

Understanding the Systematics of Major Phytopathogenic Fusarium Species

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Abstract:

This paper provides a comprehensive overview of key Fusarium species that cause plant diseases and produce harmful mycotoxins. Our understanding of Fusarium diversity and evolution has greatly expanded in the past 15 years through advanced molecular analysis techniques. Scientists now estimate there are at least 300 distinct Fusarium species, though less than half have been officially classified. The most significant plant pathogens fall into four main groups: the *F. fujikuroi* complex (causing diseases like rice Bakanae and pine pitch canker), the *F. graminearum* complex (primarily causing wheat and barley diseases), the *F. oxysporum* complex (causing wilting in over 100 crop species), and the *F. solani* complex (causing root rot in various plants). The paper also briefly covers other Japanese Fusarium pathogens. The scientific community now favors using the single name "Fusarium" rather than multiple alternative names. Researchers seeking to identify Fusarium species are directed to use two specific online databases: Fusarium-ID and Fusarium MLST.

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Introduction:

The genus *Fusarium* contains numerous plant pathogens that affect crops and produce toxic compounds called mycotoxins. Scientists have identified approximately 300 distinct *Fusarium* species through DNA analysis, though many haven't been formally described yet. These fungi typically live in soil

and can interact with plants in various ways - as parasites, harmless inhabitants, or disease-causing agents. While *Fusarium* classification was traditionally based on physical characteristics (with key works published by researchers like Booth, Gerlach, Nirenberg, Nelson, Wollenweber, and Reinking), the field

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has been transformed over the last 20 years by molecular techniques that analyze multiple genes to define species boundaries. The paper aims to examine both traditional morphological and modern molecular classifications of the most important plant-pathogenic *Fusarium* groups, while also discussing future opportunities and challenges in this field.

Molecular systematics has revolutionized *Fusarium* taxonomy

Fusarium fungi are members of the Nectriaceae family within the broader classification of Ascomycetes. The genus was first identified by Link in 1809 and formally recognized by Fries in 1821. Before 2013, scientists could use two different names for the same *Fusarium* species - one for its asexual form and another for its sexual form (like *Gibberella*). However, this dual naming system was abolished by new international naming rules adopted in 2011 at a botanical congress in Melbourne. The scientific community has widely embraced using just the name "*Fusarium*." Before 1997, scientists classified *Fusarium* species solely based on their physical characteristics observed in laboratory cultures from various sources like diseased plants, animals, soil, and water. A major milestone in *Fusarium* classification came with Wollenweber and Reinking's 1935 publication "Die Fusarien," which identified 16 subgroups

(now considered outdated), 65 species, and various subspecies. While they provided detailed methods for identifying species based on physical characteristics, many scientists, particularly outside Europe, found their system too complex as it required detailed microscopic analysis. In contrast, Snyder and Hansen later proposed a much simpler but scientifically questionable system that recognized only nine species.

Most plant pathogens are nested within four species complexes

(1) *Fusarium fujikuroi*

What we now know as the *F. fujikuroi* species complex would have been classified simply as *F. moniliforme* in Snyder and Hansen's simplified system, or as part of section *Liseola* in Wollenweber and Reinking's classification. Different taxonomists recognized varying numbers of species within section *Liseola*, ranging from one to nine. A breakthrough came with the development of mating type tests, which helped identify 13 biological species within this complex. Each of these species has been formally named and described in its asexual form, including important species like *F. verticillioides*, *F. fujikuroi*, and *F. circinatum*. Scientists now recommend abandoning the practice of referring to these species as mating populations of *Gibberella fujikuroi*, since only one species (*F. fujikuroi*) actually corresponds

to this sexual form. In Japan, several members of this species complex cause important plant diseases, including bakanae disease in rice (*F. fujikuroi*), pitch canker in pine trees (*F. circinatum*), and various other plant infections caused by species like *F. fractiflexum*, *F. guttiforme*, and *F. phyllophilum*. All 13 species in this complex that can reproduce sexually require two different mating types (heterothallic reproduction).

Pitch canker disease, caused by *F. circinatum*, was first discovered on Virginia pine in North Carolina in 1946 and has since spread to other pine species worldwide. The fungus responsible for this disease has gone through several name changes as scientific understanding evolved. It was initially called *F. lateritium* f. *pini*, then renamed to *F. moniliforme* var. *subglutinans*, and later known as *F. subglutinans* f. sp. *pini*. Finally, after detailed morphological studies and DNA analysis, it was classified as a new species, *F. circinatum*, in 1998. The disease has been reported across the globe, including the southeastern and western United States, Haiti, several European countries (Spain, Italy, Portugal), South Africa, Chile, Mexico, and parts of Asia. In Asia, it was first identified in 1989 on *Pinus luchuensis* in Japan's Amami Island, Kagoshima Prefecture, later spreading to Okinawa Prefecture. Korea reported its first cases in Kyunggi Province in the mid-1990s.

Three Japanese samples that were originally classified as *F. moniliforme* var. *subglutinans* were later confirmed as *F. circinatum* through both physical examination and genetic analysis.

(2) *Fusarium graminearum*

Fusarium head blight (FHB) is a globally significant disease affecting wheat and barley. It's particularly destructive because it not only reduces crop yields but also contaminates grains with harmful compounds like trichothecene mycotoxins (DON and NIV) and substances that mimic estrogen. While several *Fusarium* species can cause FHB, *F. graminearum* was long considered the main culprit and thought to be a single species that could freely interbreed. However, research over the past 15 years using genetic analysis has revealed that what was thought to be a single species actually comprises at least 16 distinct species, now known as the *F. graminearum* species complex (FGSC). Analysis of 12 genes suggests these species evolved separately in different regions: Asia, North America, South America, and either Australia or Africa. Traditional classification methods based on physical characteristics could only identify 6 distinct species and 3-4 species groups within this complex, likely because these species evolved relatively recently and still look very similar. Scientists are continuing to study these pathogens to

understand their diversity, toxin-producing capabilities, and geographic distribution. They've developed a genetic testing method that helps identify species and predict their toxin-producing potential, which has been valuable in discovering new species and tracking changes in pathogen populations. Interestingly, all 16 species in this complex can self-fertilize (homothallic), though they appear to have evolved from ancestors that required cross-fertilization (heterothallic), like their close relatives *F. pseudograminearum*, *F. cerealis*, *F. culmorum*, and *F. lunulosporum*.

(3) *Fusarium oxysporum*

The *F. oxysporum* species complex (FOSC) includes some of the most destructive and widespread *Fusarium* plant pathogens. These fungi are found globally in soils and plants, causing various diseases including vascular wilts, damping-off, and root rots in many economically important crops. In Japan alone, FOSC members affect more than 130 different plant species. Scientists have identified over 100 specialized forms (*formae speciales*) and races of *F. oxysporum*, reflecting their importance in plant pathology. The concept of *forma specialis* was introduced by Snyder and Hansen in 1940 to classify strains based on which specific plants they infect. While this classification isn't officially recognized by botanical nomenclature rules, plant pathologists still widely use it for both

FOSC and the *F. solani* species complex. Genetic studies have revealed that many of these specialized forms evolved independently multiple times. For example, the Panama disease pathogen of bananas evolved at least five separate times. This suggests that the ability to infect specific hosts developed convergently, possibly through horizontal gene and chromosome transfer between strains. While no sexual reproduction has been found in FOSC, the presence of mating-type genes suggests it might occur cryptically. Scientists have found that vegetative compatibility groups (VCGs) - groups of fungi that can fuse and share genetic material - better reflect genetic relationships than *forma specialis* classifications. VCGs are identified using nitrate non-utilizing mutants, following a method developed by Puhalla and improved by Correll. Over 125 VCGs have been identified among plant-pathogenic FOSC strains, representing more than 30 *formae speciales*. The relationship between races and VCGs varies - in some cases, there's a one-to-one correspondence, while in others, the relationship is more complex.

(4) *Fusarium solani*

Fusarium solani has been traditionally viewed as a single species that causes diseases in various plants and animals, including humans. However, genetic studies have revealed it actually comprises at least 60

distinct species. When first classified by Wollenweber and Reinking in 1935 as section *Martiella*, it included 5 species and various subspecies. Snyder and Hansen later simplified this by grouping all these taxa under *F. solani*. Scientists discovered seven different biological species within this complex that could sexually reproduce only with certain partners (heterothallic). These were initially classified as mating populations of *Nectria haematococca* or as specialized forms (*formae speciales*) of *F. solani*. Each *forma specialis* was associated with specific host plants - for example, one caused foot rot in cucurbits, another affected sweet potatoes, and others impacted mulberry trees, Japanese pepper, peas, and black locust. Molecular studies have revealed three main evolutionary groups (clades) within the *F. solani* complex, with distinct geographical distributions. These studies confirmed the genetic distinctness of the seven biological species but showed that some *formae speciales* evolved independently multiple times. Due to this complexity, scientists developed a numbering system using Arabic numbers and letters to identify species within the medically and agriculturally important clade 3. The name *F. solani* is now considered problematic since it appears in all three clades, and scientists recommend avoiding its use until it's properly assigned to a specific genetic group. With the adoption of a

single naming system for *Fusarium*, only the *Fusarium* form of the name needs to be used in publications. However, this is complicated by the fact that the genus *Neocosmospora* is nested within clade 3, leading to some species being renamed. Studies of clade 2 species revealed they share a distinctive feature in producing multi-septate spores on tall aerial structures called "Acremonium-like conidiophores."

Future challenges

Although molecular phylogenetics has significantly advanced *Fusarium* systematics, a comprehensive synthesis informed by these methods remains incomplete. With the vast amount of available data and the increasing need for reliable identification techniques, accessible online databases and resources are expected to play a pivotal role in providing tools to the scientific community. Additionally, genomic data is accumulating at an exponential rate, and it is anticipated that complete genome sequences for all major phytopathogenic *Fusarium* species will soon be available. This wealth of genomic information is expected to uncover more phylogenetically informative loci, enhancing our understanding of relationships and species boundaries within the genus. This influx of data promises a second molecular revolution in *Fusarium* systematics, although challenges in computational and analytical approaches to

phylogenomic datasets, especially for large taxa groups, remain substantial.

Looking forward, a 21st-century synthesis of *Fusarium* systematics is envisioned, integrating phylogenetic trees based on multiple loci, species descriptions, ecological, pathological, and physiological data, as well as web-based tools for accurate species identification, comparative genomics, and user collaboration. On the classical taxonomy front, challenges arise due to the abandonment of dual nomenclature after January 1, 2013, as mandated by the International Code of Nomenclature for algae, fungi, and plants. This change requires a single scientific name for holomorphic fungi like *Fusarium*, which produce teleomorphs. However, names published before the cut-off date, such as the anamorphic name *Fusarium* and teleomorphic names like *Gibberella*, compete for priority. Despite this, the broad consensus among researchers supports the unitary use of *Fusarium* as it is monophyletic, widely used, and encompasses nearly all phytopathogenic and medically significant species. Sorting through approximately 1,500 species epithets associated with *Fusarium*, scattered across several genera, to establish a phylogenetically informed "one name—one fungus" framework is a challenging task. However, the extensive molecular and genomic resources available are expected to

ease this process. For accurate identification of *Fusarium* isolates, researchers are encouraged to utilize online platforms such as *Fusarium-ID* and *Fusarium MLST*, which are dedicated to the molecular identification of *Fusarium* species.

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