Philosophical Transactions of the Royal Society B

Fungal pathogens impact trade in food and fibre: names are not enough

Pedro W. Crous[1,2,3], Johannes Z. Groenewald[1], Bernard Slippers[4], and Michael J. Wingfield[2]

[1]CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands
[2]Department of Microbiology and Plant Pathology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, P. Bag X20, Pretoria 0028, South Africa
[3]Microbiology, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands
[4]Department of Genetics, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, P. Bag X20, Pretoria 0028, South Africa

Author for correspondence:
Pedro W Crous
e-mail: p.crous@cbs.knaw.nl

Global trade in food and fibre crops is seriously impacted by fungal pathogens. Fungal species that cause plant diseases have hitherto mostly been recognized based on their morphology; knowledge of which is communicated via a binomial naming system. However, names based on a phenotype are generally disconnected from crucially important knowledge such as mating types, host specificity, life cycle stages and population structures of the fungi. Despite these problems, the majority of the fungal species are described without even basic barcoding information, let alone ecological or genomic data. Such information is essential to accurately identify most fungi, and to understand their potential impact on productivity or natural ecosystems. Because international trade in agricultural and forestry products, and consequently the introduction of pathogens to new areas will continue and likely grow, there is an urgent need to reconsider the manner in which fungal pathogens linked to trade are identified and treated. The Linnaean naming system is insufficiently informative to deal with future challenges. To address these issues, scientists must embrace new technologies to provide the required knowledge. A new information system to govern the manner in which pathogens linked to trade are treated is required, including the data needed in everyday decision making policies.

Keywords: cryptic species; food and fibre; global trade; naming of fungi

1. Introduction

Global trade in food and fibre products has become a way of life, and this will increasingly underpin a healthy global economy. Current estimates of a world population of 9.1 billion people projected by 2050, changing diets and consumption patterns, and the increasing inability of some regions of the world to produce sufficient food for local consumption (www.fao.org), suggest that 1) intercontinental movement of agricultural and forestry produce will increase, and 2) production of produce will need to become more efficient to meet ever increasing needs. Thus pre- and post-harvest losses, whatever the cause, will be increasingly intolerable.

Importing countries will always be vulnerable to accidental introductions of new and potentially devastating plant pathogenic fungi (Desprez-Loustau *et al*. 2007; Hantula *et al*. 2014; Wingfield *et al.* 2015). Quarantine systems, including trade restrictions from areas where pathogens occur, required treatment of goods and inspections for infected material, are intended to reduce this risk. Given the increasing volume of trade around the world, including in live plants and fresh produce, the capacity to apply these systems is wholly inadequate. Furthermore, the rate at which goods move is also increasing, which further exacerbates the risk. For example, bananas grown in South America are served in European households within days of harvest. This implies that the window of opportunity to intercept, identify and act on a potential invasion is minute at best (Liebhold *et al*. 2012).

The challenge to quarantine systems is complicated by the fact that many pathogens remain undetected as latent infections in apparently healthy tissue (Palmer & Skinner 2002; Slippers & Wingfield 2007). It is also relevant that most well-known fungal plant pathogenic species are primarily known from a specific suite of disease symptoms and general morphology based on only a part of their life cycle (Wingfield *et al.* 2012). Once they are studied more intensively, especially utilising modern molecular tools, they are commonly found to represent species complexes (Crous & Groenewald 2005). Pathogen detection that relies on visual inspections based on morphology is quite evidently unable to effectively identify the threats posed by fungi found in traded plant and plant product exports.

Quarantine systems have traditionally relied on fungal names, which is increasingly being shown as simplistic and ineffectual. Beyond the species level, knowledge relating to mating types, and even clones of particular pathogens, is crucially important when seeking to understand or manage fungal invasions (McDonald & Linde 2002, McTaggart et al. 2016). Or, for example, small dispensable chromosomes carrying genes involved in pathogenicity, which can be present or absent in isolates belonging to the same species, resulting in the loss or gain of the ability of a species to infect a specific host, e.g. *Alternaria alternata* (Woudenberg *et al.* 2015), and *Fusarium oxysporum* (Jonkers *et al*. 2014). To further complicate matters, quarantine lists with names as actionable organisms are found only in inaccessible national databases that are frequently not linked to relevant data, or that are not consistent with modern taxonomic treatments of the species in question.

Although it is unknown how many species of fungi occur on Earth, and estimates range anywhere from 1.5 to several million (Hawksworth & Rossman 1997; Blackwell 2011; Crous *et al*. 2015), we must conclude that the majority of species have not yet been seen or recorded (Hibbett 2016). Communication relating to these species by means of the Linnaean naming system that remains largely linked to the phenotype, and detached from the genotypic reality (Hibbett & Taylor 2013; Hibbett 2016). It is clearly not sufficiently informative to deal with future food and fibre security challenges. In this review we consider several of these issues, and approaches that could help traverse seemingly unnecessary barriers to efficient identification procedures and management of fungal threats linked to global trade in agricultural and forestry products. We illustrate our examples by using a broad range of common fungal pathogens important to agriculture and forestry. They have been chosen from the *Dothideomycetes* and *Sordariomycetes* because these fungal classes include thousands of well-studied plant pathogenic species.

2. One fungus, but which name?

Scientific names remain the basis of how we communicate regarding species of phytopathogenic fungi, also with regards to quarantine. Names are ideally linked to knowledge of the biology, distribution, ecology, host range, control, and risks associated with fungal pathogens. The concept of pleomorphism relates to the fact that many ascomycetous fungi are known by either their sexual, asexual or synasexual morphs, to which different names have been attributed based on their morphology; commonly referred to as dual nomenclature (Hawksworth 2011; Taylor 2011, Crous *et al.* 2015).

In practise, this means of identification has meant that a single fungus could be listed on the quarantine list of a country under any one of three valid names (e.g. apple scab caused by *Venturia inaequalis*, asexual morph *Fusicladium pomi*, or synasexual morph *Spilocaea pomi*; Schubert *et al*. 2003), and this is in a conservative scenario where known synonyms are also not considered. Other than having different names to contend with, quarantine officers are also faced with the difficult reality that many reported asexual-sexual relationships have never actually been experimentally confirmed, and might thus be incorrect. For example, *Cylindrocladium parasiticum*, the causal agent of Cylindrocladium pod rot of peanut was linked to *Calonectria ilicicola* (Crous *et al*. 1993), while *Cylindrocladium ilicicola* was later shown to be the asexual morph of *Calonectria lauri* (Lechat *et al*. 2010).

Following the "*One Fungus: One Name*" symposium, and the publication of the "*Amsterdam Declaration on Fungal Nomenclature"* (Hawksworth *et al*. 2011), several radical changes were proposed to the code of nomenclature that govern the naming of fungi (Hawksworth 2011). This subsequently led to the amendment of International Code of Nomenclature for Algae, Fungi and Plants (ICN) (Article 59) to abolish the use of dual nomenclature, as well as other sensible changes such as registration of nomenclatural details of fungal novelties in a database such as MycoBank (Crous *et al*. 2004), the acceptance of electronic and English (as alternative to Latin) publication of new names and descriptions (Hawksworth 2011; Taylor 2011).

Moving to a single name for a plant pathogen was strongly supported by the plant pathology community (Wingfield *et al*. 2012) that needed to have meaningful names for species associated with important plant diseases. In the short term, the changes to the ICN code, together with the increased understanding of systematic relationships amongst fungi based on more representative DNA sequence based phylogenies, has resulted in a large number of taxonomic revisions in recent years. While these name changes might have caused confusion for plant health and quarantine practitioners in the short term, the more accurate application of generic names based on solid genetic support will ensure longer-term stability in the use of names. Appropriate names of fungal pathogens was also important for fundamental plant pathology research, such as various 'omics' approaches aimed at a fundamental understanding of plant-pathogen interactions through comparisons amongst related species. Past taxonomic treatments lead to confusion in this regard such as for example, genome comparisons of "*Mycosphaerella*" that were frequently among members of different genera, e.g. *Zymoseptoria tritici* (Quaedvlieg *et al*. 2011; Stukenbrock *et. al*. 2012), *Pseudocercospora fijiensis* (Crous *et al.* 2013; Chang *et al.* 2016), and *Dothistroma septosporum* (Barnes *et al*. 2004; de Wit *et al.* 2012). The same applied to genera treated under the name "*Magnaporthe*", e.g. *Nakataea* versus *Pyricularia* (Zhang *et al*. 2011; Klaubauf *et al*. 2014), "*Botryosphaeria*" (Crous *et al.* 2006; Phillips *et al*. 2013), "*Ceratocystis*" (De Beer *et al.* 2014), and *Fusarium* (Lombard *et al*. 2015; O'Donnell *et al.* 2015).

Unfortunately, many genera and species remain unrevised or devoid of critical data that would allow for accurate identification and phylogenetic placement. During the period 2000–2013, 1833 fungal genera were described for which only 155 (8.4 %) have types linked to reliably annotated ITS nrDNA sequence data in public databases (Crous *et al*. 2014). This implies that the number of newly described fungi lacking DNA data continues to increase rather than decrease. In an attempt to alleviate this problem, "The Genera of Fungi" project was launched, with the aim of sequencing, restudying and/or recollecting the type species of genera of fungi, focusing on a subset of names that are currently accepted (Kirk *et al*. 2013; Crous *et al*. 2014). Furthermore, to assist plant pathologists to know which generic names they should apply to pleomorphic genera, committees under the auspices of the International Commission for the Taxonomy of Fungi have been tasked with preparing lists of accepted names recommended for use, i.e. *Dothideomycetes* (Wijayawardene *et al*. 2014; Rossman *et al*. 2015b), *Erysiphales* (Braun & Cook 2012), *Eurotiales* (Samson *et al.* 2014; Visagie *et al*. 2014), *Leotiomycetes* (Johnston *et al*. 2014), *Diaporthales* (Rossman *et al.* 2015a), *Hypocreales* (Rossman *et al*. 2013; Quandt *et al.* 2014), *Magnaporthales* (Zhang *et al.* 2016), *Microascales* and *Ophiostomatales* (De Beer *et al.* 2013), and plant pathogenic fungi in general (Rossman & Palm-Hernández 2008; Rossman *et al*. 2015b, 2016). These names will be evaluated by the Nomenclature Committee for Fungi, and formally accepted or not at the Nomenclature Session of the 2017 International Botanical Congress to be held in Shenzhen, Southern China. It is critically important that plant pathologists take note of these efforts and support them with urgency.

3. Latent or endophytic fungal infections

There are a great many plant pathogenic fungi that cause latent infections. These represent a particularly difficult challenge for international trade and associated quarantine measures. Latent infections involve a parasitic relationship between a pathogen and a host that might remain asymptomatic for some period of time but that eventually induce disease symptoms (Verhoef 1974). In this situation, a pathogen remains latent until environmental or nutritional conditions or the stage of maturity of the host or pathogen induces it to produce symptoms of disease (Agrios 2005). A few pertinent case studies are discussed below.

Species of *Colletotrichum* are commonly associated with anthracnose diseases on numerous host plants worldwide (Cannon *et al*. 2012). Anthracnose disease of strawberry is a particularly serious problem for commercial fruit production (Freeman & Katan 1997), which resulted in *C. acutatum* being listed as a regulated plant quarantine pest by the European and Mediterranean Plant Protection Organization (EPPO) and the EU Council Directive 2000/29 Annexes I and II from which it was removed in 2009. Sources of inoculum include infected plants, weeds and other hosts (McInnes *et al.* 1992; Parikka *et al.* 2006), while the pathogen is also well-known to survive via latent infections on strawberries (Parikka & Lemmetty 2004). Because these infections are frequently not observed by visual inspections, they ultimately cause major post-harvest problems, which can lead to huge economic losses (Everett 1997). To complicate matters further, Damm *et al*. (2012) recently separated the morpho-species *C. acutatum* into 31 taxa, of which 21 were shown to represent novel species. Furthermore, *C. acutatum* was shown to be rare in Europe, and then mostly on ornamental plants, while five other species in the *C. acutatum* complex were found to actually occur on strawberries (Fig. 1). Under these circumstances, it is difficult to imagine how quarantine can be applied through attempts at visual inspection for symptoms or morphological identification of species.

The genus *Botryosphaeria* is commonly associated with stem cankers, leaf spots and fruit rots of many hosts (Mehl *et al*. 2011). Diseases caused by *Botryosphaeriaceae* mostly follow the onset of stress (Slippers & Wingfield 2007). Smith *et al*. (1996) first demonstrated that species of this family commonly occur as latent infections in apparently healthy tissue.

Many species of *Botryosphaeriaceae* are known to exist via localized, latent infections in their hosts, which appears to be a common characteristic of this group. The eventual outcome of these infections are often unclear; some species of *Botryosphaeriaceae* can remain latent for many years as localized infections deep inside woody or other tissues. *Diplodia sapinea* for example, which is a commonly occurring pathogen of *Pinus* spp., is well-known to exist via latent infections in its hosts, including in wood of stems, branches, twigs, seed cones and (to a limited extent) seed (Burgess *et al.* 2001; Smith *et al.* 1996, 2000; Bihon *et al.* 2011). It has evidently been introduced with its host multiple times around the world (Burgess et al. 2001; Bihon et al. 2011). Similarly, *Botryosphaeria protearum* was isolated as latent pathogens on South African *Proteaceae* in their native habitat, and also from Australia, Madeira Islands and Portugal where these plants are grown commercially (Denman *et al.* 2003). Many of these species have broad host ranges, such as *Neofusicoccum parvum*, *Botryosphaeria dothidea*, *Lasiodiplodia theobromae* and others (Slippers et al. 2004; Slippers & Wingfield 2007). Once introduced in a new area as latent infection or endophyte on one host, they can easily move to other hosts where these otherwise “innocent” endophytes become serious pathogens.

The *Mycosphaerellaceae* comprises one of the largest families in the Phylum *Ascomycota*, in which some species have evolved as latent pathogens, saprophytes or symbionts. For example, while studying species in the genus *Lecanosticta*, including the important pine needle pathogen *L. acicoloa*, Quaedvlieg *et al.* (2012) described several phylogenetically closely related novel species isolated as latent pathogens from asymptomatic pine needles collected in Mexico. Species of *Pseudocercospora* are commonly associated with leaf spots, with some taxa such as *P. angolensis* on *Citrus* (Quaedvlieg *et al.* 2012), and *P. fijiensis*, *P. musicola* and *P. eumusae* on *Musa* (Chang *et al.* 2016) being of major quarantine concern. Other than these examples, a great number of species from diverse genera in the *Mycosphaerellaceae* are commonly isolated as latent pathogens, occurring on a wide range of asymptomatic host plants (Crous *et al.* 2013).

During a recent study on Citrus greasy leaf spot disease in China, numerous species of *Cercospora*, *Pallidocercospora*, *Passalora*, *Pseudocercospora*, *Verrucisporota* and *Zasmidium* were isolated as latent infections from greasy leaf spot-like disease symptoms (Huang *et al.* 2015). Several novel *Zasmidium* species were recognized on *Citrus*, and one, namely *Z. citri-griseum*, appeared to have a wide host range including *Acacia*, *Citrus*, *Eucalyptus,* and *Musa*, as well as a global distribution (Huang *et al.* 2015). Host specificity, or the lack thereof, adds a different level of risk to exporting produce harbouring plant pathogenic fungi. Other genera that include species commonly encountered as latent pathogens, and that frequently also have wide host ranges are *Chrysoporthe* (Rodas *et al.* 2005; Nakabonge *et al.* 2006), *Diaporthe* (Gomes *et al.* 2013), *Pestalotiopsis* (Maharachchikumbura *et al.* 2014), *Alternaria* (Woudenberg *et al.* 2015), *Phoma* (Chen *et al.* 2015), and *Fusarium* (Herron *et al.* 2015), to name but a few. The key issue illustrated by these examples is that many genera include important plant pathogens that have a latent phase in their life cycles. This easily leads to unwanted introductions, further complicated by the fact that these pathogens frequently also have wide host ranges.

4. Cryptic species, mating types and clones

When does a quarantine organism stop being regarded as an “actionable organism”, e.g. when does it become accepted as established and “present” in a specific country? An important fact to consider in this regard is that a species is not ‘one dimensional’ as a name on a list suggests. Rather, it is a complex or pool of different “sexes” or mating types, virulence factors and genes, linked to a host or hosts, forming a relationship that is influenced by climate and a range of other environmental factors. Furthermore, many pathogens harbour cryptic species that pose a particular problem with regards understanding invasion and potential quarantine (e.g. Perez et al. 2011; Sakalidis et al. 2013). Crous & Groenewald (2005) stated “*Show me a plant pathogen, and I will show you a species complex*” capturing the fact that this is virtually true for all pathogens that have been thoroughly studied.

Ascomycetous fungi can reproduce either asexually or sexually, and in the latter case typically have two sexual mating types that are needed for mating to occur (Ni et al. 2011; Taylor et al. 2015). Understanding these cycles is critical for disease management. This is because it significantly affects the ability of the fungus to overcome resistance mechanisms of its host; with sexually reproducing strains having an advantage (McDonald & Linde 2002). Mating types should therefore have significant relevance for the status of quarantine organisms. For instance, *Dothistroma septosporum*, the causal agent of Red Band Needle Blight, has been introduced into many countries. By generating the mating-type primers for this pathogen, Groenewald *et al*. (2007) were able to show that although the species was introduced into South Africa, Australia and New Zealand, both mating types were present in South Africa (i.e. sexual recombination possible), but only a single mating type can be found in Australia and New Zealand (i.e. sexual recombination not possible). It is, therefore, not only the species, but also the mating types that are of quarantine concern.

In addition to mating types, specific and even clonal lineages within a pathogen population have relevance to quarantine. Bananas represent one of the important global staple food crops, having evolved in the Indo-Malayan archipelago. Panama disease, which is caused by *Fusarium oxysporum* f.sp. *cubense* (Foc), appears to also have originated in Southeast Asia (Ordonez *et al*. 2015). Based on molecular studies, it appears that Foc is a haploid asexual pathogen with a clonal population structure, and that temporal and spatial dispersal of Tropical Race 4 is actually due to a single clone (Ordonez *et al*. 2015). If additional clones were thus to move from Southeast Asia, the disease would become even more difficult to manage because a broader range of cultivars are likely to be affected. Furthermore, horizontal gene and chromosome transfer provide a means for lineages to broaden their host range, and influence their pathogenicity, which has been noted in several genera, including *Fusarium* (Mehrabi *et al*. 2011).

In some genera of phytopathogenic fungi, the name masks variation in host specificity and pathogenicity that is present below the species level. Although such variation in plant pathogenic fungi is often found to represent several cryptic species, the opposite situation also occurs. One case in point is the *Alternaria alternata* species complex, to which the quarantine species *A. mali*, causal agent of Alternaria blotch of apple, belongs. Woudenberg *et al*. (2015) employed whole genome and multi-gene analysis to reduce 35 *Alternaria* morpho-species to synonymy under the older name, *A. alternata*. The authors concluded that it is the presence or absence of the gene cluster that codes for a specific toxin that is of quarantine concern, and not necessarily a specific synonym of *A. alternata*.

5. Host range and assessing risk

The host range of fungal pathogens can vary greatly, from those that are cultivar-specific to others that infect numerous host families or orders. For the majority of fungi that are known, the true host range is poorly understood. For the undescribed fungi, which represent the vast majority, host range is impossible to predict. This creates particular problems with the naming of plant pathogenic fungi, but also for using the Linnaean binomial system to assess quarantine risk of fungi. For example, above we discussed the *Botryosphaeriaceae* that are frequently introduced into new regions as latent infections on plants or plant products, from where they can spread to a large number of other hosts with unpredictable disease outcomes. There are many other such examples, of which we present three that are particularly prominent.

In the past, the names of many fungi were based on the host from which the fungus had initially been isolated. The now famous quote by F.C. Deighton regarding the way that plant pathologists have treated the cercosporoid fungi in the past, reflects on this approach: *"If a sparrow flies to a cherry tree, it's a cherry tree sparrow. If the same sparrow sits in an apple tree, its an apple tree sparrow"*. With literally thousands of hosts, and a very reduced suite of available morphological characters, this system was only contested once pathologists began to cross-inoculate *Cercospora* species on vegetables and finding that single species thought to be host-specific actually had wide host ranges (Groenewald *et al.* 2013). Based on morphology, Crous & Braun (2003) treated 281 morphologically similar *Cercospora* species as synonyms of *C. apii sensu lato.* The advent of DNA sequence -based phylogenetic studies has shown that many of these are actually distinct operational species units, namely *C. apii* on *Apium graveolens* (celery) and *C. beticola* on *Beta vulgaris* (sugarbeet) (Groenewald *et al*. 2005). A radiation of species within this complex has also been observed in subsequent studies (Groenewald *et al*. 2013; Bakhshi *et al*. 2015), suggesting that Deighton was not necessarily incorrect and that in many cases these were in fact distinct taxa; Deighton merely underestimated the number of similarly looking "birds" that can visit the same "tree". In *Diaporthe,* however, host specificity seems to be the exception, rather than the rule. In studying Diaporthe cane and leaf spot of grapevines, Van Niekerk *et al*. (2005) identified 15 species, many of them known to occur commonly on other hosts. The same phenomenon has also been observed in more recent studies on this group, e.g. Gomes *et al*. (2013). Although some species are host specific, the general trend for the *Diaporthe* appears to be a lack of host specificity, suggesting that published literature predating 2005 must be treated with great caution.

Uncertainty about names linked to specific hosts can extend well beyond different plant hosts. Pathogens that are reported to cause disease in both plants and humans tend to attract considerable attention. A particular example are species the genus *Phaeoacremonium* (Crous *et al*. 1996), which is associated with Petri Disease of grapevines, where they can cause up to 50 % losses in newly planted vineyards (Pascoe & Cottral 2000). Importantly, species of *Phaeoacremonium* also cause opportunistic phaeohyphomycosis in humans. In a study on clinical isolates, Mostert *et al*. (2005) described nine new species, six of which were associated with opportunistic human infection. Presently seven *Phaeoacremonium* species have been isolated from woody plants and human infections (Gramaje *et al*. 2015), with numerous species shown to have wider host ranges on different genera of plants. *Phaeoacremonium* species infecting humans can grow at 37 °C, with the exception of *P. inflatipes* that has a maximum growth temperature of 35 °C. Published reports suggests that arthropods, collembolans and mites could carry *Phaeoacremonium* spores adhering to their body (Edwards *et al*. 2001), but many questions remain unanswered relating to their pathology, ecology and sexual reproductive strategies where some species are homothallic while others are heterothallic (Mostert *et al*. 2006). These examples not only illustrate the problem of using host range to justify novel species descriptions, but also the difficulty to predict risk to other hosts.

Species of *Phyllosticta* are common plant pathogens associated with a broad host range, causing leaf and fruit spots. The genus includes taxa such as *P. capitalensis,* which is isolated as a common endophyte from a very wide host range and distribution, where it frequently co-occurs with plant pathogenic species (Wikee *et al*. 2013a). Other species appear to be more host-specific and of quarantine concern, e.g. *P. citricarpa,* the cause of citrus black spot (Baayen *et al.* 2002; Glienke *et al.* 2011), as well as *P. citriasiana*, *P. citrichinaensis* and *P. citrimaxima,* which also cause similar disease symptoms on *Citrus* (Wikee *et al*. 2013b). Recent surveys of *Phyllosticta* species associated with citrus black spot disease symptoms suggest that the general symptomatology on *Citrus* fruit, and simplistic *Phyllosticta* morphology, has clouded the true variation that occurs in this this disease complex. Freckle disease of banana, which was in the past associated with *Phyllosticta musarum,* has also recently been revealed to be associated with a complex of *Phyllosticta* species, all of which are specific to their banana hosts (Wong *et al.* 2012). Prior to the common application of DNA sequenced-based phylogenetic inference species of *Phyllosticta* have mainly been named based on their host association. However, it is now clear that the genus includes both host-specific and plurivorous species. Consequently, a concerted effort will be required to recollect fungi linked to the approximately 3000 names known in the genus and thus to clarify questions relating to their host specificity.

6. Conclusions

Global trade in food and fibre is facing major challenges related to fungal pathogens. Although we have tried to address some of these issues in this review, it is clear that major fundamental hurdles remain. A major issue is the present ICN, which governs the naming of fungi, and essentially allows plant pathogenic fungal species to be described without DNA data. This leaves researchers and practitioners trying to play “catch-up” at huge additional cost, having to recollect and thus provide molecular data for described plant pathogens. If the ICN does not address this problem, mycologists will have to seriously consider suggestions to adopt their own code of nomenclature (Taylor 2011; Hibbett & Taylor 2013). There is an urgency in this regard given the extent to which the current code hampers progress and application of broadly accepted best practices. This is not only to the detriment of mycology, but also to global food and fibre production, as well as ecosystem health. A new system must also allow for more permanent and traceable names or codes linked to environmental sequences (where no culture might exist) to be described, as well as diversity below the species level.

A second major constraint to effective quarantine is the poor linkage between resources that carry layers of information about plant pathogens. Unfortunately there is a general lack of support to maintain and link databases such as Q-bank (http://www.q-bank.eu/), MycoBank (http://www.mycobank.org/), Index Fungorum (http://www.indexfungorum.org), UNITE (https://unite.ut.ee/), GenBank (http://www.ncbi.nlm.nih.gov/), and the ARS-USDA fungus-host distribution database (http://nt.ars-grin.gov/fungaldatabases/fungushost/fungushost.cfm), to name but a few. Each of these databases includes unique information about species, their identification, strains, hosts and much more. Linking them appears to be “low hanging fruit” from a global quarantine and plant health management perspective. Doing so would immediately unlock large amounts of data for important pathogens around the world. Only specialists who understand the intricacies of navigating this maze of data resources can currently access much of this information.

A third major constraint is the general lack of proper, well-characterised reference specimens and/or cultures of quarantine and related species in public-accessible collections (see review by Stackebrandt *et al*. 2014). Such biological resource centres also are under constant threat of decreasing budgets and increasing costs, which could result in invaluable cultures being lost to future generations of mycologists, plant pathologists and other end users. These reference specimens are critically important for the establishment of a reliable barcoding system. Yet, as handy as DNA barcodes are as tools for species recognition, the real value of these collections will emerged once the fungal genomes have been analysed, e.g. using secondary metabolites to infer ecology, the identification of pathogenicity factors, transposable elements, as well as life-cycle and population structure (Orton *et al*. 2011; McTaggart *et al.* 2016). There is a growing realization that not only future biological studies, but also future quarantine and management will be reliant on this information. If we are serious about reducing the impact of fungal pathogens on trade in food and fibre, a fundamental change in how we operate will be required. Names, morphology and visual inspection for fungal pathogens are simply not enough.

Figure 1.

Parsimony phylogeny depicting the host range and geographic distribution of strawberry-associated species belonging to the *C. acutatum* species complex. Strains from *Fragaria* are indicated in red text and the branches and micromorphology photos of the different fungal species are colour-coded. The species *C. godetiae* and *C. nymphaeae* include the largest number of strains isolated from *Fragaria*. The tree was rooted to *C. orchidophilum* CBS 632.80 and the length of the outgroup branch represents 77 changes. The alignment is based on a subset of the 6-locus alignment of Damm *et al*. (2012), which was downloaded from TreeBASE (study number 12762; http://purl.org/phylo/treebase/phylows/study/TB2:S12762). All species that did not include *Fragaria* isolates were removed from the alignment, as well as additional isolates from the same host and country per *Colletrichum* species. GenBank accession numbers, detailed collection information and additional photoplates per species are available in Damm *et al*. (2012).

References