Biodiversity and population studies in *Fusarium*

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Representatives of the genus *Fusarium* occur in a wide range of ecological niches in most geographical regions of the world. The form genus exhibits a remarkable degree of variability in morphological, physiological and ecological attributes. Such high level of biodiversity or variation has led to considerable difficulties in the development of a stable and widely accepted taxonomic treatment of the genus. The combination of mycogeographic surveys with morphological and physiological studies as well as studies at the molecular level have provided new approaches to assess the nature of biodiversity and adaptation in *Fusarium*. The present paper illustrates the application of these approaches by reference to three species, *F. graminearum*, *F. acuminatum* subsp. *armeniacum* and *F. compactum* and populations related to each of these species.

Keywords: biodiversity, ecology, taxonomy.

(Abstract and keywords provided by the journal)

The form genus *Fusarium* exhibits a remarkable degree of biodiversity in respect of morphological, physiological and ecological attributes. Thus, it is not surprising that representatives of the genus occur in a wide range of ecological niches in most geographical regions of the world. This high level of biodiversity or variation, however, led to considerable difficulties in the development of a stable and widely accepted taxonomic treatment of the genus.

The ideal taxonomic system should reflect the genetic relatedness of taxa. It should also recognise, at an appropriate level, taxa which are distinguished by practically significant aspects of their pathogenicity, mycotoxicology or ecology without unnecessary splitting of genetically unified populations. The history of *Fusarium* systematics has shown marked swings between excessively narrow species concepts and those which are so broad that practically useful information on pathogenicity and toxigenicity has been lost. Contemporary studies of biodiversity in *Fusarium*, which have led to the description of several new specific and infraspecific taxa, 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.

Prior to 1900 there was a proliferation in the number of species described and this may be attributed partly to the variability in any *Fusarium* population as well as to inadequate criteria for delimiting taxa. H. W. Wollenweber pioneered taxonomic research on *Fusarium* through a systematic life-long study of a wide range of cultures from different climatic regions, the results of which were published in a series of publications culminating in his classic work with O. A. Reinking (1935). It is apparent that Wollenweber encountered difficulties in defining the limits of some populations leading to different taxonomic arrangements in successive publications (Wollenweber, 1913; Wollenweber & Reinking, 1925, 1935). Despite these difficulties, however, Wollenweber and Reinking significantly reduced the number of taxa through consolidation, as illustrated in „Die Fusarien" (Wollenweber & Reinking, 1935). This monograph became the foundation on which all subsequent taxonomic systems have been based (Toussoun & Nelson, 1975). Modifications to the system proposed by Wollenweber and Reinking appear to have been prompted mainly by different concepts of the limits of variation within a species.

Snyder & Hansen (1940, 1941, 1945) studied variability in *Fusarium* sections *Elegans*, *Martiella* and *Ventricosum* using cultures initiated from single conidia and showed that morphological and cultural characteristics exhibited a significant degree of overlap between the species. On this basis these authors reduced all taxa in section *Elegans* to synonymy with *F. oxysporum* Schlecht. emend. Snyder & Hansen, and all taxa in sections *Martiella* and *Ventricosum* to synonymy with *F. solani* (Mart.) Appel & Wollenw. emend. Snyder & Hansen. These reductions have been accepted widely (Booth, 1971; Burgess & al., 1994; Nelson & al., 1983). Snyder and Hansen then proceeded to reduce the number of *Fusarium* species they accepted to nine (Snyder & Hansen, 1940, 1941, 1945). This included the reduction of all taxa recognised by Wollenweber & Reinking (1935) in *Fusarium* sections *Arthrosporiella*, *Discolor*, *Gibbosum* and *Roseum* to synonymy with *F. roseum* Link (Snyder & Hansen, 1945). Such radical synonymy received limited acceptance, primarily by plant pathologists, but it was not generally accepted because some of the economically important species treated as synonyms of *F. roseum* were considered distinctive and could be distinguished consistently from other species on a morphological basis, e.g. *F. culmorum* (W. G. Smith) Sacc. and *F. graminearum* Schwabe. In an attempt to reconcile these objections, Snyder & al. (1957) proposed that these distinctive populations be designated cultivars of *F. roseum*. The cultivar concept was not widely accepted because the authors did not formally define the criteria on

which cultivars were to be based (Snyder & al., 1957). The radical consolidation of species in four sections into *F. roseum* by Snyder & Hansen and the widespread use of this epithet in published work has led to the loss of a large body of valuable information on the pathology and toxicology of populations subsumed into this species (Marasas & al., 1984; Thrane, 1989).

During the last decade mycologists and plant pathologists have reached a reasonable degree of consensus on the taxonomy of *Fusarium* species. The basic approach proposed at the Fifth International Fusarium Workshop in Sydney in 1983 and illustrated by Burgess & Liddell (1983), Burgess & al. (1988, 1994) and Nelson & al. (1983) has been accepted by many workers and is based largely on „Die Fusarien" (Wollenweber & Reinking, 1935) and the work of Gordon (1952) and Booth (1971). Since 1982 a number of new species have been recognized (Burgess & al., 1982; Burgess & Trimboli, 1986; Marasas & al., 1985, 1986, 1987; Nelson & al., 1987; Summerell & al., 1995) and some species have been amended (Burgess & al., 1985) or transferred to another genus [e.g. *Fusarium stoveri* Booth to *Microdochium stoveri* (Booth) Samuels & Hallett].

Recently, Burgess and co-workers have described a number of newly recognised populations as subspecies (Burgess & al., 1993; Sangalang & al., 1995a) based on the guidelines for subspecies proposed by Hawksworth (1974). It is not surprising that additional populations distinctive enough to be recognised as new taxa have been identified as it is only in the last two decades that intensive and extensive surveys of *Fusarium* populations associated with various crops and soils in the hot semiarid and subtropical regions of the world have been completed (Burgess & al., 1975, 1988; Marasas & al., 1988; Sangalang & al., 1995b). Prior to that time *Fusarium* taxonomy had been based largely on materials collected in cool temperate regions, although Wollenweber & Reinking (1925), Reinking & Wollenweber (1927), Gordon (1956, 1960), Booth (1971) and Gerlach & Nirenberg (1982) had access to cultures collected from some tropical regions. It is likely that other populations will be differentiated as further systematic surveys of *Fusarium* species are completed in arid and tropical regions, where information on the nature and distribution of *Fusarium* populations is limited.

The recognition of ecologically distinct populations as subspecies has the advantage that they can be described formally to indicate their morphological affinity with other *Fusarium* populations while acknowledging a degree of overlap in morphological characteristics and distribution. Some subspecies will probably be raised eventually to the rank of species as information on their morphological and ecological characteristics is accumulated and limits established. The reverse procedure also might occur.

It should be emphasised here that these species and subspecies are form taxa. Thus, morphologically similar populations may not necessarily be closely related in genetic terms. The development of molecular techniques to study the affinity between fungal populations has provided opportunities for assessing genetic affinity of form taxa.

Indeed the combination of extensive mycogeographic surveys with morphological and physiological studies as well as studies at the molecular level have provided powerful new approaches to assess the nature of biodiversity and adaptation in *Fusarium*. The application of these approaches can be illustrated by reference to three species, *F. graminearum*, *F. acuminatum* Ell. & Ev. subsp. *armeniacum* Forbes, Windels & Burgess and *F. compactum* (Wollenw.) Gordon and populations related to each of these species.

F. graminearum

Purss (1969, 1971) reported that cultures of *F. graminearum* isolated from wheat affected by crown rot differed in pathogenic ability from cultures of this species isolated from maize affected by stalk rot. Francis & Burgess (1977) established the existence of two populations, designated Groups 1 and 2, within *F. graminearum*, based on the examination of a large number of cultures derived from samples of diseased wheat, maize and other hosts during extensive surveys in eastern Australia (Francis & Burgess, 1975; Burgess & al., 1975). Although cultures of each group could be differentiated consistently on the basis of secondary taxonomic characters when grown under standard environmental conditions they did not differ in respect of the primary criterion for species differentiation, namely the shape of the macroconidium. The presence or absence of perithecia in cultures initiated from single macroconidia is the most reliable practical characteristic for differentiating the two groups. Wild-type cultures of Group 1 do not form perithecia in culture on carnation leaf piece agar (CLA) (Fisher & al., 1982) whereas wild-type cultures of Group 2 form abundant perithecia on CLA (Francis & Burgess, 1977).

The Group 2 population should be referred to by its teleomorph binomial, *Gibberella zeae* (Schwein.) Petch. It also forms abundant perithecia in nature and has been reported widely from temperate and subtropical regions of the world as the cause of head blight of cereals, stalk and cob rot of maize and other diseases. In contrast, the Group 1 population very rarely forms perithecia in nature and causes crown rot of cereals and grasses. It has been reported from Australia, South Africa, northern Africa, Italy and California and Washington State in the U.S.A. The two groups produce similar mycotoxins with minor differences in the relative amounts of each mycotoxin (Blaney & Dodman, 1988).

Based on the similarity in morphological characteristics, the overlapping niches on cereals and grasses and the similarity of the teleomorph, Francis and Burgess (1977) postulated that the existence of these populations was the result of microevolutionary changes. The authors designated these two populations as groups because it was considered that there were no appropriate formal taxonomic categories (Burgess, unpublished).

The senior author has examined over a thousand wild-type cultures of *F. graminearum*, Groups 1 and 2 from four continents since 1975. Cultures with characteristics intermediate between the two groups were not encountered during these examinations. This suggests that the two groups are more distinct genetically than was implied by Francis & Burgess (1977).

Schilling & al. (1994) reported studies on genetic diversity within and between *F. graminearum*, *F. culmorum* (W. G. Smith) Sacc. and *F. crookwellense* Burgess, Nelson & Toussoun using RAPD markers. Cultures of the three species and the two groups within *F. graminearum* were distinguished by RAPD patterns. Furthermore, cluster analysis (UPGMA) and principal coordinate analysis indicated that *F. graminearum* Group 2 cultures have greater genetic affinity to *F. culmorum* and *F. crookwellense* than to *F. graminearum* Group 1.

Similar findings have been made independently by Benyon & al. (unpublished) employing the method of Restriction Fragment Length Polymorphism (RFLP) analysis. Cultures of *F. graminearum*, *F. culmorum*, *F. crookwellense* and *F. sambucinum* Fuckel were distinguished by RFLP patterns. Distance analyses calculated using Dice's coefficient and represented as a dendrogram by the neighbor-joining method indicated greater affinity between *F. graminearum* Group 2, *F. culmorum* and *F. crookwellense* than with *F. graminearum* Group 1. *F. sambucinum* showed greater affinity to the species in section *Roseum*.

Such independent findings derived using different molecular techniques suggest that consideration should be given to assigning species rank and a species epithet to the population, *F. graminearum* Group 1.

F. acuminatum subsp. *armeniacum*

This subspecies was described formally by Burgess & al. (1993). It was assigned the rank of subspecies on the basis of its macroconidia which, although larger, are similar in shape to the macroconidia of *F. acuminatum sensu lato*. It also differs from *F. acuminatum* Ell. & Ev. subsp. *acuminatum* Burgess & al. in respect of colony morphology and growth rate. The two subspecies intergrade with respect to some morphological and ecological characteristics.

Cultures of *F. acuminatum* subsp. *armeniacum* were first noted in Minnesota and recorded under the name *F. roseum* (Link) emend. Snyder & Hansen 'Gibbosum' (Kommedahl & al., 1979; Windels, pers. comm.). Independently Burgess and coworkers had noted the occurrence of atypical cultures of *F. acuminatum* from maize and soil and described these informally (Burgess & Liddell, 1983), and made them available for examination at the Fifth International Fusarium Workshop in 1983. Cultures of this subspecies were later reported from South Africa (Rabie & al., 1986; Marasas & al., 1988), again as atypical isolates of *F. acuminatum* and Rabie & al. (1986) reported that some of these isolates produced high levels of T–2 toxin. Further studies by Logrieco & al. (1992a) and Wing & al. (1993a, b) confirmed that cultures of *F. acuminatum* subsp. *armeniacum* could produce medium to high levels of T–2 toxin and neosolaniol and were highly toxigenic whereas cultures of *F. acuminatum* subsp. *acuminatum* only produced trace levels of T–2 and were not toxigenic. These results are noteworthy as high levels of T–2 production have only been reported previously by cultures of *Fusarium sporotrichioides* Sherb. (Marasas & al., 1984). These findings suggest that *F. acuminatum* subsp. *armeniacum* may have closer genetic affinity with *F. sporotrichioides* than with *F. acuminatum* ssp. *acuminatum*. Thrane (1989) has suggested that secondary metabolite data should be used to supplement other taxonomic criteria in delineating species.

Substantial evidence indicates that there is a close phylogenetic relationship between *F. acuminatum* subsp. *armeniacum* and *F. sporotrichioides* based on comparisons of partial ribosomal RNA sequences (Logrieco & al., 1992b) and electrophoretic karyotype analysis (Nagy & Hornok, 1994). The latter authors also probed the karyotypes of the two subspecies of *F. acuminatum* for the trichodiene synthase gene *Tox*5 and obtained hybridisation signals only in cultures of *F. acuminatum* subsp. *armeniacum*.

Further molecular studies are justified to clarify the nature of the genetic affinity between *F. acuminatum* subsp. *armeniacum* and *F. sporotrichioides* more precisely before the taxonomic status of *F. acuminatum* subsp. *armeniacum* is reviewed.

F. compactum

This species is relatively abundant in semi-arid and arid soils of the warmer regions of Australia (Burgess & Summerell, 1992; Gott & al., 1994; Sangalang & al., 1995b; Summerell & al., 1993) and South Africa (Marasas & al., 1988). It is also highly toxigenic (Greenhalgh & al, 1991; Wing & al., 1993a) and has been associated with a mycotoxicosis involving sandhill cranes in the United States (Cole & al., 1988;

Nelson & al., 1990; Windingstad & al., 1989). It is rarely reported from cool temperate regions.

This taxon was first described as a variety of *F. scirpi* by Wollenweber (1931), but was later placed in synonymy with *F. equiseti* (Wollenweber & Reinking, 1935). Gordon (1952) considered it sufficiently distinct to raise it to species rank, a view shared by Gerlach & Nirenberg (1982) but not by Booth (1971). Nelson & al. (1983) considered that red-pigmented isolates formed a distinctive group, but provisionally retained them in *F. equiseti*. All of these workers had seen only a small number of isolates.

Examination of several hundred cultures from central and northern Australia led Burgess & Liddell (1983) and Burgess & al. (1988, 1994) to regard *F. compactum* as a distinct species, in which both red and brown pigmentation occur. The ecology of *F. compactum* is quite different from that of *F. equiseti*, and the two species may be unambiguously distinguished by growth rates at 30 C and 35 C and by colony morphology. *Fusarium compactum* cannot be reliably separated from *F. equiseti* on the basis of the shape of the macroconidia.

Recent unpublished studies by Burgess and coworkers on *F. compactum* indicate a remarkable degree of variability in the length of the macroconidia both within and between cultures of this species on CLA. While macroconidia in a single culture of most isolates are relatively uniform, in other cultures macroconidia from different sporodochia may show almost the full range of size found in the genus. For example, in one CLA culture of F6346 initiated from a single macroconidium, mean length of macroconidia in each of 3 sporodochia ranged from 38 µm to 60 µm and the differences between sporodochia were significant at $P = 0.01$ by analysis of variance (Levic & al., unpublished). Similarly, mean length of macroconidia in different cultures from a single geographic region, which are otherwise similar in colony morphology, pigmentation and growth rates, and show no sign of degeneration, can range from less than 40 µm to greater than 75 µm (Levic & al., unpublished).

The authors have had difficulty differentiating cultures of *F. compactum* which produce very long macroconidia from cultures of *F. longipes* Wollenw. & Reinking, which consistently forms very long macroconidia. Both species belong to the Section *Gibbosum* and thus the macroconidia exhibit the strong dorsi-ventral curvature characteristic of species in this section. Cultures of *F. compactum* with very long macroconidia have been isolated most commonly from the tropical regions of northern Australia, the only region from which *F. longipes* has been recovered in this country (Backhouse & Burgess, 1995). Cultures of *F. longipes* are not toxigenic (Wing & al., 1993a). Cultures of *F. compactum* with very long macroconidia can only be

differentiated from cultures of *F. longipes* by secondary morphological criteria. *F. compactum* forms diffuse confluent sporodochia on the leaf pieces and in mycelium in the agar on CLA whereas *F. longipes* forms discrete sporodochia, often columnar, on the leaf pieces. The 'foot' at the base of the basal cell of macroconidia of *F. longipes* is typically longer and has a more distinct 'heel' than that of macroconidia of *F. compactum*. A study of the genetic variation and affinity of these two species and indeed the other species in section *Gibbosum* using RAPD or RFLP techniques would contribute significantly to a better understanding of these common soil fungi.

Conclusions

The above are examples of taxa of pathological and toxicological significance which were only distinguished by the careful examination of large numbers of cultures representing the limits of biodiversity within the relevant populations and related taxa. Understanding the affinity between species and infra-species populations, and hence the development of an adequate taxonomy, of form genera such as *Fusarium* has been difficult because of the paucity of reliable morphological and physiological characters. The availability of a range of molecular techniques has made possible precise studies on the genetic affinity and phylogeny of such populations. Furthermore, the development of species specific probes offers the potential for the precise identification of cultures which cannot be clearly differentiated on morphological criteria.

There is now a strong case for the 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. It is critical, however, that studies on genetic diversity within and between species populations be based on the analysis of a large number of cultures derived from a wide range of substrates and geographic origins.

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