

Keynote paper

Fusarium wilt of banana: Global problems and perspectives

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Summary

Fusarium wilt of banana is recognized as one of the most destructive diseases of banana worldwide. In addition to an overview of the history of research into fusarium wilt of banana, a precis of the current global problems posed by this disease to producers and consumers of bananas is presented in this paper. Key issues and opportunities facing scientific researchers in their attempts to find solutions to the management of this disease are also discussed, with reference to the notion of sustainable agriculture.

Keywords: Fusarium wilt, banana.

Introduction

It is a privilege to be invited to present this keynote paper for the international seminar and workshop 'Banana fusarium wilt: Towards sustainable cultivation'. The aim of this paper is to provide a brief overview of the importance of the banana crop, the described history of fusarium wilt of banana and our current understanding of the fusarium wilt pathogen, *Fusarium oxysporum* Schlecht. f. sp. *cubense* (E.F. Smith) Snyder & Hans. (FOC). Some of the unsolved problems posed by fusarium wilt disease to producers and consumers of bananas today will also be presented. Finally, specific problems, key issues and opportunities facing scientific researchers in their attempts to find solutions to this disease will be discussed in reference to the challenge of delivering solutions for sustainable agriculture.

The crop: Bananas, including the many dessert, plantain, cooking, ornamental and native varieties, are an important source of food, fiber and income for millions of people throughout our world, the vast majority of whom are small-holders or subsistence farmers. Globally, the starchy fruit produced from this hardy perennial crop is estimated to be in excess of 76 million tons each year (FAO 1993). Only about 14% of this produce is for export trade. The crop has significant economic importance in many countries where it is grown for national domestic markets and international export trades.

The *Musaceae* is a family of monocotyledons which, through natural events and human selection and domestication over thousands of years, have come

to hold a strong cultural significance in many countries where the diverse *Musa L.* species are grown. From Buddhist temples where specific varieties of fruit hold religious significance, to their vital and colorful place in produce markets, to the production of fiber and intoxicating beverages, the banana is an important part of human culture as well as our diet and livelihoods.

The disease: Plant diseases also influence our culture and history. Fusarium wilt, or Panama disease, of banana is recognized as one of the most widespread and destructive plant diseases in the recorded history of agriculture. In the book *Famine on the Wind*, Carefoot and Sprott (1969) rank fusarium wilt of banana equal in destructive potential as another well known soilborne pathogen *Phytophthora infestans* (Montagne) de Barry which caused the potato famines of the mid 1800s. In the following excerpt, the political nature of plant diseases is also highlighted in the author's analysis of export plantation owners in Central America faced with epidemics of disease in plantations of Gros Michel: "both the Panama disease and Sigatoka tended, through their depredations, to shift the control of land from the small owner to the large and absentee owners . . . the banana companies that were near failure tried to counter every decline in production with larger land grants and other concessions from government in power" (Carefoot & Sprott 1969).

The first description of fusarium wilt of banana was published in 1876 by Joseph Bancroft who described diseased plants of the 'Sugar' (Silk/Pisang Rasthali, AAB) variety observed in Brisbane, Australia. The efforts of Erwin Smith, who in 1910, recovered a fungus from diseased banana tissue from Cuba and named it *Fusarium cubense* E. F. Smith (Smith 1910), were followed by several other workers who reported this pathogen and contributed to its characterization and naming including, Ashby (1913), Brandes (1919), and Snyder and Hansen (1940).

Eras of research on fusarium wilt of banana

i) *The Gros Michel era.* It is meaningful at the time of this symposium to revisit some of the history and context of previous research in fusarium wilt of banana. The first comprehensive review of this disease was provided by Stover (1962), who discussed possible origins and research associated with the Gros Michel epidemics in the American tropics. Although the disease was widely reported around the world by the early 1900s, little sustained research was conducted until the middle of the century. We must gratefully acknowledge the scientific investigations from this time, several of which were carried out in association with the United Fruit Company, for much of our current understanding of this host and disease. Many of the monographs by Norman Simmonds, Harry Stover, Ivan Buddenhagen, Ben Waite, John Rishbeth, Nader Vakili, Carl Beckman, Luis Sequeira and others remain as seminal texts for this host and disease. Research in this era was primarily driven by the widespread destruction of the key export variety, Gros Michel (AAA). Fortunately for the export trades, but not for *Fusarium* research, the strains of FOC that had earlier been introduced into the Americas from their

Asian homelands did not include Cavendish-competent strains and the agronomically superior Cavendish (AAA) clones replaced Gros Michel. Research into fusarium wilt of banana in the American tropics soon came to an end after the resistant Cavendish clones were deployed in the 1960s (Stover & Buddenhagen 1986). Can we imagine a similar situation occurring again when superior disease-resistant varieties are developed and deployed around the world, this time with relevance to the needs of subsistence farmers in different localities, as well as the export trades?

ii) *The Cavendish era: The past decade.* More recently, research into genetic diversity of the pathogen, but not the disease per se, has been influenced by three main factors:

- 1) the development and application of analytical methods such as vegetative compatibility group (VCG) and molecular biology have enabled studies on pathogen diversity and distribution and hypotheses on origins, phylogeny and dispersal;
- 2) the realisation that Cavendish varieties were not immune to fusarium wilt in some parts of the sub-tropics and even in the tropics where they had been commercialized;
- 3) the increased impetus of banana breeding programs targeted at creating bananas resistant to black sigatoka leaf streak disease (*Mycosphaerella fijiensis* Morelet) and at developing new and novel types of bananas.

In 1989, the first international conference on fusarium wilt of banana was held (Ploetz 1990). Much has happened during the past decade that has stimulated more research on pathogen and host diversity, but little on the disease itself. The most striking development that has precipitated more research has been the rapid devastation of more than 5000 ha of newly established Cavendish plantations in tropical Indonesia and Malaysia and more recently in the Northern Territory of Australia, and the fear that this has generated of possible spread to other major export banana producing regions. Some research support has subsequently been generated for collection and genetic analysis of strains of FOC from the centres of *Musa* and FOC origin, evolution and domestication in Asia and has enabled meaningful analysis of the diversity, origin and dispersal of the pathogen (refer to papers by Bentley *et al.* and Ploetz in these proceedings). Also, an increased global effort, primarily through the auspices of INIBAP and also the CFC/FAO-IGGB/World Bank Banana Improvement Program, has enhanced efforts of the collection, identification and maintenance of *Musa* germplasm.

Progress has been made in the past decade, notably in the areas of pathogen diversity studies (Pegg *et al.* 1966, Kistler & Momol 1990, Bentley & Bassam 1996, Koenig *et al.* 1997, Bentley *et al.* 1998, O'Donnell *et al.* 1998), banana breeding and varietal development (notably the programs of FHIA in Honduras, IITA in Nigeria and Uganda, EMBRAPA-CNPMF in Brazil, CIRAD-FLHOR in Guadeloupe and TBRI in Taiwan) and molecular

biotechnology (Sági *et al.* 1998, ProMusa Supplement 1999, refer also to review of the recent symposium on molecular and cellular biology of banana by Ploetz in these proceedings). It is interesting to look back through the papers published from the fusarium wilt meeting held in 1989 (Ploetz 1990) and see that we have answered many of the questions that were posed during that meeting. However, after the two recent decades of research effort and millions of dollars in research funding, banana producers still lose their livelihoods and profits to this disease. Despite our understanding of how this pathogen is spread, the disease is still spreading and threatening the livelihoods of many more communities and increasing the areas of FOC infested agricultural land. For example, recent analyses conducted by the authors confirm that strains of FOC have been moved eastward from Indonesia into Irian Jaya as far as the border with Papua New Guinea, in infected banana suckers (Davis *et al.* 2000). Some of the isolates analysed from these recent outbreaks included the 'tropical' race 4 strain of FOC (VCG 01213/16). These areas were previously free from the disease which poses a great danger to the many unique native *Musa* species and banana varieties grown on the island of New Guinea. Many of the native varieties collected from this region in previous germplasm collecting missions, were found to be highly susceptible to races 1 and 4 of FOC in field evaluation trials conducted in Australia, indicating that they have little natural resistance to this disease (K.G. Pegg, unpublished).

In addition to the failure to put in place effective local protocols to prevent the movement of this disease into new areas, there are also many gaps in our knowledge and understanding of the biology and ecology of this pathogen and we still have a long way to go towards developing and effectively implementing strategies for its management in different banana production systems throughout the world. Some problems and perspectives currently facing the research effort on this disease are subsequently presented.

Problems

The problems associated with this disease are many and offer opportunities for novel and useful research. Some of the current problems presented by this disease have been divided into three categories below namely, undelivered practical outcomes, gaps in our current scientific knowledge and some constraining factors due to the nature of the pathogen itself. While some progress has been made on some of these issues in individual countries or regions, they remain as significant challenges for research programs throughout the world.

1. Practical outcomes yet to be fully delivered

1.1 Reduction in spread of disease by the movement of infected planting material. The lack of application of exclusion protocols and lack of provision to farmers of alternatives to infected vegetative planting material (e.g. tissue culture-derived plantlets, clean vegetative planting material derived from dedicated

disease-free schemes or treatments for rhizome/seed pieces) continues to encourage the dissemination of the pathogen. The lack of appropriate information disseminated locally to reduce the spread and impact of this disease for smallholders is also of major concern in many parts of the world. In addition, the practice of initiating banana germplasm collections by directly planting suckers collected from other regions has also contributed to the spread of this pathogen in some areas of the world. Much more effort is immediately required by local research stations and banana research networks throughout the world to address this practical issue.

1.2 Elimination of shifting agriculture to maintain banana production. The practice of shifting banana production into 'clean' land, often obtained by the clearing of forested areas, to maintain production continues. This is not sustainable and combined with the lack of application of basic farm hygiene and disease management practices to exclude the pathogen from the new areas, they too become infested with the pathogen. For example, with infected planting material or through introduction of contaminated soil attached to vehicles, machinery and implements.

1.3 Widespread deployment of disease resistant cultivars. Resistance to some strains of FOC has been identified in some of the new varieties released from banana breeding programs in recent times e.g. FHIA 01 ('Gold Finger') and FHIA 18 to races 1 and 4 of FOC in Australia (refer to paper by Moore *et al.* and report by Orjeda on IMTP global disease evaluations in these proceedings). However, we still rely heavily on the banana breeding and development programs to generate more cultivars with combined resistance to other pests and diseases (e.g. sigatoka leaf diseases, nematodes, and viruses) to satisfy the unique national and local requirements of smallholders as well as large-scale exporters.

1.4 Decreased susceptibility of tissue culture-derived plants to fusarium wilt. While the adoption of tissue culture-derived planting material in many commercial banana operations has significantly decreased the spread of many banana pathogens, the incidence of fusarium wilt in plants derived from tissue cultured is considerably higher than that observed in plants propagated from suckers or rhizome pieces (Smith *et al.* 1998). Refer to the papers by Smith *et al.* and Hernandez *et al.* in these proceedings for recent developments and to point 2.5 below.

1.5 Enhanced diagnostic capabilities for viruses in tissue-cultured banana plants. Although reliable indexing protocols exist for several viruses of banana, diagnostic capability for a wider range of viruses would improve the safe international movement of banana germplasm. For example, detection of viruses such as banana streak virus (BSV) is sometimes difficult due to incorporation of the virus in the host genome, particularly in varieties with *M. balbisiana* heritage (Geering *et al.* 1999, Harper *et al.* 1999, Ndwora 1999). Improved detection systems are vital for the safe and effective movement of banana germplasm globally and for maintenance of diverse germplasm banks

stored as tissue culture collections.

1.6 Disease control measures for susceptible varieties. Although attempted over many decades, long-term control measures are not yet available for susceptible varieties. Flood-fallowing yielded promising results for the control of fusarium wilt in amenable production systems in Central America in the 1960s (Stover 1962), although Stover later speculated that over time this practice had likely destroyed the wilt suppressive nature of the soils concerned (Stover 1990). Short-term disease management is obtained in some parts of Asia by rotating favoured but highly susceptible banana cultivars (e.g. Pisang Rasthali) with paddy rice, which likely reduces the number of viable spores of FOC due to prolonged anaerobic conditions in the soil. However, if infected banana suckers are then used to re-initiate the banana crop, the FOC population is also maintained. If disease-free plants of these varieties were made available for replanting and basic farm hygiene measures were put in place to prevent the re-introduction of the pathogen into such rotations, it is likely that a nett reduction in the FOC population could be obtained over time allowing the continued production of susceptible clones. In countries where commercial banana plantations are grown as an annual or biennial crop, improvements to this sort of system, for example by the introduction of biofumigant green manure crops or biocontrol agents between each rotation may also have application in allowing the production of susceptible yet highly favoured clones in areas where FOC occurs. The survival of FOC in the rhizosphere of potential rotation crops is largely unknown. Likewise, the long term effect on populations of FOC in soil after incorporation of biofumigant crops such as Vetch (*Vicia villosa* L.) or fodder rapes and mustards (*Brassica* L. spp.) is also unknown and is an area where research is warranted.

1.7 Need for expanded 'race' classification system. The current race classification system for fusarium wilt of banana is in urgent need of an overhaul to allow more meaningful interpretation of the many strains of FOC that have recently been described, particularly since the application of new methods of analysis, expanded disease surveys and more comprehensive isolate collections. Also, the original 'race' system is based on a narrow range of cultivars, primarily the two of greatest importance to export trades, Gros Michel and Cavendish, and does not include many of the varieties and landraces that are currently of interest. While the term race is not strictly correctly applied to this pathosystem, since the differential host cultivars on which it is based are not genetically defined, it has become an accepted term of convenience to broadly describe disease reactions from some strains of FOC to a narrow range of banana cultivars.

Modern methods of analysis including VCG, DNA amplification fingerprinting (Bentley & Bassam 1996, Bentley *et al.* 1998 and Bentley *et al.* in these proceedings), restriction fragment length polymorphism (RFLP) and gene sequencing (Kisler & Momol 1990, Koenig *et al.* 1997, O'Donnell *et al.* 1998) have defined many correlated groups within this pathogen. However,

the pathogenicity of many of these recently described unique groups (VCGs 0123, 0126, 01214, 01217, 01218 and 01219 for example) to a wide range of banana varieties is unknown as they have limited geographic distribution and their host range has thus far only been inferred from the varieties from which the isolates were recovered. In the absence of comprehensive field trials in these areas to determine host ranges, the development of a robust and reliable pathogenicity test that uses small tissue culture banana plants would greatly assist in closing this gap in our knowledge and would contribute valuable information towards a more comprehensive 'race' or host range classification for the many strains of FOC. Furthermore, the inclusion of strains collectively referred to as 'race 3' in any new FOC host range system must be reviewed. In keeping with the original intentions of the host based classification system of *formae speciales* of *F. oxysporum* (Snyder & Hansen 1940), and its subsequent reviews (Gordon 1965, Armstrong & Armstrong 1981), it is proposed by the authors that strains of *F. uluvarum* pathogenic to non-banana hosts such as *Heliconia* L. would more correctly be described in their own *forma specialis* and subsequently their own VCGs (Katan 1999).

2. Gaps in our scientific knowledge

2.1 Resistance mechanisms. What are they in banana and how are they triggered? Are they different for the *acuminata* and *balbisiana* genotypes? At the conference held in Florida in 1989, Carl Beckman highlighted the need for research to understand the recognition systems of host plant tissue and the pathogen and how this translates into responses that successfully defend, in the case of resistant varieties, the plant from systemic colonisation by FOC and subsequent disease development (Beckman 1990). By measuring infection quotients and defense reactions in resistant and susceptible varieties of banana and tomato (*Lycopersicon esculentum* L.) after exposure to pathogenic strains of FOC and of *F. oxysporum* f. sp. *lycopersici* (Sacc.) Snyder and Hans., respectively, Beckman postulated that resistant type reactions may be governed by factors that become immediately operational (i.e. within one hour) of the pathogen coming in contact with host cells, suggesting that a difference in recognition systems may contribute to the resistant or susceptible type reactions. Beckman stressed the importance of understanding the interaction of surface molecules on the cell walls of both host and pathogen in recognition systems as a key to enabling manipulation to improve defense reactions in the host. Little published research from other groups the past decade has significantly furthered our understanding of these issues in the banana-FOC pathosystem.

2.2 Resistance genes. More recently, with the development of transformation systems for banana, efforts have been intensified towards identifying resistance genes for fusarium wilt, black and yellow sigatoka, viral and nematode diseases. Recent advances in the application of biotechnology to banana and plantain were reported at the 'International Symposium on the Molecular and Cellular Biology of Bananas', held at the Boyce Thompson

Institute in Ithaca, NY, USA in 1999 (ProMusa Supplement 1999, see also summary by Ploetz in these proceedings). In brief, genes for resistance to any strain of FOC have not yet been identified but advances have been reported for other fungal pathogens (Sági *et al.* 1999, Wiame 1999).

Once identified, how long, realistically, will it be before these genes can be introduced into the varieties of choice, and reliably maintained and expressed in host plants? Then how long until the transformed resistant varieties can be evaluated in the field and finally disseminated to where they are most needed?

2.3 Markers for resistance. Where host plant resistance is stable and unlikely to break down quickly after deployment, markers to assist in the mapping or identification of resistance genes, in theory, provide significant assistance to conventional and biotechnology assisted breeding programs (Michelmore 1991). Considerable field evidence of durable host plant resistance in banana to some strains of FOC exists. For example, the Cavendish cultivars deployed over vast areas in Central and South America infested with race 1 strains of FOC (VCGs 0124/5) have remained resistant to these strains for more than 40 years. Elsewhere in the world, Cavendish varieties also rarely succumb to these strains of FOC except where plants are grown in sub-optimal condition (Pegg *et al.* 1995). However, in host plants such as the banana that have mostly sterile female fruit, expedient methods to identify markers linked to disease resistance such as bulked sergeant analysis have not been easily applied. While molecular techniques such as isozymes, restriction fragment length polymorphism, random amplified polymorphic DNA, variable number tandem repeats and secondary metabolites have been applied to banana for clonal identification, genetic and systematic studies (Jarrett & Gawel 1995, Ortiz *et al.* 1995), we still lack a definitive molecular or biochemical markers for resistance to the various strains of FOC. Refer to paper by Sariah Meon and Lim in these proceedings for report on recent investigations into biochemical markers for FOC.

2.4 Transformation systems for Cavendish. Transformation systems have successfully been developed for Bluggoe (ABB) and other banana varieties including Pisang Rasthali (ProMusa Supplement 1999) but systems for the favored export clone Cavendish have not been as straightforward in their development. Several groups have been working towards the transformation of the Cavendish clone Grande Naine and some have recently reported success including the group at the Catholic University of Leuven in Belgium (Sági *et al.* 1998, Perez-Hernandez *et al.* 1999) and the Queensland University of Technology in Australia (Becker *et al.* 1999). It is interesting to review the conclusions from the roundtable sessions of the meeting held in Florida more than a decade ago, where Ploetz (1990) reports that "*The genetic transformation of banana with resistance genes remains a distant possibility . . . before more is known of the genetic control of resistance in banana, it is not clear what or how many genes must be transferred in order for resistance to be conferred to recipient lines. Certainly these methods hold promise, but considerable work needs to be done*

before useful results could be expected from such work".

2.5 Stimulation of plant defenses for higher levels of protection against FOC. Research efforts are currently underway in Australia and South Africa to investigate plant defence activators for their efficacy in protecting immature, tissue culture-derived banana plants from infection by FOC and for their ability to induce systemic acquired resistance (SAR) in mature plantations of susceptible cultivars (see papers by Severn-Ellis *et al.*, Smith *et al.* and Moore *et al.* in these proceedings). Promising results have been obtained in Australia using plant defense activators such as BION[®] alone and in combination with strobilurin fungicides (e.g. Amistar[®]) against fungal leaf and fruit pathogens of other crops such as avocado (*Persea americana* Mill.) and passionfruit (*Passiflora edulis* Sims.). Full evaluation against FOC in banana is yet to be completed (refer to paper by Moore *et al.* in these proceedings). If the mode of action of successful SAR agents is to 'turn on' generalized resistance mechanisms in the whole banana plant, such agents may have application against leaf spot fungi as well as vascular fungal pathogens like FOC.

2.6 Reliable glasshouse protocols for assessing resistance in immature banana plants. Although several attempts have been made in the past to develop such a test, reliable data for resistance reaction is still only available by assessing mature plant reaction (to at least first and preferably second ratoon) in fields infested with single strains of FOC. This presents a major time constraint to breeding programs and a drain on research funds, as field evaluation trials are costly and time-consuming to conduct. A reliable small plant test would not replace the need for large scale field evaluations of new varieties or parental breeding lines but it would be useful in reducing the number of varieties selected for inclusion in large scale field evaluations and further development. Such protocols would presumably also have application in determining the efficacy of biological and other disease control treatments in the glasshouse. Refer to paper by A.A. Mohamed *et al.* in these proceedings for update on a new protocol for the evaluation of banana plants.

2.7 Understanding of biological control mechanisms and wilt-suppressive soils. We are still a long way from understanding and applying biological control mechanisms for this pathosystem. Despite the prediction of Marois a decade ago that induced resistance or cross protection would be the most promising approaches for biological control of fusarium wilt of banana (Marois 1990), few protocols giving long-term or broad-scale success by using fungal or bacterial organisms have been widely adopted (see papers by Severn-Ellis *et al.* and Smith *et al.* in these proceedings). Many biological control agents have been reported for fusarium wilts of other crops, several for some decades now (Cook & Baker 1983, Marois 1990, Alabouvette 1999), and yet the principles have not been adopted with broad success for fusarium wilt of banana. Is more research needed to capitalize on previous findings and to develop robust systems for application and establishment of biocontrol agents in banana plantations?

Although wilt-suppressive soils have previously been reported for banana (unpublished work by Volk and Reinking reported by Stover in 1962, Louvet *et al.* 1981, Cook & Baker 1983 & Marois 1990), we still do not fully understand how the mechanisms operate in these soils. Understanding may lead to options for disease control that would be particularly appropriate for sustainable agricultural practices. To undertake such studies for banana will require a long-term commitment of funds and research effort and collaboration with experts in other disciplines such as soil microbiology and biochemistry.

2.8 Simple techniques for quantifying populations of FOC in soil. The development of an easier system for quantifying viable spore numbers or colony forming units of FOC in soil would greatly assist studies of biological and cultural control methods and ecology of FOC populations in association with new banana varieties and potential rotation and biofumigant crops. At present, soil dilution plating can be conducted (Meynell & Meynell 1970), but even with the use of selective media, pathogenic colonies cannot be readily differentiated from non-pathogenic colonies of *F. oxysporum*. Each colony must be analyzed using VCG or DNA fingerprinting methods for reliable identification of the number of colonies that are FOC to enable the subsequent application of most probable number methodologies (Meynell & Meynell 1970). Such analyses are time and resource consuming and preclude the analysis of large numbers of samples. DNA technology and our improved understanding of the genetic diversity between strains of FOC present an opportunity for developing quantitative soil assays for the different strains of FOC that would allow more rapid analysis of large numbers of soil samples. DNA detection systems for the strains of FOC, and the wilt pathogen of cotton (*Gossypium hirsutum* L.), *F. oxysporum* f. sp. *vasinfectum* (Atk.) Snyd. & Hans. that are found in Australia are currently being developed by the authors.

3. Considerations due to the nature of the pathogen

3.1 FOC is a survivor! VCG and molecular data support the theory that this pathosystem is many centuries old and possibly older, and has been distributed around the world from its centre/s of origin by Man. For example, highly popular varieties such as 'Silk' or Pisang Rasthali, have been collected and distributed over several centuries [e.g. Portuguese and Spanish traders are thought to have introduced this variety to the Western Hemisphere (Stover 1962)]. Isolates of FOC collected in South America today are in the same VCG (0124/5) and share the same DNA fingerprint as isolates collected from Pisang Rasthali growing in India and other parts of Asia (Dentley *et al.* 1996). Large banana suckers and rhizomes can remain viable for long periods, as can chlamydospores of FOC if protected inside soil or plant matter, and it is feasible to surmise that with the introduction of bananas to new lands, the strains of FOC with which they were infected were also inadvertently introduced. Modern techniques such as VCG and DNA analysis show that many of the strains of FOC that have been collected from many parts of the

world are identical (Bentley *et al.* 1998) and that most of these strains also occur in Asia.

We now know that the different strains of FOC are very stable over time even despite different host genotypes and different geographic locations (see paper by Bentley *et al.* in these proceedings). This evidence suggests that VCGs are stable, clonal populations and are unlikely to mutate into other more virulent strains as was once supposed. It also suggests that VCG and DNA fingerprint groups are stable markers with evolutionary significance. Current information gathered on this pathogen also presents little evidence that new pathogenic strains readily arise from non-pathogenic populations of *Fusarium oxysporum*. Also, some countries have been 'fortunate' to receive only a small proportion of the total diversity of strains of this pathogen. With consistent enforcement of quarantine measures to prevent the movement of infected planting material, many districts have a good opportunity to remain free from this disease or to limit the strains of FOC to those that are already present.

3.2 Wild and native pathosystems remain unknown. Few in-depth studies have been conducted to understand the ecology of *F. oxysporum* in relation to the many wild and native bananas of the world. One imagines that such studies, particularly in the centre/s of co-evolution of the banana and FOC, could yield useful knowledge with application to understanding resistance and for managing the disease in the domesticated (e.g. plantation) pathosystem.

3.3 Interpretation of modern methods of analysis applied to a diverse pathogen. In applying new and more sensitive analytical methods to this pathogen around the world, we must endeavor to coordinate the results of different analyses to avoid conflicting or unnecessary over-complication of systems to describe this pathogen. It is also of ultimate importance that this characterization of diversity is related to pathogenicity or into useful terms for disease control.

The example of excessive and conflicting description of VCGs will be used to illustrate this point. In conducting several thousand VCG tests over the past decade, variable amenity amongst the Nit M tester mutants used for VCG analysis (Correll *et al.* 1987) has been increasingly observed by the authors and other researchers. A misunderstanding of this trait in the interpretation of VCG test results (based on heterokaryon formation) has in the past led to the inadvertent numbering of 'new' VCGs. With further testing, however, several of the newly numbered VCGs have been shown to be compatible with previously described VCGs and, therefore by definition, members of the same VCG. The application of DNA fingerprinting technology has allowed further insights into the level of genetic diversity and relationships of isolates within and between VCGs of FOC (Bentley 1998, refer also to papers by Bentley *et al.* and Ploetz in these proceedings). Recently, Kistler with the endorsement of many of the researchers involved in conducting VCG and DNA analysis of *F. oxysporum*, nominated an international VCG coordinator (Dr Talma Katan) and proposed protocols to

follow in the testing and description of 'new' VCGs of *F. oxysporum* and its many *formae speciales* (Kistler *et al.* 1998). Corrections, reviews and new information can now be coordinated through this system (Katan 1999, Katan & Primo 1999). In light of recent insights gained from DNA analysis, some of the duplicate VCG numbers for FOC may in future be combined or reverted to their original numerical code to avoid unnecessary complication and over-description of VCGs. For example, the authors were responsible for the numbering of VCG 01216, the strain of FOC known colloquially as 'tropical' race 4. After the generation of more Nit M testers to enable more rigorous VCG testing, it was found that isolates in this group were compatible with isolates in the previously described VCG 01213, hence the current notation indicating cross-compatibility between the VCGs 01213/16. When DNA analysis was applied to this group, it confirmed that isolates in VCGs 01213 and 01216 shared the same DNA fingerprint consistent with the isolates belonging to the same VCG (Bentley 1998).

Perspectives

In this section, some broad perspectives will be presented to stimulate thought about current and future research directions for this disease in the wider context of global developments such as sustainable resource use and biotechnology. Increasingly government policies and funding organizations require 'triple bottom line' (i.e. economic, social and environmental) accounting as a feature of research programs and funding initiatives in agriculture. Not only must research programs demonstrate cognizance of these issues but also they are increasingly required to deliver tangible outcomes and benefits in these areas. Three issues that have implications for future to research into plant disease management are presented here.

1. Sustainability

This symposium is titled 'Banana fusarium wilt: Towards sustainable cultivation'. The notion of sustainability in relation to this disease of banana and potential solutions for its management is not an easy concept to describe. It is also difficult to generalize about the application of such ideals to the diverse banana production needs and systems throughout the world. However, the principles of such notions must be addressed at the local level if improvements in food production are to be made in order to feed an ever-growing world population and to achieve another much talked about global ideal of 'food security'.

Such concepts can be interpreted in many ways. What does the tenor of sustainability mean in relation to plant diseases and how does it impact on future research into management of fusarium wilt of banana? We might we need to develop different disease control strategies to suit new or modified production systems in the near future? For example, in many countries, irrigation water for agricultural production is becoming a depleted resource and new farming systems involving minimum tillage and alternative

irrigation systems are being introduced to conserve soil moisture and reduce irrigation run-off. What impact will this have on the spread and epidemiology of soil-inhabiting pathogens like *Fusarium*? In Australia, water use efficiency is emerging as an essential issue in sustainable farming systems and considerable savings have been made by the installation of below ground drip irrigation systems (e.g. T-tape®) in conjunction with 'permanent bed', minimum tillage and precision farming regimes. Such systems have also been shown to provide benefits to the crop by providing more even moisture in the rhizosphere. However, early gains in water use efficiency and increased crop vigor with such systems in the production of watermelons (*Citrullus lunatus* (Thunb.) Mansf.) have been marred in areas where fusarium wilt occurs. The melon wilt pathogen, *Fusarium oxysporum* f. sp. *niveum* (E.F. Smith) Syd. & Hans., has been reported to spread much more quickly through melon fields where permanent below ground irrigation systems have been introduced (J.K. Kochman, pers. comm.). Control measures for this disease require the use of irrigation system to deliver disease control directly to the plant rhizosphere are not yet available, but they must be found to enable production to continue in the absence of wilt resistant melon varieties. Great potential exists to use these types of irrigation systems to deliver biological or other agents directly to the rhizosphere to enable disease control. Such systems are already used to deliver liquid fertilizers and some systemic pesticides, but without control measures for diseases like fusarium wilt, long term benefits will not be realized for many melon producers. This is just one example highlighting the importance of developing disease control measures in concert with changes in production systems. As plant pathologists, plant breeders, agronomists and extension officers, our recommendations for the future management of diseases do impact on, and contribute to, the efficacy of global efforts towards sustainable food production and we must be mindful of future directions. The development of recommendations for new banana varieties and production systems are examples with potential impact in this area.

How do we presently interpret the notion of sustainability in regard to diseases of banana? Where disease control is currently dependent on heavy annual usage of chemicals, for example for black sigatoka or nematode diseases, one answer is immediately obvious: develop effective non-chemical control solutions that are cheaper for producers and less toxic to the environment and workers. With regard to sustainability and options for control of fusarium wilt, we could interpret our aims narrowly in terms of seeking measures to prop up the continued production of a small number of varieties or a narrow range of cultivation and production methods, e.g. develop a Cavendish with resistance to all strains of FOC. Or, as biological scientists, we could take a broader view of our research in terms of contributing to farming systems that also promote the sustainability of our natural resources (e.g. land - in particular the soil, water and vegetation) as well as enabling disease management. For social and environmental benefit and better cost benefit from research dollars expended today, the second option represents better long term value, particularly if one also considers

the cost of not moving towards environmentally compatible production methods including the future costs of environmental remediation. Such issues may require a change of thinking for some researchers which may more readily be brought about through more focussed setting of priorities and policies governing research funding providers.

2. *Modern technologies and trends in organic production – two different approaches to sustainability*

2.1 *Biotechnology.* It is virtually impossible to work in agriculture today and not be aware of the impact that advances in biotechnology have made to many aspects of research into food and fiber production. This is not the forum for an extensive debate on the virtues or otherwise of biotechnology research and transgenic bananas, but in the context of considering perspectives that may influence future research, a few points are raised in relation to this disease. Due to the expensive nature of biotechnology research and limited funding resources, collaboration to avoid duplication of research efforts in biotechnology should be encouraged. This raises the related issue of ownership of resultant technology and the necessity of ensuring availability of the final products to smallholders in resource poor countries.

While progress in the area of developing and optimizing novel techniques in the field of plant biotechnology has been impressive, in some cases maybe even revolutionary, the time frames originally predicted for the delivery of tangible practical outcomes from this research have been significantly oversold. Many of the claims made over a decade ago have not been realized by banana growers on their farms today. With the exception of some viral pathogens, the identification and manipulation of resistance genes to the pathogens of banana, including FOC, has been more intractable than originally predicted. Furthermore, can we be sure that when such products are finally produced they will be freely available to those in need or will the associated costs and intellectual property issues be prohibitive? Comment on the application of biotechnology to plant, and banana, breeding has been made by Buddenhagen (1996), Ortiz *et al.* (1995), Sági *et al.* (1998) and Vuylsteke (1999). At this point in time, however, it is only the programs that are applying more traditional approaches to breeding or mutation and selection that have successfully released improved banana varieties to banana producers. For example, a combined total of more than 35 new varieties of banana and plantain have been made available to farmers from the FHIA, IITA, EMBRAPA-CNPMP and TBI programs in the past decade.

2.2 *Increasing demand for organic produce.* In many banana export markets such as Japan and Europe, the past decade has seen an enormous increase in the demand for high quality, organically produced fruit. It has been predicted that by 2010, 30% of all food in Europe will be sold as organic (Bauman 2000). In Japan, the market for organically produced food is expected to reach between US\$30 and \$40 billion within the coming decade (Bauman 2000) making Japan the largest per capita consumer of organic produce in

the world. In the United Kingdom, indications are that the increase of 21% a year in consumer demand for fresh and processed organic products is outstripping supply, despite the area of land being farmed organically, or in conversion to organic systems, having more than doubled in the past year to 250 000 ha. These trends suggest that markets for 'clean and green' bananas will only increase in the immediate future and that much opportunity exists for banana producing countries to expand into these markets, particularly with varieties that are amenable to organic production requirements.

2.3 A balanced approach. Extensive organic production is characterized by little or no use of synthetic chemicals to control pests and diseases of traditional or conventional varieties, lower yields (of, in some cases, arguably better tasting produce), greater requirements for land area and labor intensive production. There is a perception that food produced in this way is 'safe' for human consumption and has minimal deleterious impact on the environment. In contrast, genetically modified crops for intensive agriculture systems are characterized by varying degrees of chemical usage depending on whether the varieties have been successfully transformed for multiple pest and disease resistance, a higher yield to land area ratio and relatively lower labor inputs. Perceptions about the 'safety' and environmental integrity of food produced in this way vary widely and are certain to be much debated (hopefully in an informed way!) in the immediate future. Where do the solutions really lie to feed the predicted world population growth in balance with environmental values and the Earth's limited resources? Perhaps they lie in adopting a balanced approach by developing lower intensity production systems that use organic, permaculture or other environmentally responsible principles, supported by a range of genetically modified or traditionally bred varieties with improved pest, disease and drought tolerance and increased yields. It is unlikely that any one global ideal will be broadly applied, as production systems must be adapted for relevance to local situations.

3. Changing consumer needs and trends in fresh and manufactured food

As well as the increasing demand for organically produced foods in lucrative export markets, changes are also occurring in the way that consumers in these markets purchase and consume food. At the recent national banana industry conference in Australia, Professor David Hughes, Chair of Agribusiness and Food Marketing at the University of London's Wye College, highlighted that food marketing is working out what consumers value and are willing to pay for (Hughes 1999). Changes in the European market place included increased consumer demand for greater diversity in the variety of bananas (size, color, price, stage of ripeness, organically produced), more conveniently packaged smaller and sweeter fruit, more processed products with an emphasis on nutritional value (e.g. banana added to dairy products such as yoghurt), and an increased range of outlets now selling food. Many of these changes are being driven by a demand for convenience. The retailing sector is responding to the reduced weekly shopping time of consumers and their desire for high quality, nutritious and convenient foods. The potential

for bananas to expand into these markets is great.

Immediate issues for future research on fusarium wilt of banana

To conclude the following brief list of key points is presented to bring focus to issues that will affect the immediate success of research on this disease and which require our immediate action and collaboration to address.

- Fusarium wilt researchers in every country have a responsibility to instigate practical protocols to avoid spreading FOC to disease-free districts and to avoid the introduction of new strains into areas where limited diversity already exists. This must be enforced as a matter of urgency on a local and regional basis to avoid the needless spread of disease to disease-free production areas and to maintain the production of popular yet susceptible banana varieties in some areas. To be effective, education of banana producers to the real risks of spreading this pathogen and schemes to provide alternatives to infected planting material must be provided. Alternatives to eliminate the practice of 'shifting agriculture' must also be encouraged as part of this initiative.
- Banana breeding and development efforts must continue to be supported to obtain disease resistant varieties. Resistant varieties will be the cornerstone of long-term management of this disease. Coordination and compilation of resistance evaluation data from multiple locations is needed before disease resistant varieties are recommended.
- In evaluating and adopting new, disease resistant varieties in different locations we must be more open minded to the vast range of different attributes of the banana. Banana growers must be encouraged to optimize cultivation, harvesting and ripening practices for new varieties according to varietal characteristics that may be quite different to the susceptible varieties to which they are familiar. Wasted resources and misinformation can be avoided if local banana growers and industries agree to test and adopt new varieties in a progressive and coordinated way with help from local banana specialists or researchers. Ideally, such protocols need to be agreed and put in place before new varieties are released. Effective local systems for the proliferation and distribution of high quality planting material and information on new varieties must also be established, preferably prior to the release of a new variety.
- Critical thought and coordination is required about how to best apply research funds to avoid needless duplication and to focus research effort on delivery of practical outcomes to address local and regional problems.
- Collaboration between individual researchers on fusarium wilt, and other areas of agriculture, is essential for delivery of research outcomes as quickly as possible to banana producers and in response to the global trend toward funding fewer but larger R&D projects. The thematic working groups that have been formed through the INIBAP network to

address some of the current global priorities facing banana production have an opportunity to influence this effort by providing fora for communication, joint priority setting and sharing of research protocols and outcomes. Effectiveness in this aim will require organizations to be supportive of research staff in maintaining and developing links within and beyond the current fusarium wilt research network. Close collaboration between researchers and end users (banana producers and consumers) is also essential for success. The trend toward 'participatory science', where farmers and communities become involved in conducting the research has been shown to be very beneficial in increasing the uptake of new technologies and research outcomes.

We must focus and coordinate our efforts squarely towards these issues if we are to overcome them with meaningful research, development and extension programs that deliver lasting solutions for disease management that are both effective at the local level and relevant to banana production in the future.

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References

- Alabouvette C. 1999. Fusarium wilt suppressive soils: An example of disease-suppressive soils. *Australasian Plant Path.* 28(1): 57-64.
- Armstrong G.M. & J.K. Armstrong. 1981. *Formae speciales and races of Fusarium oxysporum causing wilt diseases in Fusarium: Diseases, biology and taxonomy* (P.E. Nelson, T.A. Toussoun & R.J. Cook, eds.). The Pennsylvania State University Press, PA, USA. 457 pp.
- Ashby S.F. 1913. Banana diseases in Jamaica. *Bulletin of the Department of Agriculture, Jamaica.* 2: 95.
- Bancroft J. 1876. Report of the board appointed to inquire into the cause of disease affecting livestock and plants. Queensland. 1876. *Votes and Proceedings 1877(3):* 1011-1038.
- Bauman T. 2000. *Advancing food and fibre.* Vol. 5. Department of Primary Industries Publications, Brisbane, Australia.
- Becker D.K., B. Dugdale, M.K. Smith, R.M. Harding & J.L. Dale. 1999. Genetic transformation of Cavendish banana (*Musa* spp., AAA group) cv. 'Grand Nain' via microprojectile bombardment in *Abstracts from the international symposium on the molecular and cellular biology of bananas*, Boyce Thompson Institute, Ithaca, NY, USA March 1999, *InfoMusa* 8(1) June 1999. 16pp.
- Beckman C.H. 1990. Host responses to the pathogen in *Fusarium* wilt of

- banana (R.C. Ploetz, ed.). APS Press, St. Paul, MN, USA. 140 pp.
- Bentley S. & B.J. Bassam. 1996. A robust DNA fingerprinting system applied to analysis of genetic variation within *Fusarium oxysporum* f. sp. *cubense*. *J. of Phytopathol.* 144: 207-213.
- Bentley S., K.G. Pegg, N.Y. Moore, R.D. Davis & I.W. Buddenhagen. 1998. Genetic variation among vegetative compatibility groups of *Fusarium oxysporum* f. sp. *cubense* in banana. *Phytopathology* 88: 1283-1293.
- Brandes E.W. 1919. Banana wilt. *Phytopathology* 9: 339-389.
- Buddenhagen I.W. 1996. Modern plant breeding: An overview in *Biotechnology and integrated pest management* (G.J. Persley, ed.). *Biotechnology in Agriculture Series No. 15*. CAB International, Wallingford, UK. 475 pp.
- Carefoot G.L. & E.R. Sprott. 1969. *Famine on the wind*. Angus and Robertson, London, UK. 222 pp.
- Cook R.J. & K.F. Baker. 1983. *The nature and practice of biological control of plant pathogens*. Amer. Phytopath. Soc., St Paul, MN, USA. 539pp.
- Correll J.C., C.J.R. Klittich & J.F. Leslie. 1987. Nitrate non-utilising mutants of *Fusarium oxysporum* and their use in vegetative compatibility tests. *Phytopathology* 77: 1640-1646.
- Davis R.I., N.Y. Moore, S. Bentley, T.G. Gunua & S. Rahamma. 2000. Further records of *Fusarium oxysporum* f. sp. *cubense* from New Guinea. *Australasian Plant Path.* 29: 224.
- FAO. 1993. *FAO Yearbook Volume 46*. Rome: Food and Agriculture Organisation.
- Geering A.D.W., L.A. McMichael, G. Dahal, N.E. Olsewski, B.E.L. Lockhart & J.E. Thomas. 1999. The origins of banana streak badnavirus in *Proceedings of the 12th Biennial Conference of the Australasian Plant Pathology Society*, Canberra, Australia. September 1999. 380 pp.
- Gordon W.L. 1965. Pathogenic strains of *Fusarium oxysporum*. *Canadian J. of Bot.* 43: 1309-1318.
- Harper G., J.O. Osuji, J.S. Heslop-Harrison & R. Hull. 1999. Integration of banana streak badnavirus into the *Musa* genome: Molecular and cytogenetic evidence. *Virology* 255: 207-213.
- Hughes D. 1999. Global food industry developments - What do they mean for us? Keynote address, 3rd Australian Banana Industry Congress, Gold Coast, Australia. May 1999. Extracts reproduced in *BGF Bulletin*, NSW Banana Industry Committee, Murwillumbah, Australia. 63(4) p.1-5 and 63(5) p.10.
- Jarret R.L. & N. Gawel. 1995. Molecular markers, genetic diversity and systematics in *Musa* in Bananas and plantains (S. Gowen, ed.). Chapman and Hall, London, United Kingdom. 612 pp.
- Katan T. 1999. Current status of vegetative compatibility groups in *Fusarium oxysporum*. *Phytoparasitica* 27 (1): 51-56-64.
- Katan T. & P. Di Primo. 1999. Current status of vegetative compatibility groups in *Fusarium oxysporum*: Supplement (1999). *Phytoparasitica* 27 (4): 273-277.
- Kistler H.C. & E.A. Momol. 1990. Molecular genetics of plant pathogenic *Fusarium oxysporum* in *Fusarium wilt of banana* (R.C. Ploetz, ed.). APS

- Press, St. Paul, MN, USA. 140 pp.
- Kistler H.C., C. Alabouvette, R.P. Baayen, S. Bentley, D. Brayford, A. Coddington, J. Correll, M.J. Daboussi, K. Elias, D. Fernandez, T.R. Gordon, T. Katan, H.G. Kim, J.F. Leslie, R.D. Martyn, Q. Migheli, N.Y. Moore, K. O'Donnell, R.C. Ploetz, M.A. Rutherford, B. Summerell, C. Waalwijk & S. Woo. 1998. Systematic numbering of vegetative compatibility groups in the plant pathogenic fungus *Fusarium oxysporum*. *Phytopathology* 88: 30-32.
- Koenig R.L., R.C. Ploetz & H.C. Kistler. 1997. *Fusarium oxysporum* f. sp. *cabense* consists of a small number of divergent and globally distributed clonal lineages. *Phytopathology* 87: 915-923.
- Louvet J., C. Alabouvette & F. Rouxel. 1981. Microbial suppressiveness of some soils to *Fusarium* wilts in *Fusarium: Diseases, biology and taxonomy* (P.E. Nelson, T.A. Toussoun & R.J. Cook, eds.). The Pennsylvania State University Press, PA, USA. 457 pp.
- Marois J.J. 1990. Biological control of diseases caused by *Fusarium oxysporum* in *Fusarium* wilt of banana (R.C. Ploetz, ed.). APS Press, St. Paul, MN, USA. 140 pp.
- Meynell G.G. & E. Meynell. 1970. *Theory and practice in experimental bacteriology*, 2nd Ed. Cambridge University Press, USA. 287 pp.
- Michelmore R.W., I. Paran & K.V. Kesseli. 1991. Identification of markers linked to disease-resistance genes by bulked segregant analysis: A rapid method to detect markers in specific genomic regions by using segregating populations. *Proceedings of the National Academy of Sciences, USA* 88: 9828-9832.
- Ndowora T., G. Dahal, D. LaFleur, G. Harper, R. Hull, N.E. Olszewski & B. Lockhart. 1999. Evidence that Badnavirus infection in *Musa* can originate from integrated pararetroviral sequences. *Virology* 255: 214-220.
- O'Donnell K., H.C. Kistler, E. Cigelnik & R.C. Ploetz. 1998. Multiple evolutionary origins of the fungus causing Panama Disease of banana: Concordant evidence from nuclear and mitochondrial gene genealogies. *Proceedings of the National Academy of Sciences USA*. 95: 2044-2049.
- Ortiz R., R.S.B. Ferris & D.R. Vuylsteke. 1995. *Banana and plantain breeding in Bananas and plantains* (S. Gowen, ed.). Chapman and Hall, London, United Kingdom. 612 pp.
- Pegg K.G., R.G. Shivas, N.Y. Moore & S. Bentley. 1995. Characterisation of a unique population of *Fusarium oxysporum* f. sp. *cabense* causing *Fusarium* wilt of Cavendish bananas at Carnarvon, Western Australia. *Aust. J. of Agric. Res.* 46: 167-178.
- Pegg K.G., N.Y. Moore & S. Bentley. 1966. *Fusarium* wilt of banana in Australia: A review. *Austr. J. of Agric. Res.* 47: 637-650.
- Pérez-Hernández J.B., R. Swennen, G. Saúco & L. Sági. 1999. *Agrobacterium*-mediated transformation of banana embryonic cell suspension cultures in Abstracts from the international symposium on the molecular and cellular biology of bananas, Boyce Thompson Institute, Ithaca, NY, USA March 1999, *InfoMusa* 8: (1) June 1999. 16pp.
- Ploetz R.C. (Ed.) 1990. *Fusarium* wilt of banana. APS Press, St. Paul, MN, USA. 140 pp.

- ProMusa Supplement. 1999. Abstracts from the international symposium on the molecular and cellular biology of bananas, Boyce Thompson Institute, Ithaca, NY, USA March 1999, InfoMusa 8: (1) June 1999. 16pp.
- Sági L., G.D. May, S. Remy & R. Swennen. 1998. Recent developments in biotechnological research on bananas (*Musa* spp.). *Biotechnology and Genetic Engineering Reviews* 15: 313-327.
- Smith E.F. 1910. A Cuban banana disease (Abstr.). *Science* 31: 754-755.
- Smith M.K., A.W. Whiley, C. Searle, P.W. Langdon, B. Schaffer & K.G. Pegg. 1998. Micropropagated plants are more susceptible to *Fusarium* wilt than plants grown from conventional material. *Aust. J. of Agric. Res.* 49: 1133-1139.
- Snyder W.C. & H.N. Hansen. 1940. The species concept in *Fusarium*. *Amer. J. of Bot.* 27: 64-67.
- Stover R.H. 1962. Fusarial wilt (Panama disease) of bananas and other *Musa* species. Commonwealth Mycological Institute, Phytopathology Paper 4. 117pp.
- Stover R.H. 1990. Fusarium wilt of banana: Some history and current status of the disease. pp. 1-7 in *Fusarium wilt of banana* (R.C. Ploetz, ed.). APS Press, St. Paul, MN, USA. 140 pp.
- Stover R.H. & I.W. Buddenhagen. 1986. Banana breeding: Polyploidy, disease resistance and productivity. *Fruits* 41: 175-191.
- Vuyksteke D.R., J. Hartman & A. Tenkano. 1999. Breeder's perspective on biotechnology for *Musa* improvement in Abstracts from the international symposium on the molecular and cellular biology of bananas, Boyce Thompson Institute, Ithaca, NY, USA March 1999, InfoMusa 8: (1) June 1999. 16pp.
- Wiame I., I. Engelborghs, R. Swennen & L. Sági. 1999. Characterisation of resistance gene analog and adaptation of cDNA-AFLP in banana in Abstracts from the international symposium on the molecular and cellular biology of bananas, Boyce Thompson Institute, Ithaca, NY, USA March 1999, InfoMusa 8: (1) June 1999. 16pp.