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IN SEARCH OF NEW *FUSARIUM* SPECIES

ABSTRACT

Fusarium is a large fungal genus, but scientists who work with it continue to search for new species to help bridge perceived phylogenetic gaps and to assess the biogeography of species origin and distribution. Potential new sources for species include collections made from plants and soil in native ecosystems and subsistence agriculture farms. These ecosystems are less likely to have suffered anthropomorphic changes and may offer the best hope for identifying previously undescribed species and for obtaining reliable data on species distribution. In addition to new collections, new species also may result from the break-up of a number of large species complexes that are held together primarily by morphological similarities. The two approaches are complementary and should collectively help to increase the number, diversity and quality of the species known within the genus.

Key words: Fusarium, native ecosystems, species concept, subsistence agriculture.

INTRODUCTION

Fusarium is a genus in which the number of species has ranged from less than 10 to more than 1000, with the current number of described and generally accepted species between 70 and 500 (Kirk *et al.*, 2001; Leslie *et al.*, 2006). The focus in the genus has been on species whose strains either can produce mycotoxins or cause a disease on an economically important plant. Yet these fungi are ubiquitous in soil from almost any location in any climate worldwide, with many of these fungi placed into one of two large species complexes, *Fusarium oxysporum* or *Fusarium solani* and little characterization beyond a quick mor-

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phological characterization. These fungi and those that are found in non-agricultural areas or associated with subsistence cropping systems are largely uncharacterized. Until recently, when such strains were identified, they were often placed into an already known well-described species, even if the fit was "not quite right." Thus, it is likely that the evaluation of strains from previously unexamined habitats as well the redescription of strains that fit poorly into previously described species could result in new species within *Fusarium*.

The introduction of DNA analyses for the evaluation of species status has provided an alternative way of characterizing these strains. The variations in DNA sequence are far more numerous and less likely to undergo changes in culture than the morphological features available for traditional identifications. The number of differences at individual sites usually provides enough variation so that the changes can be analyzed as a composite rather than weighting particularly heavily any single character. The process allows the ready identification of genetic lineages and clusters of strains that can then be assessed to determine whether they warrant description as a new species. These molecular techniques enable the identification of new lineages even when the number of strains in the lineage is relatively small. The key is to use these techniques on existing and novel sets of strains to discern new genetic lineages.

SPECIES AND GENERIC CONCEPTS

Species within *Fusarium* have been based primarily on morphological characters for most of the 200+ year history of the genus. These characters include shape and size of macroconidia, microconidia and chlamydospores, and the cells on which they are borne, with secondary characters including pigments and other secondary metabolites produced, growth rate and colony morphology. For separating the major species, or groups of pathogenic species, these characters work reasonably well, and taxonomic treatments of the genus relied solely on these characters through the 1980s. There were disputes between taxonomists over the value of particular characters for delimiting species, and in some cases disputes regarding nomenclatural issues as well that clouded the field and made diagnostics and identification very specialized processes.

Seeds of change were planted in the early 1970s when the concept of using sexual cross-fertility was first introduced into *Fusarium* by Matuo and Synder (1973) for the *Fusarium solani* species complex and by Hsieh *et al.* (1977) for the *Gibberella fujikuroi* species complex. Much of the preliminary work was consolidated by Leslie (1991), who proposed six mating populations within the *Gibberella fujikuroi* species complex and suggested that the variety names proposed by Kuhlman (1982) be elevated to species rank. The mating populations began to split some of the morphological species into smaller pieces and helped resolve some long-standing practical problems. For example, with the resolution of "*F. moniliforme*" into two mating populations (Klittich and Leslie, 1992) the

observations that some strains with the same species name were good maize pathogens and others were good sorghum pathogens suddenly had a taxonomic basis to support them. The widespread use of biological species has not progressed much beyond the *G. fujikuroi* species group at this time, but has been extremely useful in framing the species concepts discussion within this group.

Phylogenetic species concepts are based on multiple characters, usually DNA sequences with each base in the sequence viewed as a potential character. They have the great advantage of being useful with strains that have degenerated and lost critical morphological characters, *e.g.*, spore production, and with strains for which the biological species concept does not apply since no sexual stage is known. The basic concept has been applied to strains in many different portions of the genus, and many genetic lineages have been resolved. Establishing formal Latin binomials for these lineages has two major problems. One is determining which lineages should be grouped together into a common species, and the second is the realization that *Fusarium* names, unlike names for many other fungi, often have implications and usages that go far beyond those for many fungi, *e.g.*, quarantine and trade issues. Although the grouping issue is not unique for *Fusarium*, the need for care with names is, and the identification of a new species, even if it is a splitting of one that had been previously established, can result in significant non-tariff trade barriers.

SPECIES COMPLEXES IN *FUSARIUM*

Species complexes are well known in *Fusarium*. The *Fusarium oxysporum* and *Fusarium solani* complexes are holdovers from the consolidation of taxa implemented by Snyder and Hansen that reduced the entire number of species in the genus to just nine. Each of these species complexes contains numerous genetic lineages (Baayen *et al.*, 2000; O'Donnell, 2000; O'Donnell *et al.*, 2008*a*) and certainly contains more than one species. Each genetic lineage, however, is almost certainly not the equivalent of a species and care breaking these entities into species will be required. A good place to start would be the defined mating populations within *F. solani*, which are probably easily recognized as species at the biological and phylogenetic levels.

Within *F. oxysporum*, a place to begin is more difficult to discern. Initially, the various plant pathogenic form species would seem a good place to begin, but strains within a form species, while sharing plant pathogenic characters need not be closely related. In many cases, members of one form species are more closely related genetically to members of other form species than they are to one another (Baayen *et al.*, 2000). This result may be due to the localization of the genes required for plant pathogenicity on chromosomes that can be transferred horizontally between different strains (Ma *et al.*, 2010). Sorting out species limits in *F. oxysporum* thus will require special care in the selection of

genes to be sequenced, and a biological consideration of the importance for the asexual exchange of chromosomes as a part of the species definition.

The *Gibberella fujikuroi* species complex is roughly equivalent to the *Liseola* section of *Fusarium* and is the best broken out in terms of species with formal descriptions and those with known sexual stages. Yet even here the discrepancy between the number of described biological species (13) and the number of potential phylogenetic species (~50) is large. Clearly there are a large number of entities that remain to be formally described from this group as well.

Finally there is the recently defined *F. equiseti – F. incarnatum* species complex (O'Donnell *et al.*, 2009), which contains strains of two different species – *F. equiseti* and *F. incarnatum-F. semitectum-F. pallidoroseum*. These species complexes contain at least 28 different genetic lineages. Strains in this group often are recovered as weak pathogens of or secondary invaders in diseased plants, with primary disease associations relatively scarce and often difficult to prove. This group also makes no major known mycotoxin(s), so the economic need to work with these fungi has not been as strong as it has to work with strains from the other species complexes.

BIOGEOGRAPHY OF *FUSARIUM*

Much of the work that has been done with various *Fusarium* species has focused on strains that could be recovered from diseased or dying plants of economic importance in commercial agricultural settings. These species have been studied because of their economic importance and until recently making sure a strain could be fitted into one of these species was a routine diagnostic exercise. The collection of more strains from outside traditional temperate climate agricultural settings has led to the realization that the number of species could be much larger than was previously recognized. It also has led to the recognition that some species previously regarded as cosmopolitan in distribution may have a more limited distribution when strains that were previously "forced" into the species description are segregated into different groups. These groups have become very important in filling in gaps in phylogenetic trees that rely primarily on agricultural pathogens from temperate areas. There are two primary types of locations that have been particularly good sources of strains from which new species can be identified – native ecosystems and subsistence agriculture.

Native ecosystems have been a prominent source of new species of *Fusarium* the past few years. Species that we alone have described from such habitats include *F. armeniacum* (Burgess and Summerell, 2000; Burgess *et al.*, 1993), *F. aywerte* (Benyon *et al.*, 2000; Sangalang *et al.*, 1995), *F. babinda* (Summerell *et al.*, 1995), *F. gaditjirrii* (Phan *et al.*, 2004), *F. konzum* (Zeller *et al.*, 2003), *F. lyarnte* (Walsh *et al.*, 2010), *F. nurragi* (Benyon *et al.*, 2000; Sangalang *et al.*, 1995) and *F. werrikimbee* (Walsh *et al.*, 2010). These species often are of little or no agricultural or economic importance, and may never have been isolated

from an agricultural crop even though the native area from which they were collected is in the midst of a significant agricultural growing area. Yet these species can be critical for filling in gaps in phylogenetic trees and in providing tests of biogeographic and phylogeographic species distribution hypotheses. The number of species of *Fusarium* described so far that are known only from native areas is few. However the ease with which such species can be detected when they are intentionally searched for suggests that many additional species remain to be described. Our experience thus far suggests that grasslands will be a particularly productive ecosystem to evaluate for new species and that the species set recovered from above-ground plant parts may be very different from the species set recovered from root, soil and other below-ground sources (Bentley *et al.*, 2007; Leslie *et al.*, 2004*a*).

Subsistence agriculture differs significantly from commercial agriculture in many respects. Yields are usually much lower, mono-cropping is much less frequent, and field sizes of 1-2 hectares often are considered large. The crops grown under these conditions might be the same as those seen in larger commercial farms, *e.g.*, maize, or they may be minor crops that are very limited geographically or that have desirable local uses, *e.g.*, finger millet and tef. The differences in cropping systems and hosts often results in pathogen patterns that are quite different from those normally observed in commercial fields. The possibilities associated with both the minor crops and the subsistence cropping system need a more thorough exploration. The minor crops are likely to host species that either do not colonize or colonize poorly hosts other than these minor crops. Many of these minor crops also are grown relatively near their projected centers of origin. This location means that pathogen species that might not have travelled with the host crop when it was planted elsewhere might still be present. The selection pressure in subsistence agriculture might also enable the persistence of pathogens that would no longer be found in a commercial agricultural field of the same crop. If these pathogen populations are older than those found on the commercial crops, which seems likely, then they would be expected to contain more genetic variation and to be more amenable to changes in host and cropping system than their counterparts isolated from a commercial field of even the same crop might be. Effectively we are suggesting that subsistence agriculture cropping systems may provide refugia for plant pathogens that allows a more ancient form of the species to be evaluated. The differences in genetic variation amongst pathogen populations from commercial and subsistence agriculture may be used as a means of assessing the evolution of the commercial pathogen population of well-established species in addition to identifying previously undescribed species.

WHAT DOES IT TAKE TO BE A SPECIES?

Definitive criteria for what is and what is not a species remain an elusive target. In general, morphological species of *Fusarium* are more likely to contain multiple biological or phylogenetic species than the other way around. Biological and phylogenetic species concepts often identify the same groups whenever it is possible to apply both definitions to a group of strains. If the biological and phylogenetic species concepts are inconsistent with one another with respect to a group of strains, then it is possible that this group of strains represents an entity that is in the process of evolution and is preparing to fission into distinct groups. Identification of new species on the basis of only a single species concept, usually the phylogenetic concept is riskier, since it is not always clear where to draw the line resolving two entities. That this line is not in the same place for every pair of species makes this task even more difficult. A few prominent problems serve to illustrate this issue.

The incomplete resolution of mating boundaries can be problematic for the resolution of different biological species. *Fusarium proliferatum*, *Fusarium fujikuroi*, *Fusarium subglutinans* and *Fusarium circinatum* are generally recognized as distinct species. Phylogenetic distinctions for these groups generally are clear, but may be quite small. Each of these species has a known sexual stage and female-fertile tester strains that can be used to test for membership within any of the four associated biological species. In general these separations are clear, but on occasion strains of *F. proliferatum* and *F. fujikuroi* can intercross (Leslie *et al.*, 2004*b*) to produce fertile perithecia and viable progeny as can strains of *F. subglutinans* and *F. circinatum* (de Vos *et al.*, 2007). These species are examples of the incomplete separation referred to by Perkins (1994). Although these overlaps may make strict applications of a species definition difficult, they also enable interspecific crosses that segregate for many more traits than seen in an intraspecific cross and with new genomic techniques may enable the identification of genes that are monomorphic within a species and to identify genomic regions that are associated with speciation.

Fusarium brevicatenulatum and *Fusarium pseudoanthophilum* were originally described as two different species by Nirenberg *et al.* (1998), primarily on the basis of differences in DNA sequences, but also based on differences in the number of macroconidia produced and whether or not chlamydospores were produced. Recently these two species were synonymized (Amata *et al.*, 2010) because strains of both were cross-fertile with one another and the molecular and morphological characters became interwoven with one another as sample size inceased, *i.e.* it was clear that the two species were part of the same iceberg (Leslie *et al.*, 2001). The differences between these two species are relatively minimal and are indicative of the difficulties that result from trying to draw lines to distinguish species in the absence of significant data based on a different species description.

The division of *Fusarium graminearum* into at least 13 different phylogenetic species has been proposed (O'Donnell *et al.*, 2004, 2008*b*; Starkey *et al.*, 2007; Yli-Mattila *et al.*, 2009). The number of genes used to make this distinction is large, but there is no single gene that can be used to distinguish all of the species (Yli-Mattila *et al.*, 2009). In many cases the trees appear to have multiple radiations occurring simultaneously, which is common in populations, rather than the bifurcation that generally typifies speciation. Thus, it is only when taken as an aggregate that the DNA sequences suffice to differentiate the proposed species. Compounding this problem is the issue of sexual cross-fertility. Although *F. graminearum* is homothallic, many strains from lineages outside the widespread lineage 7 are self-sterile, although they retain the ability to serve as a male parent in a cross. To identify male-fertile strains, a special set of strains developed by Lee *et al.* (2003) is used. These strains have had the mating type gene partially disrupted and retain high levels of female fertility but are no longer homothallic. They can be fertilized by any strain that has a functional mating type gene and is otherwise capable of serving as a male parent in a cross (Bowden and Leslie, 1999). Representatives of at least nine of the phylogenetic lineages within *F. graminearum* are capable of crossing with one to several of the tester strains and producing numerous ascospore progeny (Leslie and Bowden, 2008). The level of cross-fertility in these crosses, however, is much higher than that observed in the crosses between *F. fujikuroi* and *F. proliferatum* or between *F. subglutinans* and *F. circinatum*. If the criteria proposed by Perkins (1994) are used then the level of cross-fertility observed argues for the unity of *F. graminearum* as a single species rather than for it being split into multiple species that are all but impossible to identify without significant levels of DNA sequencing.

CONCLUSIONS

With the current estimate of described *Fusarium* species between 70 and 500, the number of known species seems likely to increase significantly during the coming years, with the addition of 100-200 meaningful species over the next 10 -20 years quite likely. Many of these species will not be economically important plant pathogens, but will instead be species with hosts in native ecosystems or that are adapted to niches found in subsistence agriculture settings. These new species will certainly help to fill in phylogenetic trees and may greatly increase our understanding of the biogeography and phylogeography of the species within the *Fusarium* genus as they are much less likely to have been subjected to anthropomorphic dispersal than are their relatives that are major pathogens of economically important crops. At the same care must be taken to avoid the establishment of multiple species where only a single one is warranted. This problem is most readily dealt with by basing new species on a relatively large num-

ber of strains, and by relying on multiple species concepts as a part of the species description.

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