

## 2011 McAlpine Memorial Lecture - A Love Affair with *Fusarium*

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**Abstract** *Fusarium* is one of the most remarkable genera of the fungi. It is remarkable for its genetic and morphological diversity, its wide geographic distribution, the diversity of its relationships with plants, the diversity of plant diseases for which it is responsible, and its abundance and diversity in natural ecosystems. Evidence to support this contention is presented and discussed focusing on the author's career-long and continuing research on the genus. The diversity and socio-economic importance of *Fusarium* diseases is illustrated by reference to diseases common in the Australasian region. Examples include the *Fusarium* wilts caused by formae speciales of *F. oxysporum* and the stalk and cob rots of maize and cereal head blights caused by *F. graminearum*. The importance of *Fusarium* mycotoxins is noted. Endophytic colonization of living plant tissue by *Fusarium* species remains a poorly understood and insidious phenomenon. Examples are provided in relation to crop plants and plants in natural ecosystems. The role of natural ecosystems as reservoirs of crop pathogens and potential emerging pathogens is discussed briefly in relation to disease management and biosecurity.

**Keywords** *Fusarium* taxonomy · Biology · Socio-economic impact · Endophytic behaviour · Occurrence in natural ecosystems

### Preface

It was a privilege to present the 2011 McAlpine Memorial Lecture at the inaugural joint meeting of The 4th Asian Conference on Plant Pathology and the 18th Biennial

Australasian Plant Pathology Conference in Darwin. I thank many of the participants from across Asia for providing valuable unpublished information on *Fusarium* diseases in their countries following the lecture.

### Introduction

*Fusarium* is one of the most remarkable genera of the fungi. It is remarkable for its genetic and morphological diversity, its wide geographic distribution, the diversity of its relationships with plants, the diversity of plant diseases for which it is responsible, and its abundance and diversity in natural ecosystems.

My romance with *Fusarium* began with my PhD on *Fusarium* crown rot of wheat and barley in the northern grain belt of eastern Australia, a disease that became one of several foci of my career-long research on *Fusarium* (Burgess et al. 2001). However it was at the University of California, Berkeley, that my interest became a passionate and enduring love affair. It was there that I had the opportunity to learn from the legendary W.C. Snyder and his impressive culture collection. We disagreed on many taxonomic issues (Snyder and Hansen 1954) but I learnt from him the value of studying diversity based on cultures from a wide range of substrates and bioclimatic regions, a philosophy that has underpinned my eco-taxonomic research and that of my students since 1970. Systematic surveys across diverse bioregions of Australia have led to the discovery of fascinating new species – being the first to recognise and examine a species remains a continuing source of excitement.

In this paper I discuss the nature of *Fusarium* and some of the highlights of my taxonomic and mycogeographical studies, then comment briefly on the diversity of *Fusarium* diseases and their socio-economic importance, before focussing on the importance of endophytic colonization of crop species and wild plant populations by *Fusarium* as a key factor in

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understanding the biology of the genus, and the management of pathogenic species. The ability of *Fusarium* to colonize plants endophytically and the impact on the host plant remains poorly understood.

## Fusarium

The genus was established by Link (1809), to include species with canoe-shaped conidia, now called macroconidia that are characterised by a foot-shaped or notched base to the basal cell and variously shaped apical cells. The macroconidia vary significantly in shape between many species but are consistent in shape within a species on recommended media, although the dimensions especially length may vary between isolates. Many species, including a number of important plant pathogens, also produce one or more types of microconidia. These vary in shape, size and mode of formation. They vary in shape and size from globose (*F. beomiforme*; *F. globosum*), to clavate (*F. verticillioides*), to napiform (*F. tricinctum*) to pyriform (*F. sacchari* (Petrovic et al. 2013) and to small oval, or kidney shaped (*F. oxysporum*). They are formed from monophialides or polyphialides, often in quite elegant arrangements. They are formed singly, in false-heads, or in short, medium or long chains, and the chains are disordered in some species. Quite remarkably, in some species two different types of microconidia can be formed in a single chain or cluster. It is surprising that we know little of why different types of microconidia are formed, or indeed of their ecological significance. Similarly we know little of their role in the epidemiology of plant diseases (Ooka and Kommedahl 1977; Rowe et al. 1977; Burgess 1981). These are fertile areas for further research.

Chlamydospores, thick-walled survival spores are produced by many species including some plant pathogens such as the formae speciales of *F. oxysporum*. The significant role of chlamydospores in the persistence (over-seasoning) phase of the disease cycle was first recognised by Burkholder (1919) but their study was largely neglected until the work of W. C. Snyder's group in the 1950's (Nash and Snyder 1962).

Some species also reproduce sexually, forming perithecia in which ascospores are produced, then ejected and dispersed in the atmosphere. The pathogen *Fusarium graminearum* is a good example (Schmale et al. 2005) – it is homothallic and produces abundant perithecia in nature, and in colonies derived from single spores in culture. In contrast, some species are heterothallic, including such plant pathogenic species as *F. fujikuroi*, *F. proliferatum*, *F. sacchari*, *F. subglutinans*, and *F. verticillioides*, well-known members of the *Gibberella fujikuroi* species complex (GFSC). Sexual compatibility of isolates can provide a valuable biological marker for clarifying the limits of a species (Amata et al. 2010).

Historically *Fusarium* species were identified using morphological characteristics. Differing philosophies on what

constituted a valid species led to many taxonomic controversies and quite different taxonomic systems during much of the last century (Toussoun and Nelson 1975; Leslie and Summerell 2006). I especially acknowledge the exceptional pioneering work of Wollenweber that led to the publication of 'Die Fusarien' (Wollenweber and Reinking 1935), a monograph that provided the foundation for the modern morphological taxonomy of *Fusarium*. Wollenweber's accession records that were hand written on index cards (Wollenweber 1926) are remarkable for the clarity of the drawings and descriptions of morphological features, as well as details of the origin of cultures. His records have proved invaluable in our taxonomic research. For example they were crucial to enabling us to assign *F. scirpi* as the epithet for particular isolates from the arid grasslands of central Australia (Burgess et al. 1985; Sangalang et al. 1995b; Backhouse et al. 2001), and to understand the nomenclatural history of the species. It was a pleasure to find that the cross-shaped polyphialides of *F. scirpi* had been beautifully illustrated by Wollenweber as Accession 198, dated 1915 (Fig. 1a), under the species name *F. chenopodium* (Wollenweber 1926). Indeed this may be one of the first illustrations of a polyphialide. This species had gone unrecognised for decades, one of a number of such species that we 'rediscovered' as a consequence of continental scale mycogeographic surveys of *Fusarium* in grassland and shrubland soils. These surveys also led to the discovery of newly recognised species (Burgess and Trimboli 1986; Nelson et al. 1987; Burgess et al. 1988, 1993; Sangalang et al. 1995a; Summerell et al. 1995; Benyon et al. 2000).

However the morphological approach to taxonomy relied heavily on the experience of the researcher and could not differentiate sibling species (morphologically similar but genetically different species). Consequently advances in molecular biology over the past two decades have led to a reliance on molecular approaches for differentiating species and understanding the phylogeny of *Fusarium*. Sequencing is now accepted as a routine method for confirmation of the identity of *Fusarium* species (Geiser et al. 2004).

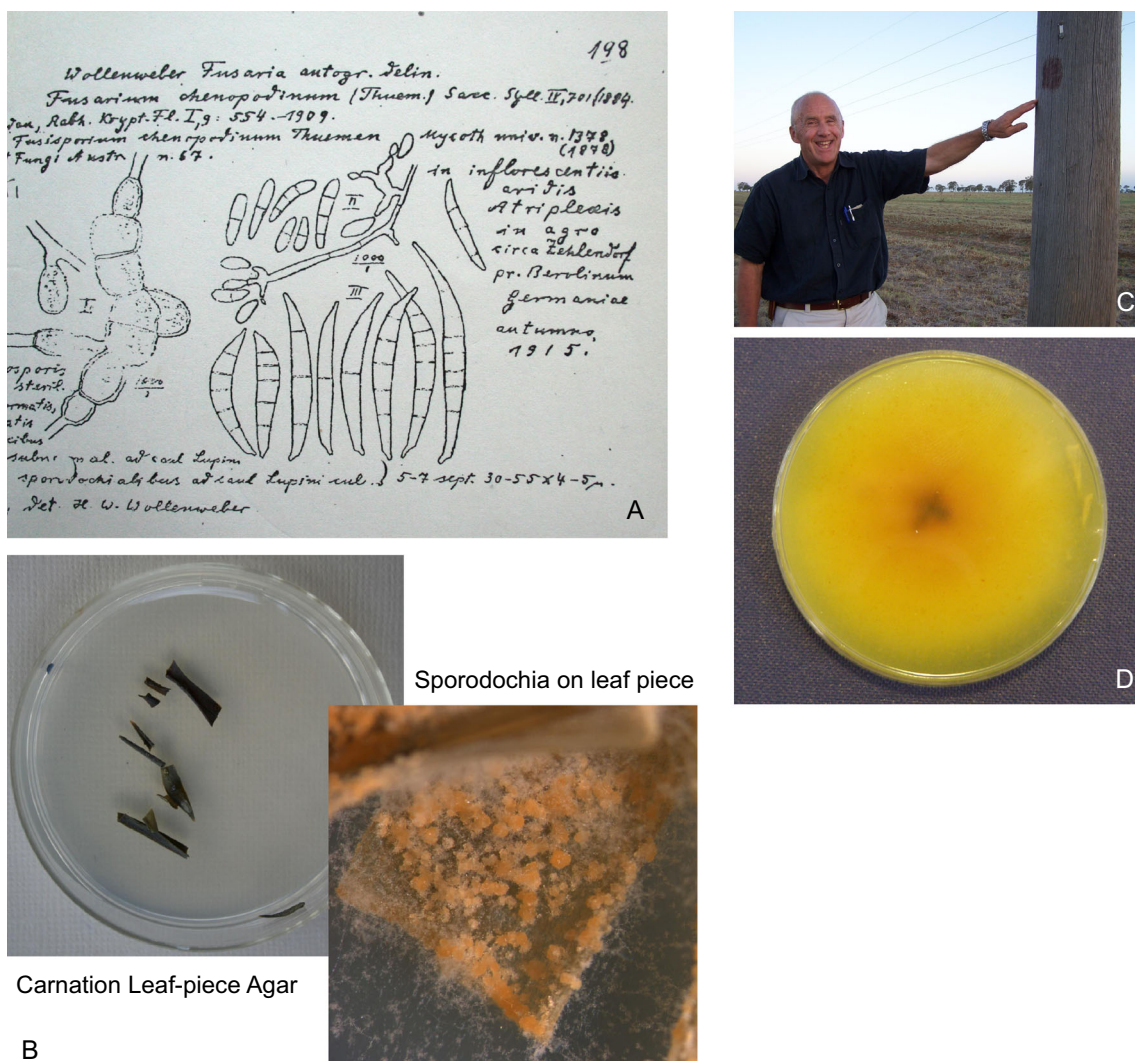
Molecular systematics has been particularly valuable in differentiating species in the GFSC (O'Donnell et al. 1998; Nirenberg and O'Donnell 1998; Kvas et al. 2009). This complex contains many important plant pathogenic and mycotoxigenic species.

I recognise that morphological identification remains a primary means of identification of *Fusarium* species in diagnostic laboratories in many countries where resources are limited. Thus it is important for plant pathologists to understand the importance of using standard procedures for culturing *Fusarium* to ensure reliable morphological identification, and equally importantly to avoid cultural degeneration and loss of virulence by pathogenic isolates. Furthermore the development of integrated disease management (IDM) strategies for *Fusarium* diseases depends on an intimate

understanding of the whole fungus, including the nature of survival structures, spores and spore dispersal. Thus morphological studies are an essential component of basic and applied research on *Fusarium*.

Accurate and consistent morphological identification and description of *Fusarium* depends on the use of a pure wild-type culture initiated from a single conidium, standard media, growth of cultures under standard conditions of light and temperature (Burgess et al. 1994), and the use of a reliable taxonomic reference (Leslie and Summerell 2006). Morphological identification should be considered putative and then confirmed by sequencing and other techniques where possible. I note that many reported sequences have been assigned to incorrect species epithets based on inaccurate morphological identification.

Carnation leaf-piece agar (CLA) (Fig. 1b) first used by P. E. Nelson is an indispensable medium for the production of conidia that are consistent in shape and mode of formation within a species (Fisher et al. 1982). Macroconidia are produced in sporodochia that develop on the leaf pieces (Fig. 1b), while microconidia are produced from monophialides and or polyphialides formed from hyphae mainly on the water agar. Chlamydo spores also develop in hyphae growing on the water agar and, in some species, from conidia. The mode of formation and nature of microconidia are best examined initially in situ with a X20 objective lens so that the delicate structures such as false-heads and chains can be seen properly in their 3-dimensional form. Colonized carnation leaf pieces are ideal for lyophilising (freeze-drying) for long-term preservation of cultures.



**Fig. 1** **a** Plate 198 (in part) from Wollenweber (1926) illustrating the cross-shaped polyphialides of *Fusarium chenopodium* later recognised as *Fusarium scirpi*. **b** Small Petri plate of Carnation Leaf-piece Agar, a standard growth medium for producing macroconidia and microconidia of *Fusarium* species for morphological identification. The colonized leaf pieces are also ideal for preservation of cultures. **c** The author in 2008 on

relocating grassland soil sampling site P6201 near Longreach, Queensland, 26 years after the original survey. The Longreach Yellow isolates (*Fusarium burgessii*) were recovered from this area. Such sites are now located by GPS coordinates rather than paint marks on posts, trees or rocks! **d** Yellow-pigmented agar of a typical isolate of *Fusarium burgessii* ('Longreach Yellow') on Potato Dextrose Agar

A lyophilised culture collection is the heart of a *Fusarium* research laboratory. Lyophilised cultures provide for future reference and research, including temporal studies on populations from the same substrate and geographic region (Bentley 2007). Cultures that I lyophilised 40 years ago using colonized carnation leaf pieces have retained viability and typical wild-type characteristics. The majority of cultures in our culture collection at the University of Sydney, now located at the Royal Botanic Gardens, Sydney, were isolated during mycogeographic surveys of *Fusarium* species associated with soil or plants in natural ecosystems. These cultures were collected from permanent sampling sites, so the geographic origin of these cultures is known and a site can be re-sampled. Our collection also includes cultures isolated during extensive systematic surveys of species associated with crop diseases, mainly of wheat, maize and sorghum. Lyophilisation of wild-type cultures soon after their isolation and purification minimises the risk of cultural degeneration (saltation), a major issue with many *Fusarium* species (Brown 1926; Snyder and Hansen 1954; Wing et al. 1995).

While the culture collection is the heart of a *Fusarium* research program, systematic mycogeographic (phylogeographic) surveys are the backbone! Cultures recovered during such surveys provide the fundamental basis for rigorous studies on the phylogeny, taxonomy and ecology of *Fusarium* populations. They also allow for inferences to be made on the origins and evolutionary relationships of species.

One example will suffice to illustrate the value of a living culture collection, surveys, and permanent sampling sites. In 1982 I undertook a survey of *Fusarium* species from grassland soil samples collected along a transect adjacent to the Tropic of Capricorn, from the coast to the edge of the Simpson Desert in Queensland, Australia (Burgess and Summerell 1992). A number of fascinating cultures were isolated from the Longreach region that did not correspond morphologically to any recognised species. They resembled *F. oxysporum* but differed in that they produced microconidia on very long monophialides on CLA and most cultures produced yellow pigmentation in PDA. These differences were considered relatively minor but the cultures were lyophilised and accessioned under the notation ‘Yellow Longreach/Yellow Oxysporum’. In 2008 I re-sampled the Longreach sampling sites (Fig. 1c) and Dr Matthew Laurence again isolated cultures of this population from these sites and from Idalia National Park, as part of his Australia-wide survey of *F. oxysporum* in soils of natural ecosystems. Phylogenetic studies confirmed that the ‘Yellow Longreach’ isolates (Fig. 1d) were indeed a distinct species, *F. burgessii*, in a newly recognised clade (Laurence et al. 2011). I am indebted to my colleagues for assigning this epithet.

## Socio-economic importance

Representatives of *Fusarium* occur in most bioclimatic regions of the world in natural and agricultural ecosystems (Backhouse et al. 2001). Many species are pathogenic, and are collectively responsible for a wide range of diseases including vascular wilts, root, crown, stalk and head rots, head blights, storage rots, cankers and growth distortion diseases such as the classic bakanae disease of rice and pokkah boeng of sugarcane. Bakanae (‘foolish seedling’ or ‘man seedling’) disease of rice caused by *F. fujikuroi* (Hori 1898; Sun and Snyder 1981; Amatulli et al. 2010), and Pokkah boeng (‘crazy top’) disease of sugarcane caused by *F. sacchari* (Martin et al. 1961; Egan et al. 1997) are well-known examples of growth distortion diseases caused by *Fusarium* in S. E. Asia and elsewhere.

Some species produce mycotoxins that can lead to contamination of produce including grain and forage, leading in turn to contamination of human food and animal feedstuffs and potential mycotoxicoses of humans and animals (Hagler et al. 2001; Marasas et al. 2001; Miller et al. 2001; Desjardins 2006; Bryden 2009). Consequently mycotoxin contamination has significant implications for food safety and trade, and may become more significant with global warming (Magan et al. 2011). Mycotoxins have also been implicated in plant disease (Desjardins and Hohn 1997). The following two examples illustrate the socio-economic impact of *Fusarium* diseases.

*Fusarium graminearum* is a pathogen of global significance best known as a major cause of *Fusarium* head blight (FHB) of wheat and other small grain cereals, as well as stalk and cob rot of maize (Sutton 1982; Gilchrist and Dubin 2002; Burgess and Bryden 2012) but it also has a wide host range amongst the Poaceae including domesticated and weed species.

*Fusarium* head blight re-emerged as a major problem in the USA in the 1990’s following the widespread adoption of no-till farming practices. In 1993 it caused losses estimated at a billion dollars that had devastating socio-economic consequences for rural communities (McMullen et al. 1997; Windels 2000). Furthermore it has been estimated that FHB may affect up to 70 M ha in China in epidemic years with losses of up to 2.5 M tonnes of grain (Gilchrist and Dubin 2002). *F. graminearum* also continues to cause problems with cob rot in maize in China (Li Honglian personal communication). The pathogen produces the important mycotoxins deoxynivalenol, nivalenol and zearalenone, which can contaminate infected grain, an additional impact of these diseases (Hagler et al. 2001; Desjardins 2006; Bryden 2009). The formation of abundant perithecia on host residues, a key link in the disease cycle, was a critical factor in the dramatic increase in the incidence and severity of FHB.

*Fusarium* wilt of banana (Panama disease) caused by *F. oxysporum* f. sp. *cubense*, is a destructive disease that has

caused serious socio-economic disruption in most banana growing regions of the world at some time (Reinking 1934; Stover 1962; Ploetz et al. 1990; Bin Doon 1991; Chandra 1991; Pegg et al. 1996; Moore et al. 2001; Wibowo et al. 2011). The banana, a monocotyledonous plant of S. E. Asian origin, is clonally propagated, a key factor in the spread of the pathogen.

Panama disease gained prominence in the 1940's and 1950's following devastating losses to the export industry in Latin America and the Caribbean (Stover 1962). The industry was based solely on the cultivar Gros Michel, which was very susceptible to Race 1 of *F. oxysporum* f. sp. *cubense*. Fortunately the Cavendish banana was found to be resistant to Race 1 and led to the resurgence of the export banana industry in the region.

Cavendish cultivars were also adopted for export plantings in parts of south Asia. The discovery of isolates in Taiwan able to cause wilt in Cavendish cultivars (Su et al. 1977) heralded a new era of socio-economic disruption. The new race being known as Race 4 (Moore et al. 2001) or Tropical Race 4 (TR4). In Taiwan, losses have been minimised through the use of somaclonal variants, with good levels of resistance. However the spread of TR4 has devastated plantations of Cavendish cultivars in Malaysia and Indonesia. Banana exports from Indonesia, for example, had virtually ceased by 2003 as a consequence of losses from Fusarium wilt and blood disease (Subandiyah 2011).

The above examples illustrate the socio-economic impact of Fusarium diseases. It is inevitable that the genus will continue to be a threat to crop production and food security with changing farming systems, incursions, and the emergence or evolution of new pathogenic populations as occurred with Fusarium wilt of cotton in Australia (Kochman 1995; Davis et al. 1996, 2006; Wang et al. 2004, 2006, 2010).

### Endophytic colonization of crop and other plants

Endophytic colonization of living plant tissue by *Fusarium* and other fungi remains a poorly understood and insidious phenomenon. Such colonization implies that there are no visible symptoms or signs of infection (Bacon and Hinton 1996; Yates et al. 1997). It is a feature of the biology of many *Fusarium* species that cause plant disease and can have a significant role in the epidemiology and management of the pathogen. Furthermore it has implications for biosecurity as crop pathogens may colonize some hosts solely as endophytes but may not be included in checklists of pathogens occurring on these plants (Burgess 2003). Several examples of endophytic colonization and the implications for disease management are discussed below.

*Fusarium oxysporum* – pathogen, endophyte, saprophyte

*Fusarium oxysporum* is a complex species of global importance. It includes many plant pathogenic populations known as formae speciales, each of which is normally responsible for a specific disease of one or a few hosts. A forma specialis (f.sp.) has one primary host by definition. A forma specialis can be polyphyletic, and may include cultivar specific races. The formae speciales are mainly responsible for vascular wilt diseases but also cause some crown and root rots, and tuber, bulb and corm rots. Many other members of *F. oxysporum* are common colonists of plant roots either as endophytes of symptomless roots, or saprophytic colonists of senescing or diseased roots. Indeed these populations are often mistakenly claimed to be pathogenic because of their frequent isolation from diseased roots especially in temperate regions, and the use of inappropriate pathogenicity tests involving wound inoculation and/or excessive ('inundative') levels of inoculum.

The vascular wilt diseases affect a wide range of crops, predominantly broad-leafed (dicotyledonous) species but not exclusively so. They are caused by well over 100 formae speciales. Infection normally occurs through the epidermis of the feeder rootlets. The fungus then colonizes the root cortex before penetrating the endodermis, the protective layer of cells around the vascular system or stele. It then enters the xylem vessels where it may be either restricted in its growth, or proliferate upwards through the xylem, depending on the resistance of the cultivar. Subsequently symptoms may develop, the severity depending on the cultivar. Vascular discoloration is usually obvious in susceptible cultivars but may not be present in some hosts such as members of the cucurbit family.

As the infected plant succumbs to wilt or senesces the wilt fungus forms chlamyospores in the root cortex, and also extends out from the xylem in the stem and colonizes adjacent tissues where they form chlamyospores. These pathogens persist in soil as chlamyospores formed from mycelium in the vascular and non-vascular tissues, or conidia formed on the surface of diseased stems. Most importantly these pathogens may also persist as chlamyospores formed in the root cortex of symptomless, secondary hosts (so-called 'non-hosts'), colonized endophytically (Smith and Snyder 1975). Therefore chlamyospore numbers can be regularly replenished in the absence of the susceptible primary host. Consequently crop rotation is not necessarily effective in reducing inoculum levels of wilt pathogens in soil (Smith et al. 1981). Symptomless secondary hosts can include crop species used in rotation with the primary host, in-crop weeds or weeds in the fallow. As an example Smith and Snyder (1975) provided evidence that *F. oxysporum* f. sp. *vasinfectum*, the cause of cotton wilt, could colonize barley roots, presumably the cortex, in which chlamyospores were formed, so contributing to the maintenance of inoculum levels

in the absence of cotton. The reader is referred to Davis et al. (2006) for further discussion of these issues. Non-pathogenic strains of *F. oxysporum* are also commonly isolated from symptomless roots. Indeed, I hypothesise that symptomless roots of non-host plants could be colonized endophytically by several formae-speciales in fields where several Fusarium wilt diseases occur, as well as non-pathogenic (endophytic or saprophytic) strains.

Further research is justified to assist our understanding of the nature of endophytic colonization of roots and the biology of chlamydospore formation and persistence making use of both classical and molecular techniques. It has been a relatively neglected area, despite the obvious importance to disease management.

#### *Fusarium graminearum* – pathogen and endophyte

Fusarium head blight was first reported in Australia by McAlpine (1896), and attributed to *F. culmorum*. However the disease was rarely observed except in localised areas such as coastal dairy farms in New South Wales (NSW) where maize and wheat were grown in close rotation. These outbreaks were probably caused predominantly by *F. graminearum* (Tobin 1988).

Since 1999 localised epidemics of FHB caused by *F. graminearum* have occurred in wheat planted in fields under centre pivot irrigation that have been used for maize production, or in fields in the general vicinity of these pivots, in the Liverpool Plains, NSW. No-till farming practices were adopted widely in this area from the early 1990's. Maize residues have provided the main source of ascospore inoculum dispersed both in-crop and over some distance (Davies 2011). The modern maize hybrids grown on the Liverpool Plains are tolerant to stalk and cob rot caused by *F. graminearum* and these diseases have not been reported in the area. However perithecia form abundantly on the old maize stalks indicating that *F. graminearum* had endophytically colonized the stalks. Davies (2011) tested this theory by monitoring the progress of infection and colonization of commercial irrigated maize planted into wheat residues with abundant perithecia of *F. graminearum*. He found that stalks were progressively infected and colonized through the growing season, presumably from ascospores released following each irrigation cycle, and later deposited in the leaf axils. However no symptoms of stalk rot or cob rot were observed. Davies (2011) concluded that infection and colonization of the maize was endophytic but led to the production of perithecia on the surface of the maize residues within 3 months of harvest (Burgess and Bryden 2012). Similar studies are justified with sorghum, a crop that also appears to be infected endophytically (Quazi et al. 2009). Such information will contribute to a better understanding of the role of symptomless host crops, and improved disease management practices.

#### **Endophytic colonization by species causing stress related root, crown and stalk rots of grain crops**

These diseases are most common in rain-fed crops in semi-arid regions and include: crown rot of wheat and barley; root, stalk and cob rot in maize; and root and stalk rot in sorghum. A key feature of these diseases is that the pathogens commonly infect and colonize the stem or stalk tissues endophytically through the growing season. They are not vascular pathogens. Plants may remain symptomless throughout the season unless subjected to moisture or other stressors depending on host resistance. Stress appears to alter the resistance of the host, disrupting the endophytic relationship, leading to symptom development.

#### *Fusarium pseudograminearum* – the cause of crown rot of wheat and barley

Crown rot of wheat and barley, first described by McKnight and Hart (1966), is an insidious and intractable disease caused by *F. pseudograminearum*, (Purss 1971; Burgess et al. 1981, 2001; Backhouse et al. 2004; Bentley et al. 2008). The incidence and severity of the disease increased significantly with the gradual adoption of no-tillage practices through the 1980's and 1990's as the fungus persists as hyphae in infested stubble (stem) residues for up to 3 years.

The description of the disease as insidious is a reflection of the endophytic nature of colonization of the host plant (Klein et al. 1991; Burgess et al. 2001). The fungus infects through the crown region and then extends up through the outer cortex of the stem but does not invade the vascular tissue until later in the season (Malligan 2009; Knight and Sutherland 2011). The initial symptoms are a browning of the lower stem region. Subsequently the fungus may cause more severe browning and disrupt the integrity of the vascular system leading to whitehead formation, the most conspicuous visual symptom of the disease, depending on the degree of moisture stress and resistance of the host. In seasons where soil moisture is freely available colonization is mainly endophytic and infected plants may show limited or no browning, and whiteheads are limited or absent, again depending on host resistance. However the stubble residues of such symptomless but infected plants maintain or increase inoculum levels. The absence of whiteheads in wet seasons has commonly led farmers to believe, mistakenly, that inoculum levels had declined and that it is safe to plant another wheat or barley crop. Furthermore some species, such as cereal oats (*Avena sativa*) (Nelson and Burgess 1994; Burgess et al. 2001) and the ubiquitous weed, wild oats (*Avena* spp.) are colonized endophytically and rarely develop symptoms, but maintain or increase inoculum levels. Thus an understanding of the endophytic nature of host colonization by *F. pseudograminearum* is crucial to understanding the

epidemiology of the disease, the importance of monitoring inoculum levels, and the development of management practices.

*Fusarium verticillioides* and the Fusarium root, stalk and cob rots of maize

In NSW, eastern Australia, *F. proliferatum*, *F. subglutinans* and *F. verticillioides*, members of the GFSC, and *F. graminearum* are the dominant pathogenic Fusarium species associated with these diseases (Edwards 1935; Francis and Burgess 1975; Burgess et al. 1981; Tran 2005; Watson 2009). However *F. verticillioides* is the dominant Fusarium colonist of maize stalks in crops grown under irrigation in the hot semi-arid inland areas (Watson 2009). Fusarium cob rot caused by *F. verticillioides* was common in hybrid maize crops in one of these areas, the Murrumbidgee Irrigation Area, in 2003, with severely affected crops being chopped for silage (Watson 2009). The outbreak was attributed to a combination of moisture stress and high temperatures during silking, (day temperatures >40 °C), and severe waterlogging stress after storm rains during late grain fill. Watson (2009) found that *Fusarium verticillioides* was the dominant Fusarium species isolated from grain, peduncles and stalks of affected plants. Stalk rot was not observed indicating that the fungus had endophytically colonized the stalks before invading the cob via the peduncle, a well-recognised phenomenon (Bacon and Hinton 1996). Fumonisin mycotoxins (Marasas et al. 2001) were detected in infected grain and stalks and contributed to the economic impact of the disease. This outbreak illustrates the critical influence of both the timing and severity of stress on stalk and cob rot development in maize, and the endophytic role of *F. verticillioides*. Maize farmers had been unaware of the prevalence of this fungus as previous crops were symptomless. It is presumed that they were colonized endophytically and thus produced high levels of inoculum in residues leading to the high incidence of infected plants in 2003.

### Fusarium endophytes in natural (wild) ecosystems

Fusarium species have been isolated from stems of various tropical grasses from natural ecosystems in northern Australia during systematic surveys over the past 15 years (Summerell et al. 2011). The *Fusarium* species isolated included important pathogens such as *F. proliferatum*, *F. verticillioides*, (Phan 2004), *F. thapsinum* (Walsh 2007) and *F. sacchari* (Petrovic et al. 2013) as well as the newly recognised species, *F. gaditjirrii* (Phan et al. 2004), *F. lyarnte* and *F. werrikimbe* (Walsh et al. 2010). The grasses studied included wild relatives of crop species, namely wild sorghums (*Sorghum* spp.), wild rice (*Oryza australiensis*) and *Coix gasteenii* a wild

relative of maize. The *Fusarium* species isolated are considered to have colonized the stems endophytically as they were sampled prior to senescence. The majority of the grass samples were collected from grasslands remote from intensive cropping areas. Thus it is likely that these *Fusarium* species have had a long association with their respective grass hosts. The following study illustrates the findings summarised above.

Petrovic et al. (2013) studied the *Fusarium* species associated with stems of the endemic wild rice, *Oryza australiensis*, from the Roper River area in the tropical north of the Northern Territory. This savannah woodland area is remote from the major cropping regions of Australia. The stems did not show symptoms of stalk rot on splitting longitudinally. The bakanae pathogen of cultivated rice, *F. fujikuroi*, was not recovered. However *F. sacchari*, the cause of pokkah boeng disease in sugarcane, was isolated, with an isolation frequency of 26 %. Walsh (2007) had earlier recovered *F. sacchari* from *Sorghum interjectum* in the Northern Territory with a similar frequency of isolation. Three of the isolates of *F. sacchari* from *O. australiensis* were tested for pathogenicity to *O. australiensis*, and a commercial cultivar of each of rice, sorghum and maize. These isolates were found to reduce emergence of *O. australiensis* and commercial rice but not sorghum or maize. In contrast lesions were observed on the mesocotyl and crown roots of sorghum and the crown roots of maize in the inoculated treatments. These findings indicate that the isolates tested have some degree of pathogenic potential to these hosts. The association of pathogenic *Fusarium* species with wild relatives of crop plants provides a reservoir of inoculum and a potential source of genetic diversity in respect to pathogenicity and other characteristics. Furthermore it illustrates the importance of understanding the role of endophytic colonization of symptomless hosts when compiling a list of hosts of plant pathogens such as *Fusarium* for regulatory purposes.

### Conclusions and future research challenges

Evidence has been presented to show that natural ecosystems in Australia are a rich source of genetic diversity of *Fusarium*. They are also a reservoir of known and potential pathogens. However little is known about the impact of endophytic colonization on the wild plant host. Consequently studies on *Fusarium* in these ecosystems can contribute to a better understanding of the origin of new pathogens at the species or intra-species level, and their ecology. Indeed the wider Australasian region will undoubtedly continue to be a rich source of undescribed *Fusarium* species associated with wild plant populations given the high level of diversity and uniqueness of the latter, and the wide range of bioclimatic regions. However extensive systematic surveys are also needed of *Fusarium* species in natural ecosystems of Africa, Asia and

South America for example, in conjunction with phylogenetic, host range and related studies if we are to properly understand the ecology, and the extent of genetic diversity in *Fusarium* on a global basis. The late W.C. Snyder often speculated that *Fusarium* evolved in tropical and subtropical regions and these would be a major source of diversity. I suggest that Australasia is one of the ‘hotspots’ of that diversity.

Despite well over 100 years of intensive studies on *Fusarium* diseases major research challenges remain for the younger generation. There are many intractable diseases for which we have IDM strategies that can mitigate but not prevent loss. Indeed many of these diseases still cause serious losses both in developed countries, as well as regions where research and extension services are poorly resourced, FHB being a prime example (Burgess and Bryden 2012). These diseases cause serious socio-economic disruption as discussed above. Furthermore *Fusarium* mycotoxins continue to impact adversely on human and animal health.

Some diseases are re-emerging as a consequence of changing agronomic practices such as no-tillage, an essential practice if we are to achieve sustainable land-use. However I have serious concerns about the aggressive promotion of no-tillage and residue retention practices in regions such as Africa. My concern is that the benefits of such practices may be negated or worse by a dramatic increase in the incidence and severity of diseases such as FHB, caused by residue-borne pathogens. The promotion of new practices must be considered carefully in the context of the local farming systems and culture, and the local capacity to manage the impact on disease severity. I have similar concerns about the introduction and promotion of new crops into countries where quarantine authorities are poorly resourced, and monitoring of incoming plant material is limited or non-existent. This problem is exacerbated where pathogens may be carried in seed or clonal material as endophytes.

One of the major challenges for quarantine authorities is that a checklist of pathogens of one plant species may not include serious pathogens of other plant species that are endophytes in the roots or foliar parts of the species in question. Propagating material of wild plant species is often considered low risk. However the discussion above indicates that this may not be so.

I am delighted that there are many younger scientists world-wide with a passion for *Fusarium* and a wide range of skills with which to confront the challenges outlined above. I maintain my passion for *Fusarium* and it is a privilege and pleasure to work with some of these young scientists in Australia and other countries.

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