

Genetic problems in some *Fusarium* species

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Genetic approaches to problems in *Fusarium* have been limited. At present, most studies focus on molecular techniques as a means for species or strain identification purposes, although genetic tools such as protocols for transformation and classical genetic crosses have been developed for some species. Genetic standards in terms of both strains and terminology are largely lacking at this time. Development of defined strains for laboratory use that are broadly accepted would increase the ease with which results from different laboratories could be compared. The existing terminology differences can be intimidating to those not actively working in the field. Population genetics is a discipline that is closely related to studies of speciation, and is one for which many *Fusarium* species are well-suited, given their ubiquity and relatively large population sizes. An important facet that needs to be added is a comparison of populations from native as well as agricultural ecosystems. Relatively few good models of fungal populations are presently available and work with any of several *Fusarium* spp. could help to fill this void. *Fusarium* species also are serving as models for the study of secondary metabolism and the organization and regulation of the genes involved in this biosynthetic process. Manipulation of fumonisin and trichothecene biosynthesis, to name but two groups of compounds, is of both basic scientific and economic importance. *Fusarium* species also carry traits of interest that have been studied in other fungi that should be examined in this genus to determine their comparability with their better-studied counterparts. Some of these traits include: regulation of the assimilation of metabolites, mating type, spore killer, transposable elements, karyotype composition, pathogenicity genes, and genes that govern vegetative compatibility reactions.

Keywords: *Fusarium*, genetics, vegetative compatibility, molecular biology.

The last systematic review of *Fusarium* genetics was by Puhalla (1981), although less extensive reviews on some individual species have appeared more recently (Sidhu, 1988; Van Etten & Kistler, 1988). In his 1981 review, Puhalla addressed sexual and asexual recombination, cultural variability, and nuclear composition. In this brief contribution I will update some areas covered by Puhalla while ignoring others since relatively little progress has been made in those. First, I will discuss three issues (identification and classification,

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development of standards, and genetic maps) that are needed to make *Fusarium* spp. more attractive for genetic investigations and then describe three areas (fungal population genetics, vegetative compatibility, and secondary metabolism) for which *Fusarium* spp. have particular genetic promise. It is my hope that in the coming years some *Fusarium* spp. will become important as research tools for fungal geneticists and will be of significance beyond their economic import and control.

Identification and classification

Identification and classification of *Fusarium* species relies on morphological characters, whether these characters be traditional spore morphology or molecular in nature. For genetic purposes, however, morphological characters are not relevant. Instead, a biological species definition must be used in which a species is defined as a population of organisms that share a common gene pool (Dobzhansky, 1950). Individuals in such a population can generally exchange genetic information through the production of fertile progeny without being subject to the restrictions associated with differences between species. It is possible for strains that are morphologically quite distinct, for example due to mutation or environmental conditions, to be in the same mating population, or biological species. A more common occurrence is that strains that are difficult, if not impossible, to distinguish morphologically are not sexually interfertile with one another. Within such morphological entities, however, subgroups are common in which the members are interfertile with one another, but are not cross-fertile with members of other such subgroups. These subgroups are commonly termed sibling species but may also be referred to as mating populations or intersterile groups. Also inherent in this definition is the concept that the species is typified by the population to which the individuals belong. A strictly interpreted application of the morphological concept that a species is typified by a single strain is not a part of a biological species definition, since all strains are expected to be discrete and distinct genetically.

Under a biological species definition the species are usually thought of as discrete entities which exchange no genetic information with one another under any conditions. Just as this concept does not hold rigidly for higher plants, in which traits of interest can be introgressed through extremely poorly fertile "wide" crosses, so can crosses between members of different species occasionally produce viable, fertile progeny. The view taken of such inter-species

interfertility is critical in determining whether groups of organisms should be viewed as distinct at the species level or at a sub-specific level (see Perkins, 1994 for a more detailed discussion of this topic). If morphological criteria are used for distinguishing species, then a knowledge of the heritability (and stability) of the morphological traits significantly increases the credibility of the morphological characters being used for taxonomic purposes.

Within the *Fusarium* genus the biological species concept has been applied in the teleomorphs *Nectria haematococca* and *Gibberella fujikuroi*, each of which contains several sibling species that are normally identified as mating populations. Anamorphs for *Nectria haematococca* belong to *Fusarium solani* and include both heterothallic and homothallic isolates (Daboussi-Bareyre & Parisot, 1981; Matuo & Snyder, 1973). Most genetic studies have been done with either mating population I and VI (Van Etten & Kistler, 1988). Anamorphs for *Gibberella fujikuroi* are found in *Fusarium* section *Liseola* (Klittich & Leslie, 1992; Leslie, 1991a) and the known mating populations are all heterothallic. Most genetic studies have been done with *Fusarium moniliforme* (mating population A) although some work has also been done with mating populations D (*Fusarium proliferatum*) and F (also *F. moniliforme*). Description of different mating populations together with their sexual stages as distinct species would simplify genetic work with these organisms since it would make relevant literature more accessible to researchers who do not work primarily with *Fusarium*, and preclude inappropriate comparisons between strains in different species that presently share a common name.

Development of standards

For *Fusarium* spp. to become accepted as model systems it also will be necessary to standardize protocols and terminology used within species. A major first step would be for the research community to identify suitable laboratory strains and/or genetic backgrounds for common standard usages. There are two basic methods for establishing laboratory standard strains. In the first case, a suitable field strain is identified and is used for the development of mutagenesis, sexual crossing, transformation, and related protocols. Interesting traits from other field strains would be introgressed into this background using the selected strain as the recurrent parent in a series of repetitive crosses. In *Gibberella fujikuroi*, traits that could be moved in this manner would include traits such as fumonisin non-production or the opposite mating type allele. Standard equations are

available to calculate the number of generations of inbreeding that are necessary to achieve particular isogenization levels (Leslie, 1981). If no field strain can be identified that has all of the desired attributes, then the desired strain could be synthesized by crosses between different strains to obtain the desired characters all within a single strain. Related strains, often sibs, may be sufficiently closely related to be used as alternates depending on the crossing protocol that was employed. The availability of standard strains makes it more likely that researchers with basic interests will include *Fusarium* in their studies of basic phenomena. These types of strains are available in genetically tractable filamentous fungi such as *Neurospora crassa* and *Aspergillus nidulans* and have made work with these systems much simpler than it might otherwise have been.

Standardized genetic terminology will also simplify communication and prevent the confusion that can result from different names and naming conventions. Recommendations for standard terminology were made for plant pathogenic fungi by Yoder & al. (1986), which are based on the general usage in *Saccharomyces cerevisiae*. In *N. haematococca* these guidelines have generally been followed and a summary table in which old names are transformed into their new forms has been published (Van Etten & Kistler, 1988). In *G. fujikuroi* the names used generally follow this form as well, with the exception of mating type for which an alternative format has been retained. In some cases in *G. fujikuroi* and in many cases in *F. oxysporum* the terminology that has been used follows that proposed by Demerec & al. (1966) that has been widely adopted for use in bacteria and some fungi, most notably *Aspergillus nidulans*. For researchers in a particular niche, individual terminology is convenient and may be little more than an extension of laboratory jargon, but in a broader context it adds confusion to the field. Development of a common terminology that can be used by all researchers is to be strongly encouraged.

Genetic maps

A key character of developed genetic systems is that genetic maps and other basic tools are available for general use. Genetic maps may be either physical or recombinational in nature. Each type of map has its own uses, strengths and weaknesses (see Hulbert, 1995 for a discussion). Physical maps may be as simple as identifying the chromosome band on a pulsed field electrophoresis gel to which a particular probe hybridizes. Electrophoretic karyotypes are available for a number of *Fusarium* species (Boehm & al., 1994; Fekete & al., 1993; Migheli & al., 1993; Nagy & Hornok 1994; Xu & al., 1995),

and in *Gibberella fujikuroi* mating population A the different chromosomal bands have been correlated with recombination-based linkage groups (Xu & al., 1995). Technical difficulties with the separation of large DNA molecules (>10 megabase pairs) make comparisons between laboratories difficult. At the other extreme, physical maps can also be detailed "contigs" in which physically contiguous pieces of DNA have been identified in genomic libraries constructed in phage, bacterial or yeast vectors. To my knowledge there are no contigs available for use in any *Fusarium* species.

Recombination-based genetic maps are the type of map that is usually thought of when genetic maps are discussed. The introduction of molecular markers, such as isozymes, restriction fragment length polymorphisms (RFLPs) and random amplified polymorphic DNA (RAPDs), has made the construction of recombination-based maps much more efficient. When using conventional auxotrophic and morphologic markers, the maximum number of markers that can be scored in a single cross is usually no more than 6-8 and may be as few as 2-3 depending on the interactions of the different mutant alleles. [A description of some of these difficulties and a list of the conventional mutants that are known in *N. crassa* can be found in Perkins & al. (1982).] With molecular markers, hundreds of different loci can be scored in a single cross and multiple labs can easily correlate mapping results with a single set of progeny strains. The accuracy of the map depends on the number of progeny and the number of markers scored. The progeny must be collected in such a manner that each can be assumed to have originated from a separate meiosis (Leslie, 1991b). Centromeres, which require data from tetrads, are not usually placed on these maps unless this information is available from an independent source. Conceptually it is easiest to construct these maps for heterothallic fungi, since all of the meiotic spores will have resulted from cross-fertilization. If precautions are taken to ensure that selfed progeny are excluded, then the construction of such maps with homothallic fungi, such as *Gibberella zeae*, also is possible.

Recombination-based and physical maps are usually complementary in nature and many labs use both types of maps simultaneously to achieve their objectives. In my lab (Xu & Leslie, 1996; Xu & al., 1995), we have used a combination of physical and recombinational approaches to construct a map of *G. fujikuroi* mating population A in which the physical chromosomes have been correlated with linkage groups established through recombination-based analyses. In such efforts, an average number of kb of DNA per centiMorgan is often calculated. These numbers can be useful, but must be used with caution since recombination is usually not distributed randomly throughout the genome.

An unusual phenomenon, which was first discovered in fungi in *Nectria haematococca*, is that of dispensable "B" chromosomes (Miao & al., 1991). These chromosomes have since been found in other fungi, including other *Fusarium* spp. (Xu & al., 1995). The role of these chromosomes, and the genes that they carry, has been hypothesized to be similar to that of plasmids and their loci in bacteria. One hypothesis is that genes that are involved in pathogenicity and toxin detoxification are carried on these chromosomes (Miao & al., 1991), but this hypothesis needs further testing.

The availability of strains that differ in "B" chromosome composition and in the number and size of essential ("A") chromosomes suggests that studies of genome organization could be quite interesting. For example, differences in karyotype or the relative locations of different loci could be used to study chromosome rearrangements that accompanied or confirmed speciation. The differences observed by Boehm & al. (1994) in strains of the same VCG of *F. oxysporum* f. sp. *cubense* strongly suggests that when constraints on genome organization, perhaps the lack of meiosis, are relaxed significant karyotypic divergence can occur relatively quickly. Studies of genome organization are powerful complements to the taxonomic and evolutionary biology studies that are common in these fungi.

Fungal population genetics

Fusarium spp. are widely distributed in both agricultural and native ecosystems on a worldwide scale. Population analyses need to be viewed from two different perspectives. In one case there is the study of genes that are selected for some purpose. Economically important examples would include pathogenicity determinants which are critical for understanding the epidemiology and control of pathogenic strains. Other obviously selected loci, although of little or no economic importance, include the genes governing mating type and vegetative compatibility; these loci play a critical role in determining the structure and maintenance of existing populations. If loci such as these are used for population genetic analyses, then the results can be used in conventional epidemiological models, and also may provide information on the natural history of the organism and/or the structure of the population. Data from these studies must be interpreted cautiously if protocols that assume the markers are selectively neutral are used for the analysis.

As an alternative to these potentially selective markers, there are numerous molecular markers, such as RAPDs and RFLPs, that are generally assumed to be selectively neutral. Variation for neutral

markers does not necessarily imply that there are similar levels of variation in ecologically important traits such as pathogenicity. Population structure as assayed from neutral markers is most useful for making inferences about the roles of recombination, genetic drift and gene flow.

Recombination frequencies can be important if it is possible to generate new pathotypes through recombination. Recombination is obviously of greater concern if the population is sexual than if it is asexual. In fungi where strains may be functional hermaphrodites, which includes most *Fusarium* spp., the relative numbers of hermaphrodites and female-sterile strains in the population can be an important indicator of how often sexual reproduction is occurring. Similarly, if there are large numbers of strain types present in the population, then recombination is a far more effective method for the maintenance of such diversity than is mutation.

Studies of gene flow can be important from a plant pathology viewpoint because they can help define what group actually constitutes a population, and how this group is distributed both temporally and spatially. For example, if gene flow is restricted, then quarantine measures to keep out a particular strain type and permit the cultivation of a sensitive host type would be effective agricultural practices. Hierarchical analyses of populations on different scales are usually necessary for the elucidation of such structure. Since some plants may be infected with multiple strains of a single fungus, e.g. Kedera & al. (1994), the scale of interest may be quite small. A more detailed outline for the analysis of these problems has recently been given by Milgroom (1995), and potential areas of research with *G. fujikuroi* in Leslie (1995).

Vegetative (heterokaryon) compatibility

Studies of vegetative compatibility in *Fusarium* have had two objectives. The first objective has been in population studies in which vegetative compatibility serves as a multigenic marker for the determination of strain identity. Unlike molecular fingerprint probes, however, the vegetative incompatibility (*vic*) loci are not selectively neutral in a population context and cannot be used to distinguish levels of relatedness other than identity/non-identity. At least two evolutionary models rationalizing the existence of the vegetative compatibility phenomenon have been proposed (Hartl & al., 1975; Nauta & Hoekstra, 1995), but neither has been tested and other alternatives exist. Controversy over the evolutionary origins of this

trait, however, does not lessen its utility or its inherent interest for further studies.

Work with vegetative compatibility in *Fusarium* has recently been reviewed (Leslie, 1993), but has primarily focused on testing the hypothesis that the vegetative compatibility groups (VCGs) resulting from the presence of two or more alleles at *vic* loci in populations of *F. oxysporum* are correlated with pathogenicity (Puhalla, 1985). This model assumes that pathogens rarely, if ever, participate in recombination events that could lead to the reassortment of *vic* alleles resulting in new VCGs. Under this model each VCG is essentially a clone, and VCG and pathogenicity are correlated by coincidence and not by cause-and-effect. In some pathogenic formae speciales this correlation is quite strong, e.g., *F. oxysporum* f. sp. *apii*, *cubense*, *cyclaminis*, and *melonis*, but in other cases the correlation is weak or nonexistent, e.g., *F. oxysporum* f. sp. *asparagi* and *lycopersici*. Curiously, saprobic strains are virtually always diverse, see for example Correll & al. (1986), raising the question of how this recombination-based diversity can be maintained in an organism with no known sexual stage.

A second major objective of vegetative compatibility studies is to elucidate the basic mechanism(s) that is (are) responsible for the recognition and killing/compatibility responses that accompany hyphal fusion. It is likely that there are many ways in which recognition occurs and the acceptance/killing process is initiated since there are multiple *vic* loci and the alleles at these loci usually interact only with other alleles at the same locus [but see Bégueret & al. (1994) for a summary of the system in *Podospira anserina* in which alleles at different loci may interact with one another]. The interaction probably involves some cell membrane and periplasmic space components since protoplasts behave differently than do hyphal cells, see Adams & al. (1987) for a *Fusarium* example. If the killing reaction can be induced selectively, then it may be possible to develop an environmentally friendly method for controlling selected fungal strains. It is important that studies such as these be conducted with *Fusarium* spp. if these novel methods of control are to be available for the control of these pathogens.

Secondary metabolites

No paper on *Fusarium* would be complete without some mention of the secondary metabolites that they are known to produce, see for example Marasas & al. (1984). The *Fusarium* genus has at least three pathways – trichothecenes, gibberellic acid and fumonisins – which

occur in organisms that are potentially useful for basic studies of the control of secondary metabolism. This important area is a strength for researchers who work with these organisms and should be exploited to attract other researchers to these systems. Genetic work with gibberellic acid and trichothecenes have been recently reviewed (Cerdá-Olmedo & al., 1994; Desjardins & al., 1993).

Genetic studies of the production of secondary metabolites are of interest for several reasons. First, they may provide insights into the biochemical pathway by which the compounds are synthesized. Such insights are often critical in devising control schemes to block or reduce the synthesis of these compounds. If the compound is desirable, such an analysis may identify rate-limiting steps that need to be enhanced in order to increase production. In addition to the structural genes, the regulatory genes in this process are probably of equal or greater interest. These regulators are likely to turn on many facets of secondary metabolism and not just a single pathway. To the extent that the regulation of secondary metabolism transcends taxonomic barriers, studies of these phenomena will be of interest far beyond the scope of *Fusarium* alone. Regulation of secondary metabolism will also require a better understanding of primary metabolism as well. It seems likely that differences between *Fusarium* and other model organisms in apparent primary metabolism might also reflect significant differences in secondary metabolism as well, see Leslie (1986, 1987) for differences in nitrogen assimilation regulation and proline utilization. Since *Fusarium* strains are generally good saprobes, are amenable to molecular genetic analysis, and usually have a sexual stage which can be induced under laboratory conditions, they are a good choice for this type of analysis.

Future prospects

The genetic study of *Fusarium* spp. has several areas of great potential and great need. The areas of greatest potential are: (1) studies of speciation and relatedness, especially in the area of genome organization, (2) fungal population genetics, especially if populations from natural and agricultural ecosystems are compared, and (3) studies of the synthesis and regulation of secondary metabolite production. The areas of greatest need are in basic genetic infrastructure. If *Fusarium* spp. are to be studied more widely and by researchers whose primary interest is not mycology or plant pathology, then the technical difficulties presently associated with working with many of these organisms must be greatly diminished. Once these problems are reduced, researchers with more disparate

research interests should find these organisms much more attractive research tools.

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