.* 1999; SCHAAFSMA 1995) and is commonly seed borne.

Two groups have been delineated within *F. graminearum* populations, differing in their pathological activity, mating systems and subtly in their morphology (BURGESS *et al.* 1975). Strains of group 1 are heterothallic and occur mostly in the soil, causing foot and crown rot diseases, whereas strains of group 2 are homothallic and occur on aerial parts of plants, causing scab symptoms on cereals (BALMAS *et al.* 1995). Recent data suggest that the two groups are genetically more distinct than was expected previously (BURGESS *et al.* 1997). RAPD markers, cluster analysis (UPGMA) and principal coordinate analysis indicated that members of group 2 of *F. graminearum* have a greater genetic affinity to *F. culmorum* and *F. crookwellense* than to those of group 1 of *F. graminearum* (SCHILLING *et al.* 1994).

F. graminearum produces the mycotoxins deoxynivalenol (vomitoxin, DON; 3-acetyl DON and 15-acetyl DON) and zearalenone (ZEN). DON toxins appear very soon (48 h) in spikelets of barley after inoculation with macroconidia (EVANS *et al.* 2000). The level of DON is probably not the most important factor of aggressiveness of *F. graminearum* (MIEDANER *et al.* 2000). This contrasts with some results that support the view that DON may act as a virulence factor to enhance the spread of the fungus on maize (HARRIS *et al.* 1999). Increasing temperature affects significantly the production of DON and ZEN; nevertheless, there is no correlation between fungus growth and production of either DON or ZEN (RYU & BULLERMAN 1999).

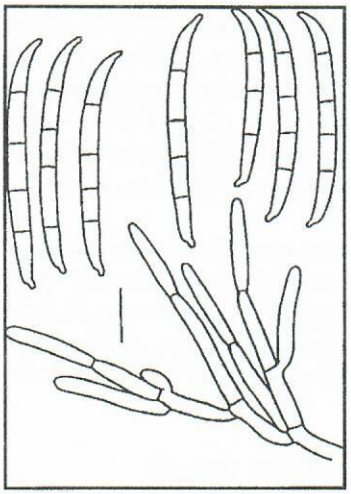
Fusarium lateritium Nees (Fig. 7)

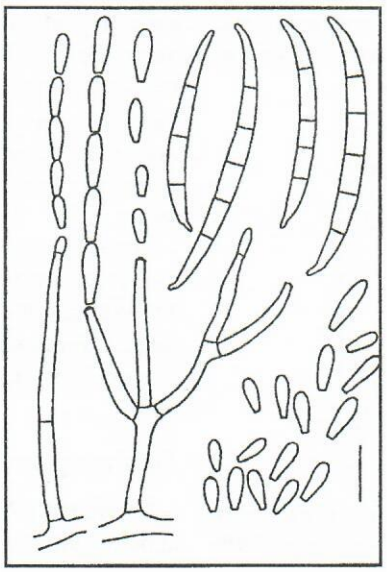
Colonies on PSA with floccose, white or pink aerial mycelium, colonies of some strains with an irregular, lobate margin. Colour of colony reverse varies between strains, beige, brown, sometimes with orange or yellow pigment. Growth rate on PSA is 20–40 mm/10 days (diam.). On SNA pale sporodochia are formed. Conidiogenous cells cylindrical, borne in dense clusters on irregularly branching conidiophores. Macroconidia 3–5 septate, 35–60 × 3.5–4 μm, cylindrical, hardly swollen in the middle, straight or slightly curved, sometimes beaked, papillate tip, basal cell with protruding pedicel. Microconidia normally absent. Chlamydospores sparse or absent.

This fungus is known on herbaceous plants (CLARK *et al.* 1990) and common on a wide range of woody host substrates as a saprophyte or as a weak pathogen causing seedling death, cankering or is associated with dieback (ELLIS & ELLIS 1997; VAJNA 2000). However, this species is also considered as endophyte (neutral fungal symbiont) and is harboured by woody stems of many trees and shrubs (DIX & WEBSTER 1995).

Fusarium moniliforme Sheld. (Fig. 8)
syn.: *F. verticillioides* (Sacc.) Nirenberg

Colonies on PSA with white or pink floccose aerial mycelium and with dark purple pigment. Growth rate is 70–100 mm/10 days (diam.). Macroconidia on SNA (1–7 septate, 30–60 × 2–3.5 μm, thick-walled, fusiform, straight or slightly curved, with pointed apical cell and pedicellate foot cell) forming in slimy droplets in the aerial myce-





7. *F. lateritium* ↑ 8. *F. moniliforme* →

Fig. 7–8. Morphology of conidia and conidiophores of *Fusarium* spp. – according to BRAYFORD (1993); scale bar = 10 μm

lium or in slimy sporodochia. Macroconidia arising from conidiogenous cells borne apically on irregularly branching conidiophores. Microconidia 5–16 × 1,5–4,5 μm, clavate with rounded apex and tapering towards their flattened base, successive spores adhering in long chains. Chlamydospores absent.

This fungus is very common in warm climates (KHAN *et al.* 1999; MACDONALD & CHAPMAN 1997), but was also detected in the Subantarctic Region (LORI *et al.* 1999). It causes stalk rot and head blight of cereals, especially maize and sorghum (CHULZE *et al.* 1995; IDREES *et al.* 1999; MA *et al.* 1998). It causes "bakanae" (abnormal elongation) and foot rot of rice, causing up to 70% losses in isolated rice fields, and air-borne microconidia may infect rice at flowering (MANANDHAR 1999). *F. moniliforme* also causes disease on a wide range of other hosts, usually on the aerial parts of the plants rather than in the soil. Very frequently is from poultry feeds and raw materials (CASTELLÁ *et al.* 1995). Production of fumonisins together with some other secondary metabolites (e.g., fusaric acid, moniliformin) may play a role in pathogenicity (JARDINE & LESLEY 1999).

Fusarium oxysporum Schlecht. (Fig. 9)

Colonies on PSA with white or pink, floccose aerial mycelium (sometimes sparse and colonies adpressed and slimy) and with pink, peach or dark purple pigment. Growth rate is 80–100 mm/10 days. Macroconidia 3–5 septate, 25–55 × 2.5–6 μm, fusiform, curved with a tapering, pointed, sometimes hooked, apical cell and distinctly pedicellate basal cell. Macroconidia arising from short monophialides. In some strains macroconidia sparse. Microconidia forming abundantly from short monophialides similar to those forming macroconidia. Chlamydospores forming abundantly. *F. oxysporum* lacks a known teleomorph. Sequence analysis of the 28S rRNA gene indicates that it is closely related to the section Liseola (GUADET *et al.* 1989; WAALWIJK *et al.* 1997a).

This fungus causes seedling blights, root and crown rots, bulb and corm rots and vascular wilt diseases of a wide range of important crop plants in temperate regions and in the tropics. However, soils also harbor large populations of nonpathogenic *F. oxysporum* (EDEL *et al.* 1997). It may also act synergistically with nematodes and is a part of disease complexes with other fungi, including other *Fusarium* species. Saprophytic strains also occur in soil and in close association with plant roots. When *F. oxysporum* acts as a primary pathogen it can cause root/crown rots, bulb rots or vascular wilt. Isolates which cause wilt diseases are usually host specific and over 100 *formae speciales* and races have been described (Table 2) (BAAYEN & WAALWIJK 1997). This large diversity can arise by mutations, transpositions and the parasexual cycle (LESLIE 1990). The genetic diversity within *F. oxysporum* has been categorized on the background of vegetative compatibility grouping (VCG) within specialized forms (KISTLER 1997; KISTLER *et al.* 1998). Enormous local and regional variation in populations of *F. oxysporum* was recognized (APPEL & GORDON 1994). Extensive polymorphism of *F. oxysporum* was found by RAPD-PCR and isozyme analyses. Isolates could be distinguished from each other by RAPD-PCR, but also by isozymes (PAAVANEN-HUHTALA *et al.* 1999). The example of *F. oxysporum* f. sp. *cubense*, causing Fusarium wilt (Panama disease), demonstrated not only a large genetic variation, but also genetic isolation suggesting that the pathogen had arisen independently, within and outside of the center of origin of the host (BENTLEY *et al.* 1998).

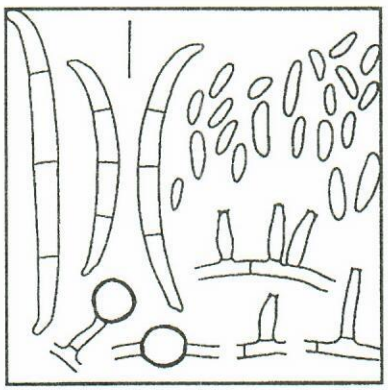


Fig. 9. Morphology of conidia and conidiophores of *Fusarium oxysporum* – according to BRAYFORD (1993); scale bar = 10 μm

Fusarium pallidoroseum (Cooke) Sacc. (Fig. 10)
syn.: *F. incarnatum* (Roberge) Sacc., *F. semitectum* Berk *et* Rav., *F. semitectum* var. *majus* Wollenw.

Colonies on PSA with pink or honey floccose aerial mycelium and peach or hazel color. Growth rate form 60 to 90 mm/10 days. On SNA two types of macroconidia are formed, dry or slimy. Dry macroconidia (3–7 septate, 20–55 × 3–6.5 μm, fusiform, strait or slightly curved, with pointed apex and conical basal cell) are formed in the aerial mycelium, arising from polyblastic cells. Slimy macroconidia (3–7 septate, 20–70 × 2.5–7 μm, curved, fusiform) arising from cylindrical monophialides are formed on the agar surface or in droplets in the aerial mycelium. Chlamydospores present in mature colonies, sparse to abundant, globose, single or in chains or clusters.

The fungus is common in tropical and subtropical regions on plant debris in soil and seeds (KHAN *et al.* 1999; MEHROTRA *et al.* 1998). It may occur as a weak plant pathogen causing seedling blights, root rot, stem rot, postharvest fruit rot on a wide range of plants (BRAYFORD 1993).

Fusarium poae (Peck) Wollenw. (Fig. 11)

Colonies on PSA with floccose white or pale pink aerial mycelium and dark vinaceous to blood colour. Growth

rate is 50–80 mm/4 days (diam.). Fresh strains on PSA with a strong fruity odour. Macroconidia on SNA 2–5 septate, 20–65 × 4–9 μm, falcate, with pointed apex and pedicellate foot cell; macroconidia sparse in many strains. Microconidia mostly 0 septate, 6–12 ×7–18 μm, globose subglobose, with a small protruding abscission papilla. Conidiogenous cells borne apically on branching conidiophores or sessile on vegetative mycelium, appearing swollen – barrel shaped, with a single conidiogenous locus. Chlamydospores absent.

This species has little direct economic significance as a plant pathogen and is considered as a weak pathogen of cereals. However, some strains are highly toxigenic, producing trichothecenes in contaminated cereal grain (BILAI *et al.* 1983; PETTERSSON & OLVANG 1995), and nivalenol, 15-acetoxyscirpenol and scirpentriol (SALAS *et al.* 1999). *F. poae* is a common member of the cereal grain mycoflora in temperate climates, but may infect leaves at the seedling stage and the flag leaf (REMLEIN-STAROSTA 1997). It can be the causal agent of Fusarium head blight (FHB) of barley, though to very limited extent (SALAS *et al.* 1999). It is rare in the tropics. *F. poae* has a trichodiene synthase gene with high sequence similarity to the *Tox5* gene of *F. sporotrichioides* (HORNOK *et al.* 1997).

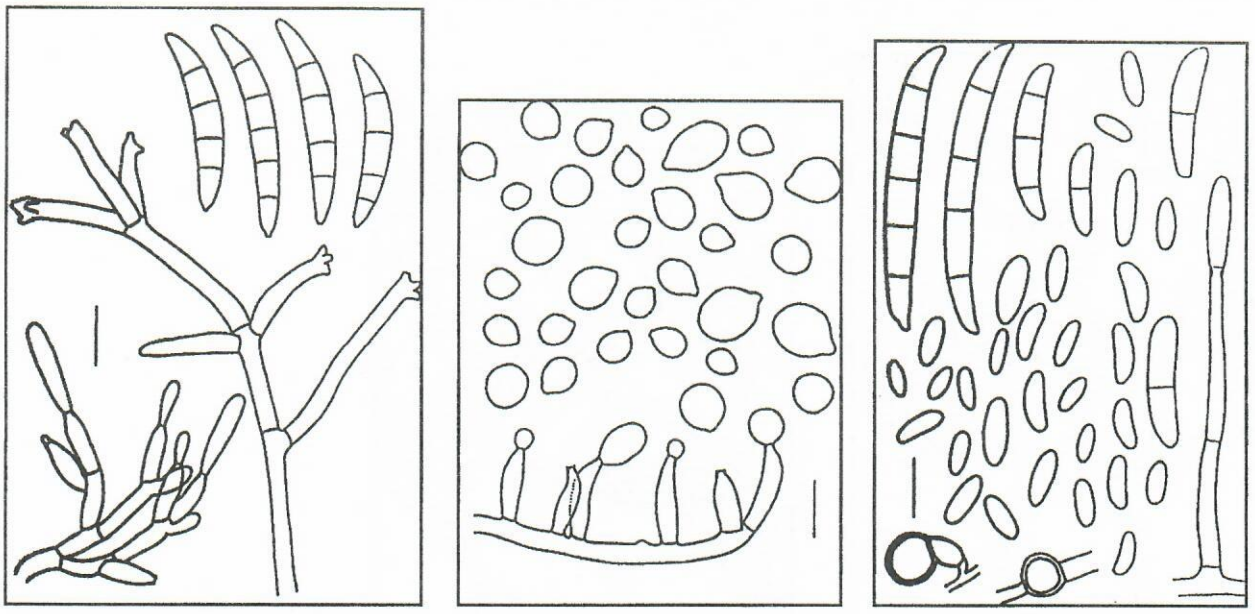
Fusarium solani (Martius) Sacc. (Fig. 12)

Colonies on PSA with floccose white or buff aerial mycelium, sometimes becoming pale brown at the centre, sometimes bluish pigment in rings. Growth rate is 70–120 mm/10 days (diam.). Macroconidia initially forming from scattered conidiogenous cells in the aerial mycelium, later forming in slimy sporodochia on the agar surface, arising from shorter phialides aggregated on irregularly branching conidiophores. Macroconidia 3–7 septate, 25–50 × 4–6 μm, cylindrical to fusoid, curved, with bluntly pointed or conical apical cell; foot cell wedge-shaped to rounded, only slightly pedicellate. Microconidia abundantly forming from erect, elongated conidiogenous cells and accumulating in small slimy droplets. Microconidia 0–1 septate, 6–25 × 3–5 μm, ovoid or fusoid. Chlamydospores present in mature cultures.

This fungus occurs in different ecological zones (SSEKYEWA *et al.* 1995) and causes disease of a wide range of host plants, often acting as part of disease complexes with other fungi, bacteria or nematodes. It may also saprophytically colonise, as a secondary invader (LORI *et al.* 1999), tissues killed by other pathogenic agents. As a primary pathogen it causes diseases of seedlings, roots, crowns, tubers or other undergrounds parts (NELSON *et al.* 1981). A number of *formae speciales* have been described within *F. solani* (Table 2).

Fusarium sporotrichioides Sherb. (Fig. 13)

Colonies on PSA with floccose white or pale pink aerial mycelium, colour of colony dark vinaceous or blood, but pigment may be lost in degenerated isolates. Growth rate is 50–85 mm/4 days (diam.). Macroconidia on SNA (35 septate, 10–20 × 2.5–4 μm, falcate, with pointed apical cell and pedicellate foot cell) arising in slimy droplets, from cylindrical monophialides. Microconidia pyriform, 0-1 septate, 5–15 × 4-8 μm and fusiform, 0–3 septate, 8–40 × 2.5–4 μm. Conidiogenous cell polyblastic. Chlamydospores usually abundant in mature cultures, globose, in intercalary chains.



10. *F. pallidoroseum* 11. *F. poae* 12. *F. solani*

Fig. 10–12. Morphology of conidia and conidiophores of *Fusarium* spp. – according to BRAYFORD (1993); scale bar = 10 μm

This species occurs mainly in cool climatic regions rather than in the tropics. It is found in soil, plant debris and in association with roots, stem-bases and lower foliage (LITTERICK & MCQUILKEN 1998). *F. sporotrichioides* is considered as a weak pathogen (SEEMÜLLER 1968); nevertheless, it can also cause Fusarium head blight (FHB) on barley, though to a very limited extent (SALAS *et al.* 1999). Strains of this species are often very toxigenic, producing high amounts of trichothecenes (Table 3), including T-2, HT-2, T-2 tetraol, DON and DAS (LOGRIECO *et al.* 1990; MARASAS *et al.* 1991; SALAS *et al.* 1999). *F. sporotrichioides* and *F. acuminatum* subsp. *armeniacum* have been found to be genetically related, and both species synthesize type A trichothecenes (ALTOMARE *et al.* 1995).

Fusarium tricinctum (Corda) Sacc. (Fig. 14)

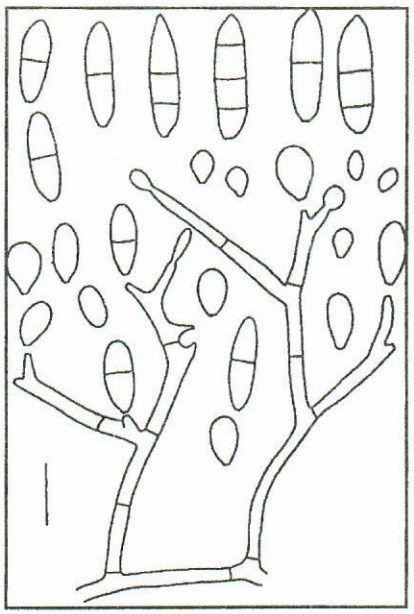
Colonies on PSA with floccose white or pale pink aerial mycelium and dark vinaceous to blood pigment. Growth rate is 30–50 mm/4 days (diam.). Macroconidia on SNA (lunate with distinct toe-like pedicel on the basal cell) sparse or developing only after 3–4 weeks incubation. Microconidia 0–1 septate, 7–18 × 3,5–8 μm, pyriform per limoniform. Conidiogenous cells cylindrical, forming apically on irregularly branching conidiophores in the aerial mycelium or on the agar surface. Chlamydospores formed sparsely.

This species occurs in plant debris in soil (LITTERICK & MCQUILKEN 1998) and is most common in cool climates. It has little plant pathogenic ability (KLAASEN & MARASAS 1998; SEEMÜLLER 1968), but can be a common contaminant of cereal grain (SHIPILOVA 1995). *F. tricinctum* and *F. acuminatum* subsp. *acuminatum* share some similarities in morphological and cultural traits and are able to synthesize enniatin and moniliformin, but not trichothecenes. These taxonomic relationships were also verified by isozyme analysis and RAPD assay (ALTOMARE *et al.* 1995).

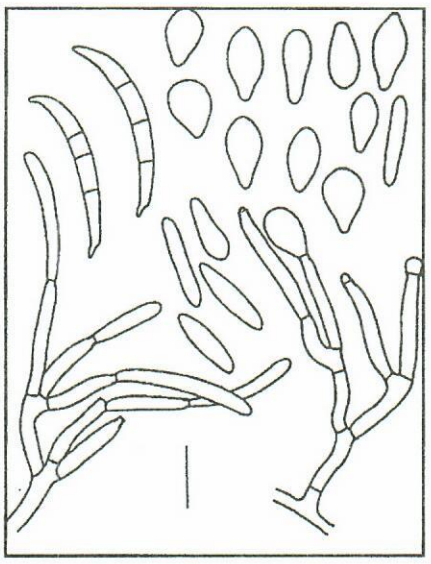
CONCLUSIONS

The systematics of the genus *Fusarium* is rather complicated. There are at least two main reasons for this: 1) the taxonomic, and 2) the cultural plasticity of *Fusarium* species (BRAYFORD 1993). The taxonomy of the genus *Fusarium*, based on morphological characteristics, has been a subject of controversy for many years (NELSON 1990). Until rather recently, *Fusarium* species have not been widely used in genetic studies of variation between and within populations (BURNETT 1984; WOO *et al.* 1998). This has changed over the last 10 years, and many species have been subjected to genetic analysis (LESLIE 1990; WAALWIJK *et al.* 1997a,b). For exact characterization it is possible to use different molecular techniques, e.g., VCGs – vegetative compatibility systems (LESLIE 1993; KISTLER *et al.* 1998; VILJOEN *et al.* 1997), RFLP – restriction fragment length polymorphism (EDEL *et al.* 1995; FERNANDES *et al.* 1997; ROSEWICH *et al.* 1999), RAPD – random amplified polymorphic DNA (HERING & NIRENBERG 1995; MULE *et al.* 1995; MULE & LOGRIECO 1997; O'DONNEL *et al.* 1999), PCR – polymerase chain reaction (BRAYFORD 1997; MOELLER *et al.* 1997; VAN DER PLAS *et al.* 1995).

Some results of molecular taxonomy suggest that the traditional grouping of the sections in some cases does not correspond with genetical relations of *Fusarium* spe-



13. *F. sporotrichioides*



14. *F. tricinctum*

Fig. 13–14. Morphology of conidia and conidiophores of *Fusarium* spp. – according to BRAYFORD (1993); scale bar = 10 μm

cies. However, it is certain that cooperation between classical taxonomists, workers applying new molecular techniques in *Fusarium* research and geneticists is necessary and useful for a more detailed understanding of the taxonomy of this genus. Recently, BURGESS *et al.* (1997) stressed that there is a strong case for acceptance of species and infra-species descriptions and taxonomic placement on the basis of data from molecular techniques as well as morphological and physiological criteria. However, as a critical is considered, that studies on genetic diversity within and between populations of species must be based on the analysis of a large number of cultures originating from a wide range of substrates and geographic areas. According to LESLIE (1997) genetic approaches to problems in *Fusarium* have been limited. From this viewpoint genetic standards in terms of both strains and terminology are lacking. Their development would facilitate comparisons of results from various laboratories.

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Souhrn

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Fusarium Link (1809) je anamorfní rod s celosvětovým geografickým rozšířením a rozsáhlým stupněm biodiverzity. Druhy rodu *Fusarium* jsou běžné v půdě a bývají nalézány na mnoha druzích cévnatých rostlin. Některé specializované druhy mohou parazitovat i na jiných houbách nebo na hmyzu. V systému hub je rod *Fusarium* řazen do třídy *Hyphomycetes*, oddělení *Deuteromycotina*. Teleomorfy jsou součástí rodů *Gibberella* a *Nectria*, řádu *Hypocreales* (třída *Ascomycetes*). Taxonomie rodu *Fusarium* není ustálená a počet druhů i sekcí je velmi různý. V současnosti existuje několik klasifikačních systémů tohoto rodu. Druhy rodu *Fusarium* bývají nejvíce studovány v souvislosti s jejich schopností způsobovat choroby mnoha ekonomicky významných plodin. Některé druhy produkují mykotoxiny a jiné metabolity, které mohou být škodlivé pro člověka i hospodářská zvířata. Je známa rozsáhlá variabilita v patogenitě a u mnoha *Fusarium* spp. jsou popsány specializované formy (f. sp.) a fyziologické rasy. V práci je shrnut popis čtrnácti nejdůležitějších půdních a fytopatogenních druhů rodu *Fusarium*.

Klíčová slova: *Fusarium* spp.; taxonomie; klasifikace; morfologie; geografické rozšíření; toxiny; jiné metabolity; patologie rostlin; *formae speciales*; rasy; růstové charakteristiky *in vitro*

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