Annu. Rev. Phytopathol. 2003. 41:177–98
doi: 10.1146/annurev.phyto.41.011703.115501
First published online as a Review in Advance on March 19, 2003

GIBBERELLA FROM *A* (*VENACEAE*) TO *Z* (*EAE*)[1,2]

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Key Words *Fusarium*, biological species, phylogenetic species, plant pathogenesis, mycotoxins

■ **Abstract** *Gibberella* species are destructive plant pathogens, although many are more familiar under their *Fusarium* anamorph names. The recent synthesis of phylogenetic, biological, and morphological species approaches has revitalized taxonomy of a genus that was first described almost 200 years ago. Twelve sexual species of *Gibberella* of agricultural importance were selected for this review to represent phylogenetic, biological, and chemical diversity of the genus. Even closely related *Gibberella* species can differ in reproductive mode, geographic and host distribution, plant pathogenesis, and production of toxins and other biologically active metabolites. *Gibberella* species have proven amenable to meiotic and molecular genetic analysis; A complete genome sequence of *G. zeae* should soon be available. Combining gene disruption strategies with new genomics technologies for expression profiling should help plant pathologists to understand the pathological and evolutionary significance of biological and chemical diversity in *Gibberella* and to identify novel strategies for disease control.

INTRODUCTION

All *Gibberella* species are sexual states or teleomorphs of *Fusarium* species. Most *Gibberella* species are destructive plant pathogens, although many of them are more familiar to plant pathologists under their *Fusarium* anamorph names. *Gibberella* species cause head blights of *Triticum aestivum* (wheat), ear rots of *Zea mays* (maize), bakanae disease of *Oryzae sativa* (rice), tuber dry rot of *Solanum tuberosum* (potato), and pitch canker of *Pinus* species (7, 61). Some *Gibberella* species have broad host ranges and worldwide distributions, whereas other species appear to have more restricted host ranges and geographic distribution. Many *Gibberella* species produce an impressive array of toxins and other biologically active metabolites (28). For more than 100 years, both chronic and acute mycotoxicoses

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in farm animals and in humans have been associated with consumption of grains contaminated with *Gibberella* species and their toxins (57).

The Ascomycete genus *Gibberella* was first described as *Sphaeria pulicaris* in 1822 in *Systema Mycologicum* by the Swedish botanist Fries (33). The genus was reclassified as *Gibberella* by the Italian mycologist Saccardo in 1877 and described in his monumental classification of known fungi, "Sylloge fungorum hucusque cognitorum" (71). Saccardo derived the genus name from the Latin *gibbera*, referring to the gibbous or hump-like shape of the perithecia. *Gibberella* perithecia are very dark blue to dark purple in color, spheroid to ovoid in shape, with a warty surface and a pronounced ostiole. Perithecia generally are borne on the surface of the substrate, scattered or in clumps. The asci contain an unordered meiotic tetrad of eight ascospores that can be straight or curved, one- to three-septate, and hyaline to pale yellow. Anatomy of *Gibberella* perithecia appears to vary little between species, but few species have actually been studied in any detail. Mycologists of the late nineteenth and early twentieth centuries described dozens of *Gibberella* species, often from perithecia that occurred in nature on woody hosts, but many of these species have not been reevaluated. Samuels et al. have published a useful key to 21 *Gibberella* species that are sexual states of *Fusarium* species found in agricultural environments (72).

During the second half of the twentieth century, filamentous Ascomycetes, or Euascomycetes, such as *Aspergillus nidulans* and *Neurospora crassa* became preferred experimental systems for genetic studies. By the 1980s, genetic approaches that had been developed for these model fungi began to be applied to *Gibberella* and to other plant pathogenic Euascomycetes. Several *Gibberella* species are proving useful for analysis of genetics and diversity of plant pathogenesis, mycotoxin biosynthesis, and other traits. *Gibberella* species are easy to maintain and manipulate using standard microbiological techniques. Many species will readily produce their sexual states in the laboratory, and thus are amenable to Mendelian genetic analysis, including tetrad analysis, since the products of a single meiosis are kept together within the ascus. Because the progeny of a sexual cross are haploid, complications of dominance are not present. Sequence analysis of mating-type (*MAT*) loci indicates that homothallism is secondary to heterothallism in *Gibberella* and that the majority of species are heterothallic (98). However, even the homothallic species *G. zeae* is able to outcross at frequencies sufficient for Mendelian genetic analysis (9). Other experimentally useful features of *Gibberella* include DNA-mediated transformation systems that allow both specific gene disruption by homologous recombination and random mutagenesis by integration at nonhomologous sites throughout the genome. Due to the relatively small size of *Gibberella* genomes (less than 50 megabase-pairs) (42, 95, 96), genes can be cloned directly and relatively easily by mutant complementation with either plasmid or cosmid vectors.

The era of *Gibberella* genomics began in the late 1990s with the public release of databases of expressed sequence tags of *G. zeae* and the related asexual species *F. sporotrichioides* through websites at Michigan State University and the

University of Oklahoma. Because of the high cost of genome sequencing and limited public resources, granting agencies such as the United States Department of Agriculture (USDA) and the National Science Foundation (NSF), and professional phytopathological societies are identifying and prioritizing fungi that present an emerging and significant threat to agriculture, through accidental or deliberate introduction. In 2002, the USDA/NSF Microbial Genome Sequencing Program provided financial support for complete sequencing and public release of the genome of a *Gibberella* species, *G. zeae*, which causes wheat head blight and maize ear rot worldwide. *Gibberella* genome sequencing projects also are under way in the private sector. Knowledge of the genomes of these plant pathogens is expected to elucidate the genetic basis of plant-fungal interactions and to accelerate the development of novel strategies for disease control.

One advantage of the genus *Gibberella* for genetic studies is the biological and chemical diversity that has resulted from its evolutionary antiquity; the Mesozoic Era beginning 250 mya is an estimated time for divergence of the Euascomycetes (4). Because the genus *Gibberella* is so large and diverse, however, this review must be selective rather than encyclopedic, despite its title. The author presents 12 *Gibberella* species of agricultural importance: their taxonomy, genetics, plant pathology, and mycotoxicology. The review is restricted to the monophyletic genus *Gibberella*, and does not include *Fusarium* species that have sexual states in other genera such as *Nectria*. The review also is restricted to sexual species of *Gibberella*, and does not include their asexual relatives such as *F. oxysporum*. The 12 species have been selected to represent biological and chemical diversity of the genus. The 12 species also have been selected to represent phylogenetic diversity of the genus, based on a consensus of efforts to establish phylogenetic relationships among a large number of *Gibberella* species (2, 5, 64, 66). Seven of the species represent a major cluster that has been called the *G. fujikuroi* species complex and which contains species formerly placed in *Fusarium* sections *Liseola* and *Dlamini*. These seven species are *G. circinata*, *G. fujikuroi*, *G. intermedia*, *G. moniliformis*, *G. nygamai*, *G. subglutinans*, and *G. thapsina*. The eighth selected species, *G. baccata*, has close affinities to the *G. fujikuroi* species complex and was previously placed in *Fusarium* Section *Lateritium*. The final four species, *G. avenacea*, *G. coronicola*, *G. pulicaris*, and *G. zeae* represent species formerly placed in *Fusarium* Sections *Roseum* and *Discolor* (*Fusarium*) (61).

G. AVENACEAE

Gibberella avenacea was described by Cook in 1967 as the teleomorph of *F. avenaceum* (18). The specific epithet *avenaceum* refers to the original isolation of the anamorph from stalks of *Avena sativa* (oats) in Germany in the nineteenth century (71). Perithecia collected in 1965 from wheat stalks in the field in Washington State yielded ascospores that produced colonies typical of *F. avenaceum*. At the Commonwealth Mycological Institute at Kew, Booth based his published description

of *G. avenacea* on this collection of material (7). Cook's study, however, lacked a demonstration that strains derived from single ascospores were able to produce perithecia, either homothallic or heterothallic. To the author's knowledge, perithecia of *G. avenacea* have not yet been produced in the laboratory.

In 1995, two *Fusarium* populations with macroconidial morphology similar to *F. avenaceum* were described from Australian soils by Burgess et al. and were designated as *F. avenaceum* subsp. *aywerte* and subsp. *nurragi* (74). Analysis of DNA sequences, restriction fragment length polymorphisms (RFLPs), and amplified fragment length polymorphisms (AFLPs) supported elevation of the two subspecies to species rank as *F. aywerte* and *F. nurragi* and also supported their genetic distinction from *F. avenaceum* strains from soils and plants in Australia (5, 59; D. Geiser, personal communication). Teleomorphs of the two new species have not been reported.

The host range of sexually fertile strains of *G. avenacea* has not been determined. Strains classified as *F. avenaceum* by phylogenetic analysis have a worldwide distribution and a very wide host range, causing root rots and ear rots of cereals, dry rot of potato tubers, and blights of plant species as diverse as *Pinus* and *Eustoma* (7, 59). Pathogenicity tests of *F. avenaceum* strains indicated that an individual strain can be pathogenic on plants as diverse as potato or *Eustoma* regardless of its host of origin (36, 59). To investigate population genetic structure of *F. avenaceum*, Geiser et al. at The Pennsylvania State University initiated a molecular phylogenetic analysis of strains from diverse hosts and geographic areas. Analysis of DNA sequences from unlinked loci showed that *F. avenaceum* strains are highly diverse but monophyletic, with no significant incongruence (59; D. Geiser, personal communication).

F. avenaceum is toxigenic: Strains that produce polyketides (fusarins and moniliformin) and nonribosomal peptides (beauvericins and enniatins) have been reported (28, 55). Enniatin-nonproducing mutants of *F. avenaceum* were produced by disruption of the enniatin synthase gene. These mutants were significantly reduced in ability to cause potato tuber dry rot, thus supporting a role for enniatins in pathogenesis on potato (36). Reports of the production of terpenoid trichothecenes by *F. avenaceum* often have been confused by incorrect identification of strains (57). When *TRI5*, an essential trichothecene biosynthetic gene from *Fusarium*, was used as a hybridization probe, the gene was not detected in a number of strains of *F. avenaceum*, suggesting that this species does not produce trichothecenes (86).

G. BACCATA

Gibberella baccata was described by Wallroth in 1833 as *Sphaeria baccata* from various woody plants in western Europe. The specific epithet *baccata* refers to the appearance of perithecia as similar to a cluster of small round fruits (71). *G. baccata* is the teleomorph of *F. lateritium*, which causes cankers and blights on a wide range of plants. Wollenweber & Reinking (94) distinguished several varieties of *F. lateritium* based on host of origin and morphological traits. In 1961, Canadian

mycologist Gordon described the species as heterothallic (34). Heterothallic strains were obtained as single ascospore isolates from perithecia on blighted branches of *Morus*, from diseased leaves of *Celosia*, and from diseased *Coffea* berries and twigs (50). Lawrence et al. (51) conducted random ascospore and tetrad analyses of morphological variants that demonstrated independent segregation of certain traits among progeny and confirmed heterothallism in *G. baccata* from *Coffea*. Interfertility of *G. baccata* strains from different hosts has not been reported.

In 1990, a *Fusarium* species that causes chlorotic leaf distortion of *Ipomea batatas* (sweet potato) was described as *F. lateritium/G. baccata* by Clark et al. at Louisiana State University (17). Some of these strains from sweet potato produced highly oxygenated trichothecenes in culture (17; S. McCormick, personal communication). To investigate the relationship of strains from sweet potato to fertile and nonfertile strains of *G. baccata* from *Coffea* and other hosts, strains were compared by vegetative compatibility group (VCG) analysis and RFLP analysis (38). These data indicated that sweet potato strains of *F. lateritium* were genetically distinct from strains from *Coffea* and other hosts, including fertile strains of *G. baccata*. DNA sequence analysis of multiple unlinked loci supported the designation of the strains from sweet potato as a new species, *F. denticulatum* (64, 66). Efforts to produce homothallic or heterothallic perithecia from sweet potato strains in culture were unsuccessful, thus the teleomorph of *F. denticulatum* is unknown (38).

Sexually fertile strains of *G. baccata* have been isolated from *Celosia* in Nigeria, *Coffea* in Zimbabwe and Papua New Guinea, *Morus* in Japan, and *Ulmus* in the United States (50). Strains classified as *G. baccata* by phylogenetic analysis have been isolated from additional hosts and geographic areas, including *Albizia* and *Pinus* from the United States, *Citrus* from New Caledonia, *Morus* from Australia, and soil from South Africa (38). Strains classified only by morphology as *F. lateritium* have a worldwide distribution and a very wide host range, causing wilt, canker, and dieback of woody trees and shrubs, and seedling blights (7). Population genetic structure of fertile strains of *G. baccata* is unknown; an analysis of *F. lateritium* found considerable genetic diversity among nine strains from hosts other than sweet potato (38). Toxigenicity of sexually fertile strains of *G. baccata* is not known. Enniatin-producing strains of *F. lateritium* have been reported, but fumonisin-producing strains have not (28).

G. CIRCINATA

Perithecia of *Gibberella circinata* were first produced by Viljoen et al. in South Africa as the eighth mating population of *G. fujikuroi*, mating population H (11, 88). Perithecia were obtained from crosses in the laboratory between strains designated *F. subglutinans* f. sp. *pini* that had been isolated from diseased *Pinus* species in South Africa, California, and Florida. DNA sequence analysis of multiple unlinked loci supported elevation of the mating population to species rank as *G. circinata*, anamorph *F. circinatum*; only the DNA sequence of the rDNA ITS2 region was incongruent with other gene genealogies (64, 66). Nirenberg & O'Donnell (64)

derived the specific epithet *circinatum* from the coiled hyphae produced by this species. Homothallic strains of *G. circinatum* have not been reported. Heterothallic strains of *G. circinatum* have been isolated from *Pinus* species worldwide (11). Random ascospore analysis of *MAT* genes and VCGs demonstrated independent segregation of these traits among progeny and confirmed heterothallism in *G. circinata* (10). Perithecia of *G. circinata* have not yet been reported from nature.

G. circinata causes pitch canker, a destructive disease of certain *Pinus* species worldwide (7). Pitch canker strains also can cause branch dieback and seedling blights on *Pinus* but are not pathogenic to other hosts. Genetic diversity and relationships of *G. circinata* populations from California, Florida, Japan, Mexico, and South Africa have been studied using VCG analysis, mating-type tests, and a variety of polymorphic DNA markers (10, 92). Higher diversity of the Florida and Mexico populations supported long-term establishment of the pathogen in those areas, whereas the presence of only one VCG in the Japan population supported very recent introduction. Although the California and Florida populations were closely related, the California population was significantly less diverse, which is consistent with reports of the pathogen in Florida by 1945 and in California only in 1986. Pitch canker first appeared in South Africa in a single nursery in 1990, and an increase in allelic diversity and number of VCGs during the next ten years suggested that sexual reproduction is occurring in the population, although perithecia have not been found in the field.

G. circinata is toxigenic: Strains have been reported to produce beauvericin, but not to produce the polyketide moniliformin or fumonisins (25). When fumonisin biosynthetic genes from *G. moniliformis* were used as hybridization probes, the genes were not detected in two mating tester strains of *G. circinata* (70). Although *G. circinata* is a pathogen of *Pinus*, a California strain of this species formed a fertile hybrid cross with a strain of *G. intermedia* from *Zea mays* ssp. *mexicana* from Mexico and produced viable recombinant progeny (25). The *G. intermedia* parent and all progeny of the initial cross were avirulent on *Pinus radiata*, but progeny of a backcross to the virulent parent showed a wide range of virulence. This interspecific hybridization event should facilitate identification of virulence determinants of the pitch canker pathogen (32).

G. CORONICOLA

Perithecia of *Gibberella coronicola* were first produced by Francis & Burgess from crosses between Australian strains designated *F. graminearum* Group 1 (31). Aoki & O'Donnell conducted DNA sequence analysis of the β-tubulin gene and elevated Group 1 to species rank as *G. coronicola*, anamorph *F. pseudograminearum* (2, 3). Genetic analysis using RFLPs of random genomic and mitochondrial DNA supported the distinction of *G. coronicola* from *G. zeae*, anamorph *F. graminearum* (5). The specific epithet *coronicola* is derived from the Latin *corona*, meaning crown, plus *cola*, meaning dweller, and refers to the crown rot of cereals caused by the fungus (3). Homothallic strains of *G. coronicola* have not been reported.

Heterothallic strains of *G. coronicola* have been isolated from *Graminae* and soils from Australia, wheat from the United States, and *Medicago* from South Africa; however, fertility of laboratory crosses is consistently very low (3, 31). Although perithecia of *G. coronicola* appear to be rare in nature, they have been reported on wheat crowns in Australia (31).

Sexually fertile strains of *G. coronicola* have been isolated mainly from wheat in Australia and South Africa (3, 31). Strains classified as *G. coronicola* by phylogenetic analysis have been isolated from various grass hosts from additional geographic areas: Canada, China, Colombia, Japan, Europe, and the United States (2). *G. coronicola* causes root and crown rot of small grain cereals, particularly in warm, semiarid areas such as Australia and South Africa (13, 31). Population genetic structure of *G. coronicola* is unknown. *G. coronicola* is toxigenic; strains that produce both the polyketide zearalenone and the trichothecene deoxynivalenol, but none that produce nivalenol, were reported in Australia (6).

G. FUJIKUROI

Gibberella fujikuroi was first described by Sawada in 1917 in Formosa (now Taiwan) as *Lisea fujikuroi* on rice stems (75). Sawada recognized the causal role of the species in bakanae disease of rice and gave it the specific epithet *fujikuroi* in recognition of his colleague Fujikuro. In 1931, Ito modified the name to *Gibberella fujikuroi* and wrote "the fungus seems to be identical with or only a variety of *Gibberella moniliformis* (Sheldon) Wineland (= *Fusarium moniliforme* Sheldon)" (39). In disagreement, Sawada & Kurosawa correctly considered G. *fujikuroi* to be distinct from *G. moniliformis*, a maize pathogen. This conclusion was based on Kurosawa's elegant experimental evidence that only *G. fujikuroi* caused the characteristic elongation symptoms of bakanae disease on rice plants (49). The distinction between these two species was again obscured when Wollenweber & Reinking published their *Die Fusarien* in Berlin in 1935, in which they considered *G. fujikuroi* to be the perfect stage of *F. moniliforme* in a broad sense, with *G. moniliformis* a synonym (94).

During the 1970s, the broader concepts of *G. fujikuroi* of Wollenweber, Booth, Nelson, and others came under challenge (7, 61, 94). Nirenberg adopted the combinations of *G. fujikuroi/F. fujikuroi* and *G. moniliformis/F. verticillioides* to distinguish between the bakanae pathogen and the maize pathogen (63). In addition, Snyder, Kuhlman, Leslie, and others began to apply a biological species or mating population concept to this group of related *Gibberella* species, which began to be designated the *G. fujikuroi* species complex. In 1971, Snyder and Sun produced perithecia by crossing strains of *F. fujikuroi* in the laboratory; then four reproductively isolated groups of *G. fujikuroi* were designated as groups A, B, C, and D, with genetically interfertile strains from rice designated as mating group C (37, 48). Additional genetic studies have identified eight biological species or mating populations, designated A-H, within the *G. fujikuroi* species complex (53, 88). All of these mating populations have now been formally recognized as

Gibberella species. The elevation of the eight mating populations to a distinct species was supported by DNA sequence analysis of multiple unlinked loci; only the DNA sequence of the rDNA ITS2 region was incongruent with other gene genealogies (66). In this article, therefore, *G. fujikuroi* will refer, as intended by Sawada & Kurosawa, only to the teleomorph of the bakanae pathogen, *F. fujikuroi*.

G. fujikuroi is predominately a pathogen of rice worldwide, and can cause seedling blight as well as the more characteristic elongation symptoms. *G. fujikuroi* occasionally has been isolated from grain of *Sorghum bicolor* (sorghum) (53). Population genetic structure of *G. fujikuroi* is unknown. *G. fujikuroi* is toxigenic: Strains that produce moniliformin and beauvericin have been isolated from rice from Asia, Africa, Europe, and the United States, but strains that produce the terpenoid fusaproliferin have not been identified (28). When fumonisin biosynthetic genes from *G. moniliformis* were used as hybridization probes, the genes were detected in two mating tester strains of *G. fujikuroi*, although these strains and other strains of *G. fujikuroi* produced little or no detectable fumonisins in culture (28, 70). *G. fujikuroi* produces high levels of terpenoid gibberellins, which by themselves can cause the characteristic elongation symptoms of bakanae disease on rice and other plants. Tudzynski and associates in Munster have characterized a gibberellin biosynthetic gene cluster in *G. fujikuroi* and also have found some of these genes in related *Gibberella* species that are not known to produce gibberellins (84, 85).

G. INTERMEDIA

Perithecia of *Gibberella intermedia* were first produced by Kuhlman as *G. fujikuroi* var. *intermedia* by crossing strains of *F. proliferatum* in the laboratory (48). The teleomorph also was reported as the fourth mating population of the *G. fujikuroi* complex, mating population D (53). Samuels et al. elevated the variety to species rank as *G. intermedia* (72), which was supported by DNA sequence analysis of multiple unlinked loci (66). Only the DNA sequence of the rDNA ITS2 region was incongruent with other gene genealogies. According to Kuhlman (48), the specific epithet *intermedia* refers to his observation that ascospores of this species are intermediate in size between those of *G. moniliformis* and *G. fujikuroi*. Homothallic strains of *G. intermedia* have not been reported. Heterothallic strains of *G. intermedia* have been isolated from diverse hosts worldwide (48, 53). Random ascospore analyses of a DNA marker, fumonisin production, and moniliformin production demonstrated independent segregation of these traits among progeny and confirmed heterothallism in *G. intermedia* (27). Perithecia of *G. intermedia* have not yet been reported from nature.

Strains of *G. intermedia* that are sexually fertile members of mating population D have a worldwide distribution and a very broad host range, including plants as diverse as *Musa*, *Asparagus officinalis*, *Mangifera indica*, maize, *Nicotiana tabacum*, *Pinus*, rice, sorghum, and wheat (53). *G. intermedia* causes a destructive crown and root rot of *A. officinalis* and an ear rot of maize. To investigate

population genetic structure of *G. intermedia*, Geiser et al. initiated molecular phylogenetic analysis of strains from diverse hosts and geographic areas. Their analysis of DNA sequences from unlinked loci demonstrated that *G. intermedia* strains are highly diverse but monophyletic and show mating compatibility despite their high levels of divergence (D. Geiser, personal communication). Wide dispersal of both mating types and a high frequency of female fertility increase the potential for sexual reproduction in this species (54). *G. intermedia* is highly toxigenic: Strains that produce beauvericin, fumonisins, fusaproliferin, moniliformin and other polyketides (fusaric acid and fusarin) have been reported (28). When fumonisin biosynthetic genes from *G. moniliformis* were used as hybridization probes, the genes were detected in two mating tester strains of *G. intermedia* (70).

G. MONILIFORMIS

Perithecia of *Gibberella moniliformis* were first produced in 1924 by Wineland by crossing strains of *F. moniliforme* isolated from maize in the United States (93). The specific epithet *moniliformis* is derived from the Latin *monilis* meaning necklace, which Sheldon used to describe the distinctive long chains of microconidia (76). The teleomorph also has been published widely as mating population A of the *G. fujikuroi* species complex (37, 48, 53). DNA sequence analysis of multiple unlinked loci supported elevation of the mating population to species rank; only the DNA sequence of the rDNA ITS2 region was incongruent with other gene genealogies (66). Homothallic strains of *G. moniliformis* have not yet been reported. Heterothallic strains of *G. moniliformis* have been isolated primarily from maize worldwide (37, 48, 53). Both mating types are widespread and strains from diverse hosts and geographic areas can be interfertile (53). Construction of a map based on the segregation of RFLPs, AFLPs, and other traits confirmed heterothallism in *G. moniliformis* (43, 95). Although perithecia of *G. moniliformis* appear to be rare in nature, Vorhees collected them from maize leaf sheaths in Florida in 1931 (89) and Burgess et al. collected them from old maize stalks in Vietnam in 1994 (80). Single ascospore cultures originating from perithecia from Vietnamese maize were crossed to tester strains and shown to be heterothallic strains of *G. moniliformis*.

Throughout the twentieth century, plant pathologists used the anamorph species name *F. moniliforme* following its identification as a maize pathogen by Sheldon in 1904 (76). However, Nirenberg rejected *F. moniliforme* as a later synonym of Saccardo's 1882 designation of *Oospora verticilloides*, which she transferred as *F. verticillioides* (63). After considerable debate, *F. verticillioides* is the presently accepted nomenclature for the anamorph of *G. moniliformis*.

Fertile strains of *G. moniliformis* are associated worldwide with maize diseases at all stages of plant development; they infect the roots, stalks, and ears, and also can be found colonizing symptomless maize plants, especially seeds. Fertile strains also have been isolated from other hosts, including *Ficus*, *Musa*, *Pinus*, rice, sorghum, and teosintes, which are wild *Zea* species native to Mexico and Central

America (25, 53). Wide dispersal of both mating types and a high frequency of female fertility increases the potential for sexual reproduction in this species (54). Vegetative compatibility group analysis also indicates high levels of genetic diversity, even among strains from a single maize or teosinte seed sample or from a single maize stalk (25, 53, 54).

G. moniliformis is toxigenic: Strains that produce fumonisins, fusaric acid, and fusarins have been reported (28). Proctor and associates at USDA characterized a fumonisin biosynthetic gene cluster in *G. moniliformis* (69). Fumonisin-nonproducing mutants were produced by disruption of the fumonisin polyketide synthase gene. These mutants were not significantly reduced in ability to cause maize ear infection and ear rot in field tests, indicating that fumonisins are not required for pathogenesis on maize ears (24).

G. NYGAMAI

Perithecia of *Gibberella nygamai* originally were produced by Klaasen & Nelson by crossing strains of *Fusarium nygamai* in the laboratory at The Pennsylvania State University (44). The teleomorph first was reported as the seventh mating population of the *G. fujikuroi* species complex, mating population G (53), and in 1996 was formally described as *G. nygamai* (44). DNA sequence analysis of multiple unlinked loci supported elevation of *G. nygamai* to species level; only the DNA sequence of the rDNA ITS2 region was incongruent with other gene genealogies (66). The specific epithet *nygamai* is an Aborginal name for *Acacia* species in the region of Australia where this species was first isolated (14). Homothallic strains of *G. nygamai* have not been reported. Heterothallic strains of *G. nygamai* have been isolated primarily from sorghum in Australia, and from soil debris and soil in Australia and Sub-Saharan Africa (44). Random ascospore analysis of mating type and fumonisin production demonstrated independent segregation of these traits among progeny and confirmed heterothallism in *G. nygamai* (45). Perithecia of *G. nygamai* have not been reported in nature.

Strains of *G. nygamai* that are sexually fertile members of mating population G have been isolated from grassland and field soils in Australia and Africa and from grain sorghum from Australia (44). Strains classified as *G. nygamai* by phylogenetic analysis have been isolated from additional hosts and geographic areas: *Cajanus* in India, rice in Morocco, *Striga* in the Sudan, and *Nicotiana* in Greece (66). Strains classified only by morphology as *F. nygamai* have been isolated from additional sources: various millets in Africa, and soils in Thailand and Puerto Rico (14, 60). *G. nygamai* has been isolated from both symptomless and diseased plant tissues, but its pathogenicity has not been reported. Population genetic structure of *G. nygamai* is unknown. *G. nygamai* is toxigenic: Strains that produce beauvericin, fumonisins, fusaric acid, and moniliformin have been reported (15, 45, 55, 56). When fumonisin biosynthetic genes from *G. moniliformis* were used as hybridization probes, the genes were detected in two mating tester strains of *G. nygamai* (70).

G. PULICARIS

Gibberella pulicaris is the type species of the genus *Gibberella* and was first described as *Sphaeria pulicaris* by Fries in 1822 (33). In his *Systema Mycologicum*, Fries described perithecia from a branch of a *Sambucus* tree, but he did not provide the etymology of the epithet *pulicaris* that he gave to this species (33). *Pulicaris* can be translated from Latin as "of or belonging to fleas" and may refer to both perithecia and fleas appearing like little black dots. In 1877, Saccardo transferred the species as *G. pulicaris*. The anamorph is *F. sambucinum*, the type species of the genus *Fusarium*. Wollenweber & Reinking (94) distinguished several forms of *F. sambucinum* based primarily on colony color and other morphological traits. Booth (7) considered Wollenweber's *F. sambucinum* f. 6 to be a distinct species, *F. sulphureum*, noted for the presence of a diffusable sulphur yellow color and for the absence of red color in the colony undersurface. Nelson et al. (61) and others included *F. sulphureum* and other forms in a broad species concept of *F. sambucinum sensu lato*.

Homothallic strains of *G. pulicaris* have not been reported. In 1961, Gordon first described production of heterothallic perithecia in mating tests in the laboratory (34). Both mating types occur worldwide, and strains from diverse hosts and geographic areas can be interfertile. For example, strain BBA 64995 from the Netherlands has produced fertile crosses with strains from Australia, Egypt, Europe, and Iran and with more than 150 strains from Canada, Mexico, and the United States (20, 21, 62). Random ascospore and tetrad analyses of mating type, colony color, resistance to phytoalexins, trichothecene gene mutations, and other traits demonstrated independent segregation among progeny and confirmed heterothallism in *G. pulicaris* (20–23).

In 1987, Nirenberg organized the *European Fusarium Sambucinum Project*, wherein a group of mainly European scientists investigated *F. sambucinum sensu lato*. Based on diverse methods, including morphology, rDNA gene sequences, DNA markers, and toxin profiles, 40 strains of *F. sambucinum sensu lato* were divided into three species: *F. sambucinum sensu stricto*, *F. torulosum*, and *F. venenatum* (62). Mating tests with European *G. pulicaris* tester strains indicated concordance between the morphological and biological species concepts of *G. pulicaris/F. sambucinum*. The data also indicated that sulphur yellow strains that had been identified as *F. sulphureum* according to Wollenweber (94) are conspecific with *F. sambucinum*. Thus, the teleomorph of *F. sulphureum* is *G. pulicaris* and not *G. cyanogena* as stated by Booth (7). A teleomorph for *F. torulosum* was suggested by Nirenberg (62), and a teleomorph for a *Fusarium* population with some affinities with *F. venenatum* has been reported in South Africa (83), but neither has been formally described.

To the author's knowledge, a phylogenetic analysis based on multiple gene genealogies of multiple strains has not been published for *G. pulicaris*. Three different sequences of the rDNA ITS2 region, designated types A, B, and C, were identified in a global collection of strains of *F. sambucinum sensu lato* (65). Subsequently, O'Donnell et al. proposed that ITS2 type A is *F. torulosum*, ITS2

type B is *F. sambucinum sensu stricto* (*G. pulicaris*), and ITS2 type C is *F. venenatum* (66). The distribution of ITS2 polymorphisms within this global collection of strains, however, was incongruent with *G. pulicaris* as defined by mating compatibility and vegetative compatibility (20, 21). For example, mating compatibility, mating-type identity, and vegetative compatibility of strain R-9146 (NRRL 13700, ITS2 type B) and strain R-9140 (ITS2 type C) indicate that these two strains from potatoes from New Brunswick, Canada, are *G. pulicaris* (20). These data indicate that the ITS2 regions are polymorphic within *G. pulicaris*, as they are within other *Gibberella* species (4, 66). On the other hand, incongruence of traits within *F. sambucinum sensu lato* may occasionally be due to interspecies fertility. For example, species-specific PCR and randomly amplified polymorphic DNA banding patterns indicated that the low fertility cross of strain R-6380 (ITS2 type B) with strain R-5920 (ITS2 type A) is a likely interspecies cross between *G. pulicaris* and *F. torulosum* (65, 97).

G. pulicaris has a worldwide distribution and a very broad host range, including plants as diverse as *Beta vulgaris*, *Brassica oleracea*, *Dianthus*, maize, *Polygonum*, *Pterocarya*, and wheat (7, 62, 65). *Gibberella pulicaris* is economically most important as a causal agent of potato dry rot, particularly in Europe and North America (20). Despite the long-established cultivation of potatoes and occurrence of tuber dry rot in the United States, diversity of *G. pulicaris* on potato tubers appears to be very low. Only one mating type was present among 121 fertile strains isolated from potato tubers from Maine to Oregon from 1963 to 1993, and only three VCGs accounted for more than 90% of these strains (20). In contrast, the widespread occurrence of both mating types and a larger number of VCGs in Canada and Europe indicated that sexual reproduction and recombination might have occurred (20, 83).

G. pulicaris is toxigenic: Strains that produce diacetoxyscirpenol and other trichothecenes, enniatins, fusaric acid, and fusarins have been reported (28). Trichothecene-nonproducing mutants of *G. pulicaris* were produced by disruption of the trichodiene synthase gene. These mutants were reduced in ability to cause root rot of *Pastinaca sativa* but were not reduced in ability to cause potato tuber dry rot, indicating that trichothecenes are important in pathogenesis on some hosts but not others (23). Potato-pathogenic strains also are able to metabolize a variety of potato defense compounds, including rishitin, lubimin, and other sesquiterpenes, and solanine and other glycoalkaloids (22, 91). Weltring et al. showed that disruption of an ABC multidrug-resistance transporter gene in *G. pulicaris* decreased tolerance to potato sesquiterpenes and virulence on potato tubers (30).

G. SUBGLUTINANS

Gibberella subglutinans was first described by Edwards in 1932 as *G. fujikuroi* var. *subglutinans* from old maize stalks in Eastern Australia (29). The specific epithet *subglutinans* is from the anamorph *F. subglutinans* and is derived from the Latin *sub glutinosus* meaning somewhat viscous, and may refer to the slimy, salmon-colored masses of macroconidia that are often present on infected maize substrates and in

laboratory cultures (29, 94). The teleomorph has been produced in the laboratory by crossing strains of *F. subglutinans* from maize from the United States and has been described as the fifth mating population of *G. fujikuroi*, mating population E (53, 61). DNA sequence analysis of multiple unlinked loci supported elevation of the mating population to species rank; only the DNA sequence of the rDNA ITS2 region was incongruent with other gene genealogies (66, 77). Homothallic strains of *G. subglutinans* appear to be rare (7). Both homothallic perithecia and heterothallic perithecia were reported by Ullstrup in 1936 in laboratory cultures of strains derived from single ascospores from perithecia that he collected from old maize stalks in New Jersey (87). Heterothallic strains of *G. subglutinans* have been isolated worldwide, primarily from maize (25, 53, 64, 77). Random ascospore analysis of mating type demonstrated segregation of this trait among progeny and confirmed heterothallism in *G. subglutinans* (25).

Strains of *G. subglutinans* that are sexually fertile members of mating population E have been isolated from maize in Africa, Asia, Mexico, and the United States, and also from teosintes, wild *Zea* species from Mesoamerica (25, 53, 77). Strains classified as *G. subglutinans* by phylogenetic analysis also have been isolated from maize from Germany and Iran (66). *G. subglutinans* is associated with diseases at all stages of maize plant development, infecting the roots, stalks, and ears, and also can be found colonizing symptomless maize plants, especially seeds (29). Application of phylogenetic species concepts has indicated that the biological species *G. subglutinans* is subdivided into more than one group (25, 77, 78). Steenkamp et al. analyzed DNA sequence data for 22 strains of *G. subglutinans* isolated from seeds of maize in South Africa, Mexico, and the central United States, and for 8 strains isolated from seeds of five teosinte species from Guatemala and Mexico. Phylogenetic analysis of combined sequence data for six nuclear DNA regions revealed the presence of two distinct groups, which appear to be genetically isolated in nature but are capable of interfertility in laboratory mating tests. The occurrence of both *MAT* idiomorphs and multiple VCGs indicated that strains in each group are not clones. To date, the two genetic groups have not been associated with host or geographic origin, or with any phenotypic traits such as morphology, toxin production, or pathogenicity.

G. subglutinans is toxigenic: Strains that produce beauvericin, fusaproliferin, fusaric acid, and moniliformin have been reported, but fusarin-producing strains have not (28). Rare strains of *G. subglutinans* have been reported to produce low levels of fumonisins in culture (28). However, when fumonisin biosynthetic genes from *G. moniliformis* were used as hybridization probes, the genes were not detected in two mating tester strains or in two additional strains of *G. subglutinans* (70).

G. THAPSINA

Perithecia of *Gibberella thapsina* originally were produced by Klittich & Leslie by crossing strains of *Fusarium thapsinum* in the laboratory at Kansas State University. The teleomorph first was reported as the sixth mating population of the

G. fujikuroi species complex, mating population F (46, 53), and in 1997 was formally described as *G. thapsina* (47). DNA sequence analysis of multiple unlinked loci supported elevation of *G. thapsina* to species level; only the DNA sequence of the rDNA ITS2 region was incongruent with other gene genealogies (66). The specific epithet *thapsina* (Greek *thapsinos*) refers to the characteristic yellow pigment produced by this species (47). Homothallic strains of *G. thapsinum* have not been reported. Heterothallic strains of *G. thapsina* have been isolated primarily from sorghum in Africa and in the United States (47). Random ascospore analysis of mating type, female fertility, and colony color demonstrated independent segregation of these traits among progeny and confirmed heterothallism in *G. thapsina* (46). Perithecia of *G. thapsina* have not yet been reported in nature.

Strains of *G. thapsina* that are sexually fertile members of mating population F have been isolated mainly from stems of sorghum, maize, and *Musa*, from sorghum roots and crowns, from grain sorghum and maize, and from plant debris in sorghum fields. Fertile strains have been reported from northern and southern Africa, Asia, Europe, and the United States (47). These surveys indicate that *G. thapsina* has a global distribution, especially as an endophyte and pathogen of sorghum. Under greenhouse conditions, some strains of *G. thapsina* can cause spreading lesions in wounded stalks of both sorghum and maize (40, 41). Although both mating types are widely dispersed, a low frequency of female fertility decreases the potential for sexual reproduction in this species (54). Vegetative compatibility group analysis also indicates lower genetic diversity in *G. thapsina* than in the closely related species *G. monilformis* (54).

G. thapsina is toxigenic: Strains that produce fusaric acid and moniliformin have been reported (28). Rare strains of *G. thapsina* have been reported to produce low levels of fumonisins in culture (28). However, when fumonisin biosynthetic genes from *G. moniliformis* were used as hybridization probes, the genes were not detected in two mating tester strains of *G. thapsina* (70). A survey of strains of *G. thapsina* from sorghum in Italy found no strains that produced either beauvericin or fusaproliferin (28).

G. ZEAE

Gibberella zeae was described by the American mycologist Schweinitz in 1822 as *Sphaeria zeae* (71). The specific epithet *zeae* refers to isolation from *Zea mays*. In 1936, British mycologist Petch examined one of Schweinitz' original specimens that had been deposited 100 years earlier at Kew and corrected the name to *Gibberella zeae* (68; see Reference 72 for photographs of the lectotype specimen at Kew). Although *G. zeae* is homothallic and self-fertile, Bowden & Leslie demonstrated that homothallic strains of *G. zeae* also could outcross in the laboratory. Random ascospore analysis demonstrated independent segregation of VCGs among progeny (9). Construction of a map based on segregation of AFLPs and other traits confirmed outcrossing in *G. zeae* (42). Perithecia occur in nature on a wide range of cereals and grasses, and production of ascospores on host residues

plays an important role in epidemiology of maize ear rot and head blight of wheat and *Hordeum vulgare* (barley) (7).

G. zeae occurs worldwide on cereal grains such as *Geum urbanum* (rye), barley, maize, oats, rice, and wheat, and also can occur on plants as diverse as *Coffea*, *Pisum*, *Trifolium*, and *Solanum* (7). *G. zeae* causes destructive epidemics of maize ear rot and wheat and barley head blight in temperate regions. DNA sequence analysis of multiple unlinked loci supported resolution of the biological species *G. zeae* into seven or more distinct phylogenetic lineages (66, 90). However, members of at least three of these phylogenetic lineages were interfertile and produced viable recombinant progeny in laboratory mating tests (9; A. Desjardins, unpublished observations). Thus, the lineages may represent geographically separated and genetically distinct populations rather than distinct species. Indeed, DNA sequence analysis found significant incongruence between gene genealogies for one of four Nepalese strains tested, indicating recombination between lineages coexistent in Nepal (67). An analysis of AFLPs, other DNA markers, and other traits among a collection of several hundred strains of *G. zeae* from Nepal has identified three genetically distinct subgroups that differ in trichothecene chemotype and virulence on wheat (16, 26).

G. zeae is toxigenic: Strains that produce deoxynivalenol, nivalenol, and other trichothecenes, fusarins, and zearalenone have been reported (28). Research groups at USDA, in Korea, and elsewhere have characterized trichothecene gene clusters in *G. zeae* (12, 52, 90). Trichothecene-nonproducing mutants of *G. zeae* were produced by disruption of the trichodiene synthase gene. These mutants were reduced in ability to cause wheat head blight and maize ear rot in the field, indicating that trichothecenes play a major role in virulence on wheat and a more minor role in virulence on maize (23, 35).

DISCUSSION

Even 20 years ago, the taxonomy of *Gibberella* and its *Fusarium* anamorphs could still have been described in the words of Linnaeus in 1751, "The order of Fungi, a scandal to art, is still chaos with botanists not knowing what is a species, what a variety" (1). A high degree of confusion was due to the fact that traditional morphological traits, such as colony color, length of microconidial chains, or the production of chlamydospores, may vary only slightly between species or be variable within species of *Gibberella*. Taxonomy of many species of the genus has been revitalized by application of biological species concepts based on reproductive compatibility and phylogenetic species concepts based on DNA sequence variation. Biological species can be defined as "groups of interbreeding natural populations that are reproductively isolated from other such groups" (58). Biological species concepts reflect the role of species as basic units of evolutionary change. Phylogenetic species concepts reflect evolutionary history and are based on the inheritance of variable traits. The fact that species are populations of variable individuals rather than fixed types was a central feature of Darwin's theory of

evolution in 1859, "No one supposes that all individuals of the same species are cast in the very same mould. These individual differences are highly important for us, as they afford materials for natural selection to accumulate" (19). One hundred fifty years after Darwin, the discovery of DNA sequence variation within and between natural populations has provided new taxonomic characters and revolutionized fungal population genetics, especially among genera such as *Gibberella* with large numbers of species and often limited morphological diversity (73).

The synthesis of phylogenetic, biological, and morphological species approaches has resolved several agriculturally important *Gibberella* species that have only subtle differences in morphology. The fumonisin-producing species *G. moniliformis* has been resolved from the moniliformin-producing species *G. thapsina*; and *G. circinatum* which causes pitch canker of *Pinus* has been resolved from *G. subglutinans* which does not. Although phylogenetic species approaches are powerful, the method does require extensive DNA sequencing and marker analyses that are technically demanding and relatively expensive to use. Biological species approaches have the advantage of requiring only simple media for reproductive compatibility tests with mating tester strains available from fungal stock centers, and thus are technically simple and inexpensive to use. Disadvantages of the biological species approach are that, even in sexual species, some strains are sterile, and some species that are closely related to *Gibberella* are asexual. In principle, mating compatibility in the laboratory indicates only that strains have retained the ability to interbreed, and does not prove that they actually recombine in nature. In fact, recent population genetic studies indicate that recombination may be rare between interfertile and apparently sympatric populations of *G. subglutinans* in Mesoamerica and *G. zeae* in Nepal. These inconsistencies between biological and phylogenetic species concepts provide interesting topics for the continuing discussion of how fungal species should be identified and defined.

In 1981, Booth wrote, "The presence of the perfect or perithecial state . . . in *Fusarium* appears, superficially at least, to be of more value to the taxonomist than the fungus" (8). At that time, Booth and other mycologists believed that perithecial production was rare in nature because opposite mating types were geographically separated. To the contrary, more extensive recent surveys of geographical distribution of mating types for heterothallic *Gibberella* species discussed in this review indicate that strains of both mating types occur together in space and time for each of the ten species for which sufficient data are available. In addition, perithecia of 7 of the 11 heterothallic species have been reported in nature, and perithecia of the homothallic species *G. zeae* are sometimes so abundant in the field that ascospores are a significant source of inoculum for wheat head blight and maize ear rot epidemics. Limited available data indicate that *Gibberella* species, in common with many other fungi (82), can demonstrate a range of asexual and sexual modes of reproduction, and that reproductive mode can vary with space and time. For example, for *G. pulicaris* from potato tubers, the population from the United States can reproduce only asexually and is strongly clonal, whereas the European population has the potential for sexual reproduction and is quite diverse. Recent

evidence for sexual reproduction and recombination in *Gibberella* in nature includes an increase in allelic diversity of *G. circinata* in South Africa during the ten years since the first outbreak of pitch canker in a *Pinus* nursery there in 1990. Similar historical approaches are unfortunately limited for most *Gibberella* species by the absence of archival strains. Inferences from current distribution are complicated by the early and extensive movement of *Gibberella* species via agricultural commodities—from the ancient caravans that crossed Asia on the Silk Road to the sixteenth century ships that brought American crop plants to Eurasia.

Whether sexual or asexual in reproductive mode, *Gibberella* species demonstrate diverse patterns of geographic and host distribution, and diverse modes of plant pathogenesis. *Gibberella* species also produce a wide array of biologically active and often phytotoxic metabolites, including polyketides, terpenoids, and nonribosomal peptides. Production of some polyketide toxins, such as fusaric acid and moniliformin, is widespread in the genus, whereas production of others, such as fumonisins and zearalenone, appears to be more restricted. Among the *Gibberella* toxins identified to date, however, only enniatins and trichothecenes have been firmly established by gene disruption as virulence factors in plant pathogenesis. Furthermore, the genomes of *G. moniliformis* and *G. zeae* contain dozens of putative genes for polyketide synthases, terpenoid cyclases, and peptide synthases, and for other virulence factors such as ABC transporters and protein kinases (96). Evaluating the pathological and ecological importance of the toxins in even one *Gibberella* species is a daunting task. However, combining gene disruption strategies with new genomics technologies for expression profiling should assist us in understanding the evolutionary significance of the biological and chemical diversity of *Gibberella*. This extraordinarily adaptive genus offers unique opportunities to address complexities of the evolution of species in space and time, "how the innumerable species inhabiting this world have been modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration" (19).

ACKNOWLEDGMENTS

I am grateful to Nancy Alexander, Robert Bowden, David Geiser, Thomas Gordon, Andrew Jarosz, John Leslie, Susan McCormick, Gary Munkvold, Paul Nicholson, Ronald Plattner, Robert Proctor, Gary Samuels, Emma Steenkamp, Gillian Turgeon, Brenda Wingfield, and Michael Wingfield for helpful discussions and unpublished data.

The *Annual Review of Phytopathology* is online at http://phyto.annualreviews.org

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