*Review*

# The Fungal Genetics Stock Center: a repository for 50 years of fungal genetics research

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The Fungal Genetics Stock Center (FGSC) was established in 1960 to ensure that important strains used in early genetics research were available to subsequent generations of fungal geneticists. Originally, only mutant strains were held. At present, any organism that has had its genome sequenced is a genetic system and so the FGSC has added many new organisms. The FGSC is well integrated in its core community and, as research came to depend on cloned genes, vectors and gene libraries, the FGSC included these materials. When the community expanded to include plant and human pathogens, the FGSC adopted these systems as well. Wild isolates from around the world have also proven instrumental in answering important questions. The FGSC holds tremendous diversity of the *Neurospora* species, which form the core of the collection. The growth in the number of strains distributed illustrates the growth in research on fungi. Because of its position near the centre of the fungal genetics effort, the FGSC is also the first to see trends in research directions. One recent example is the 300% jump in requests for strains of *Neurospora crassa* carrying a mutation that makes them sensitive to high salt concentration. These strains were seldom requested over many years, but became among our most popular resources following the demonstration of their utility in studying fungicide resistance. This exemplifies why materials need to be preserved without regard to their immediate perceived value and reinforces the need for long-term support for preservation of a broad variety of genetic resources.

[McCluskey K, Wiest A and Plamann M 2010 The Fungal Genetics Stock Center: a repository for 50 years of fungal genetics research; *J. Biosci.* **35** 119–126] **DOI** 10.1007/s12038-010-0014-6

## 1. Introduction

Founded in 1960, the Fungal Genetics Stock Center (FGSC) was a response to a need expressed by the Genetics Society of America to preserve important materials such as the strains used in the seminal demonstration of the one-gene one-enzyme hypothesis (Beadle and Tatum 1941). There was a concern that as the individual researchers retired or moved on to other avenues of inquiry, the materials used in their experimentation would not be available to future researchers. The FGSC was first housed at Dartmouth College and grew quickly. Most of the strains in the early collection were *Neurospora crassa* and *Aspergillus nidulans*, and they were limited to mutants that had an easily definable phenotype. Of the thousand strains in the collection by 1965, most were nutritional auxotrophs or morphological mutants. The availability of such high-quality stocks led to a growth of the research community, and renewal and expansion of the FGSC grant during subsequent grant cycles. This has continued until the present day and, while the FGSC has physically moved three times, its integration with the community of researchers has allowed it to survive these moves with little disruption to its mission (McCluskey 2003).

The FGSC is funded by the National Science Foundation (NSF) Living Stock Collection Programme and, as such, it is in good company. Other collections in this programme include the *E. coli* Stock Center, the *Bacillus* Stock Center, the *Drosophila* Research Center, the *Chlamydomonas* Resource Center and the *Arabidopsis* Biological Resource Center. These collections are all genetic repositories and thus represent the genetic diversity of a particular research

**Keywords.** *Aspergillus*; culture collection; fungal genetics; genomics; *Neurospora*

system. Other collections in the NSF Living Stock Collection programme include the University of Texas Culture Collection of Algae, the International Culture Collection of Arbuscular Mycorrhizal Fungi at West Virginia, and even the Mycology and Botany Collection of the American Type Culture Collection. These latter collections are type collections that emphasize the diversity of organisms within a higher taxonomic group.

While type collections typically have a strong emphasis on taxonomy, stock centres such as the FGSC emphasize the genetics of the organisms in the collection. The modest research effort at the FGSC reflects this. While type collections focus on identification of species, the research effort at the FGSC has been on identifying the underlying mutation in genetically mapped but otherwise anonymous temperature-sensitive mutants (McCluskey *et al.* 2007, 2008).

The FGSC collection has historically been highly focused. Our criterion for including materials in the collection is that an organism can be included if there is significant genetics (i.e. there are genes identified that can be manipulated and followed in a cross or population) and an active research community. In that regard, we were limited for many years to holding *Neurospora* and *Aspergillus* stocks. As the *Neurospora* research community was more willing to deposit stocks, the number of *Neurospora* stocks has always been greater than that of other species (table 1). Because we are able to store strains that have been freeze-dried or kept on anhydrous silica gel, we are able to operate on a small budget with minimal staff. The FGSC has historically had a Director who has minimal operational responsibility, a Curator who oversees and participates in the operation of the collection, and one or two full- or part-time assistants. By way of contrast, the *Drosophila* Stock Center at Indiana University has over 20 curators and assistants. The most significant difference is that *Drosophila* cannot be preserved by freeze drying; all 20 000 fly stocks must be kept alive and flying at all times.

**Table 1.** Numbers of strains in the FGSC collection[a]

| Number of strains | Species |
|---|---|
| 17 628 | *Neurospora crassa*[b] |
| 936 | *Aspergillus nidulans*[b] |
| 672 | *Neurospora intermedia*[b] |
| 532 | *Fusarium* sp.[b] |
| 306 | *Neurospora tetrasperma*[b] |
| 283 | *Neurospora sitophila* |
| 253 | *Schizophyllum commune*[b] |
| 241 | *Sordaria* sp. |
| 153 | *Neurospora discreta* |
| 136 | *Magnaporthe grisea*[b] |
| 134 | *Aspergillus niger*[b] |
| 75 | *Pichia pastoris* |
| 52 | *Neurospora* hybrid |
| 28 | *Ascobolus* sp. |
| 26 | *Gelasinospora* sp.[b] |
| 31 | *Aspergillus fumigatus*[b] |

[a]Includes only the organisms for which we have significant collections.

[b]Includes the strain that was sequenced.

## 2. FGSC holdings

The FGSC holdings include over 75 000 individual strains. These include strains in three different categories – accessioned active strains, accessioned archival strains and non-accessioned strains. As of June 2009, there were 21 640 strains accessioned into the FGSC collection and over 13 000 were active. To be considered active, a strain would have either been deposited or requested by a client within the past ten years. Nearly 8000 strains are archival and as such are not subject to the regular testing that active strains undergo. No strains are discarded because they have not been requested; rather, they are available on an as-is basis.

Of the strains accessioned in the FGSC collection, most are *Neurospora* strains (table 1) with mutants outnumbering wild-type strains by a significant margin; as of mid 2009, there were 19 341 mutant strains accessioned in the FGSC collection and only 2274 wild-type strains. The mutants include 1026 *Aspergillus* strains and 17 510 *Neurospora* strains. Over 10 470 of the *Neurospora* mutants are *N. crassa* strains carrying single targeted gene deletions deposited by the *Neurospora* functional genomics programme (Dunlap *et al.* 2007). An additional 3855 strains carry a single genetic marker; 1618 strains have two lesions and 755 have three markers. Just over 1100 strains have more than three markers and two strains have 15 markers each. Most of the strains with multiple markers are for traditional genetic mapping and as such are not requested as often as they were before genome sequences were available.

The wild-type strains in the FGSC collection were mostly collected by Dr David Perkins and most come from tropical or neotropical sites (Turner *et al.* 2001). Reflecting the natural distribution of species, the FGSC collection holds 279 wild-type *N. crassa* isolates, 611 *N. intermedia* isolates, 193 *N. tetrasperma* isolates, 152 *N. discreta* isolates, 246 *N. sitophila* isolates and 12 isolates of other *Neurospora* species. Recent studies have shown that *Neurospora* can be found in temperate zones including the US and several countries in Europe (Jacobson *et al.* 2006), and many of these temperate isolates have also been deposited in the FGSC collection. The wild strains in the FGSC collection have been used in genome sequencing efforts (table 2), and have

allowed the identification of the only transposon ever found in *Neurospora* (Sewell and Kinsey 1996). A special grant from the NSF allowed the FGSC to accession a collection of *Schizophyllum commune* strains from the University of Vermont (Raper and Fowler 2004) in 2004. These stocks are mostly characterized with regard to their mating-type alleles and as such represent the diversity of mating types found in nature for *Schizophyllum*. Finally, as the genomics revolution has swept through the fungal genetics community, the FGSC has re-evaluated what it means to be a genetic system. Because of this, we have agreed to take on stocks of most fungi that have had their genomes sequenced. In this regard, the FGSC has been aligned with both the fungal genomics initiative at the Broad Institute at MIT and the efforts of the US Department of Energy Joint Genome Initiative (table 2).

Another group of noteworthy strains in the FGSC collection are the genetically engineered strains. In addition to the previously mentioned deletion mutants of *Neurospora crassa*, this category includes several groups of strains such as *Pichia* strains carrying cell-wall degrading enzymes from *Aspergillus nidulans* (Bauer *et al.* 2006), and deletion strains of *Cryptococcus neoformans* (Liu *et al.* 2008) and *Candida albicans* (Nobile and Mitchell 2009).

In addition to the main collection, the FGSC holds materials that are non-accessioned. These fall into a number of different categories including archival and orphaned collections, special purpose collections, and sets that are intended to be used together.

Most of the archival collections are from researchers who have retired or are deceased. The first such collection

**Table 2.** Genome strains in the FGSC collection

| FGSC # | Description | Other stock # | Organization |
|---|---|---|---|
| 2489 | *Neurospora crassa* | 74-OR23-1VA | Broad Institute |
| A4 | *Aspergillus nidulans* | M139 | Broad Institute |
| 9002 | *Phanerochaete chrysosporium* | RP-78 | DOE JGI |
| 9003 | *Coprinus cinereus* | 130; Okayama 7 | Broad Institute |
| 9021 | *Ustilago maydis a1 b1* | UM521 | Broad Institute |
| 9075 | *Fusarium graminearum* | PH-1, NRRL 31084 | Broad Institute |
| A1100 | *Aspergillus fumigatus* | AF293 | The Institute for Genomics Research |
| A1120 | *A. flavus* | NRRL3357 | Aspergillusflavus.org |
| A 1121 | *A. niger* | NRRL3 | DOE JGI |
| A1143 | *A. niger* | NRRL3, ATCC 9029 | |
| A1144 | *A. niger* | NRRL 328, ATCC 1015 | |
| A1156 | *A. terreus* | NIH2624 | Broad Institute |
| 9935 | *F. oxysporum fsp lycopersici* | NRRL 34936, 4287 | Broad Institute |
| 9923 | *Ashbya gossypii* | ATCC 10895 | Ashbya Genome Database |
| 9596 | *Nectria haematococca* | 77-13-4 | DOE JGI |
| 9543 | *Rhizopus oryzae* | RA99880 | Broad Institute |
| 9487 | *Cryptococcus neoformans* | H99 | Broad Institute |
| 8958 | *Magnaporthe grisea* | 70-15 | Broad Institute |
| 10004 | *Phycomyces blakesleeanus* | NRRL1555 | DOE JGI |
| 10005 | *Phycomyces blakesleeanus* | A56 | DOE JGI |
| A1513 | *Aspergillus niger* | CBS 513.88 | DSM |
| 10173 | *Stagonospora nodorum* | SN15 | Broad Institute |
| 10136 | *Verticillium albo-atrum* | VaMs102 | Broad Institute |
| 10137 | *Verticillium dahliae* | VdLs17 | Broad Institute |
| 10138 | *Verticillium dahliae* | VdBob70 | Broad Institute |
| 10383 | *Podospora anserina* | S + | Genoscope |
| 10384 | *Podospora anserina* | S - | Genoscope |
| 10389 | *Agaricus bisporus* | JB137-S8 | DOE JGI |
| 10392 | *Agaricus bisporus* | H97 | DOE JGI |

was the Tatum lyophil collection. These stocks represent the freeze-dried specimens of *Neurospora* from the Stanford and Yale laboratories of Dr E L Tatum (Barratt 1986). Totalling nearly 1300 individual stocks, these specimens span an important time in the development of fungal genetics from 1946 until 1975 when the last stocks were added to the set. The viability of these stocks is unknown and they were not stored in controlled temperature storage from at least 1982 to 2004. However, several were opened in response to a client request a number of years ago. In that instance, we showed that samples that had been freeze-dried for as long as 53 years remained viable (McCluskey 2000). Some samples that were not as old were not viable, suggesting that strain or sample characteristics contribute directly to viability.

Another significant archival collection is the 263 *Allomyces* strains from the collection of Dr R Emerson and Dr L Olson (Olson 1984). These were sent to the FGSC in 1995 and have been maintained as dry filter paper stocks at 5°C. They are not curated in that there are no resources to test or re-preserve them, but individual stocks have been sent when requested. As the *Allomyces* research community is not large or active, these materials might otherwise not have been preserved. Since they include mutants in amino acid metabolism, mating and representatives of worldwide diversity, this was an important collection to maintain. Moreover, as chytrids have been found to be a basal group to the fungi and are implicated in the die-off of amphibians around the world, it is likely that this will be an increasingly important collection.

Because temperature-sensitive mutants offer a special perspective into genetics and cell biology, the FGSC accepted a collection of primary temperature-sensitive mutants of *A. nidulans* (Harris *et al.* 1994). These 1150 strains have been screened by a number of researchers for mutations in specific pathways, but as primary mutants (they have not been back-crossed to ensure that only one mutation is present) they are limited in their appeal.

Many scientists have sent collections to the FGSC upon their retirement and these are the last category of archival non-accessioned materials. Among these are small collections from individuals including Dr Mary Case of the University of Georgia, Dr Ann Lacy of Gaucher College, Dr Fred deSerres of Oak Ridge National Laboratory, Dr John R S Fincham of Cambridge University and perhaps, most notably, Dr David Perkins of Stanford University.

The latter collection includes strains of *Neurospora* from around the world in addition to those which are part of the main FGSC collection. Also included are genetic strains with special marker sets for a variety of purposes. While these are not formally in the catalogue, they are described in publications by Dr Perkins and his colleagues.

Ironically, the last group of non-accessioned strains is also the most numerous in the collection. These are the 48 000 *Magnaporthe oryzae*-tagged integrant strains which were produced by the Magnaporthe working group to facilitate work with this important plant pathogen (Betts *et al.* 2007). Because they are regulated by the US Department of Agriculture Biotechnology Regulatory Service, they have not been utilized as much as might have been desired. They are described online at the MGOSdb website: *http://www.mgosdb.org/*.

One distinguishing characteristic of the FGSC is its willingness to take on materials generated through developing technologies. To that end, in 1985, the FGSC began accepting molecular genetic resources for deposit into the collection. While plasmids (cloned genes and cloning vectors) have been accessioned into the collection, gene libraries are accepted with the understanding that they will be maintained only as long as they are of use to the research community. In this light, the FGSC has accessioned nearly 650 characterized molecular clones including 197 cloned genes, 308 restriction fragment length polymorphism (RFLP) probes, 53 fungal transformation and cloning vectors, and 72 additional clones for mutagenesis, gene expression or, most recently, protein-tagging vectors including green, blue, red and yellow fluorescent proteins. Because of their broad applicability, these materials have been very popular, both within the fungal genetics community and in related communities such as the plant pathology or medical mycology communities.

Because many people in the research communities were using the same genome libraries, it was possible, even before genome sequencing was common, to join cosmids into larger assemblages, now known as contigs. This may have even facilitated the early assembly of the *Neurospora* genome. As genome sequencing became more common, many investigators inquired about depositing their libraries or clone banks into the FGSC. We have continued to accept genome libraries, although we have a number of criteria that each library must meet before we add it to the FGSC collection. The first criterion is that the library needs to be mapped onto the genome sequence. This allows a researcher to identify overlapping clones and target a region of the genome in which they are interested. This approach has been used very successfully in identifying the mutation in a number of anonymous temperature-sensitive mutants of *N. crassa* (McCluskey *et al.* 2007, 2008).

The second criterion is that the organism from which a library was made is not easily manipulated in the laboratory. This allows us to focus on libraries from organisms that are difficult or impossible to grow in the laboratory, such as *Puccinia graminis* (Stem rust) or on organisms that require special permits to obtain, such as *Magnaporthe oryzae* (Rice blast).

Despite these criteria, we have continued to accept libraries that can be deposited and shipped, as pools of phage

or DNA. This has allowed us to add libraries for organisms such as *Coprinus*, *Aspergillus fumigatus*, *Fusarium verticillioides* and *F. sprorthrichioides*.

### 3. Distribution

Our distribution is global. In the past 20 years, the FGSC has shipped materials to researchers in over 50 different countries (figure 1). After an increase in the late 1990s, the number of orders received by the FGSC fell to a low of 335 in 2003. Since that time, the number of orders has nearly doubled to a high of 631 in 2007 (table 3 and figure 2). In 2008, there were 644 orders for materials from the FGSC, suggesting that this trend has continued. The number of unique users has grown as well. Most of the orders received by the FGSC are for academic research. Only about 15% of our orders are from for-profit laboratories and most of these are for molecular materials such as cloning or expression vectors. Approximately equal numbers of strains are sent to US and foreign laboratories.

The growth in orders has been spread nearly equally among the strains in the FGSC collection. In 2002, 656 *Neurospora* strains and 133 *Aspergillus* strains were distributed. In 2007, 1874 *Neurospora* strains and 211 *Aspergillus* strains were distributed. While the absolute numbers of strains is different, both have nearly doubled in the past five years while the number of other strains requested has remained more or less the same (table 4). One area that has shown a strong decrease in use is the gene libraries. The greatest number of gene libraries was distributed in 1998 when 114 individual libraries were shipped. In 2007, only 27 gene libraries were requested from the FGSC. Moreover, in the late 1990s, most libraries requested were ordered genomic libraries while in 2007, all of the libraries sent were cDNA or genomic library pools (table 4). This decrease is related to the availability of the genome sequence online for *Neurospora* (Galagan *et al.* 2003) and *Aspergillus* (Galagan *et al.* 2005). Since the FGSC began distributing gene libraries, over 550 sets have been distributed. Similarly, the distribution of cloned genes in the plasmid collection has gone down since the genome sequence became available, but there has been an increase in the distribution of individual cosmid, fosmid or bacterial artificial chromosome clones from genome-associated libraries. Overall, the number of molecular clones distributed has remained relatively stable. The high distribution in 2003 and 2004 was due to the use of RFLP marker sets for assembling the *Fusarium* and *Magnaporthe* genomes in those years.

The final and most recent category of molecular resources we make available is genomic DNA. We use a similar criterion for this as we do for accessioning ordered genomic libraries; we prepare genomic DNA for organisms that are difficult to culture or for which a special permit would be required. While the number of individual samples of genomic DNA distributed is not very large (we sent 28 samples in 2006–2008), the potential impact is significant in our ability to expand the community of researchers who include filamentous fungi in their consideration. Finally, the

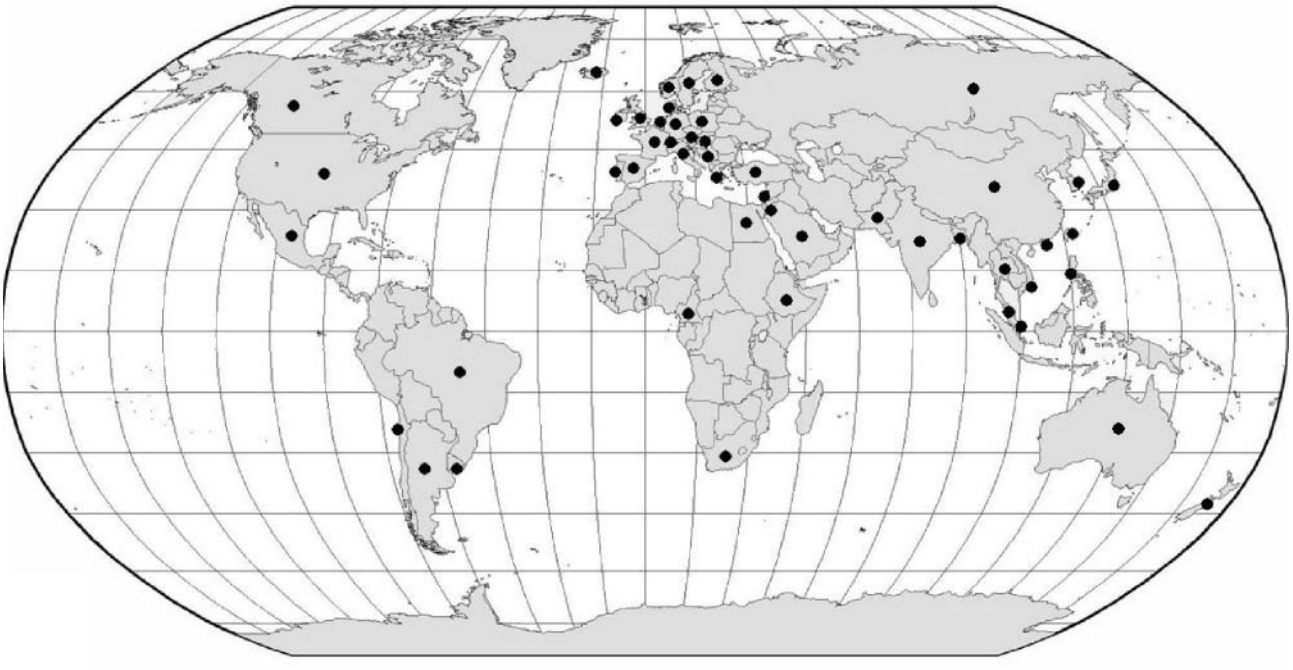

**Figure 1.** Global distribution of materials from the FGSC collection, 2004–2008.

**Table 3.** Users of materials in the FGSC collection

| | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 |
|---|---|---|---|---|---|---|---|
| Number of orders | 355 | 335 | 463 | 478 | 560 | 631 | 644 |
| Unique users | 257 | 249 | 332 | 310 | 351 | 368 | 371 |
| Academic users (foreign) | 230 (119) | 222 (114) | 297 (153) | 277 (149) | 324 (175) | 345 (182) | 341 (176) |
| Commercial users (foreign) | 21 (6) | 21 (11) | 35 (19 ) | 32 (16 ) | 27 (12 ) | 21 (8) | 30 (14) |

FGSC has, over the years, purchased and redistributed a number of resources that were either not available piecemeal, prohibitively expensive in small lots or difficult to prepare in small batches. This has included enzyme preparations for generating protoplasts, as well as Vogels 50X salt solution for growing *Neurospora*. Since the FGSC also uses a large number of specialized tubes for preparing silica gel stocks or lyophilized spore stocks (Wilson 1986), we also make available pre-sterilized silica gel blanks and lyophil tubes.

## 4. Discussion

The FGSC has largely fulfilled its mission of preserving and distributing biological resources for research on filamentous fungi. The uniform availability of strains, clones and other materials opens the field to any researcher who is interested in a question. Key discoveries made with materials in the FGSC collection include the seminal one-gene one-enzyme hypothesis, gene silencing, regulation of translation, circadian rhythms, histone modification and more. The FGSC is cited in hundreds of publications per year, demonstrating in the most fundamental way the value of the collection.

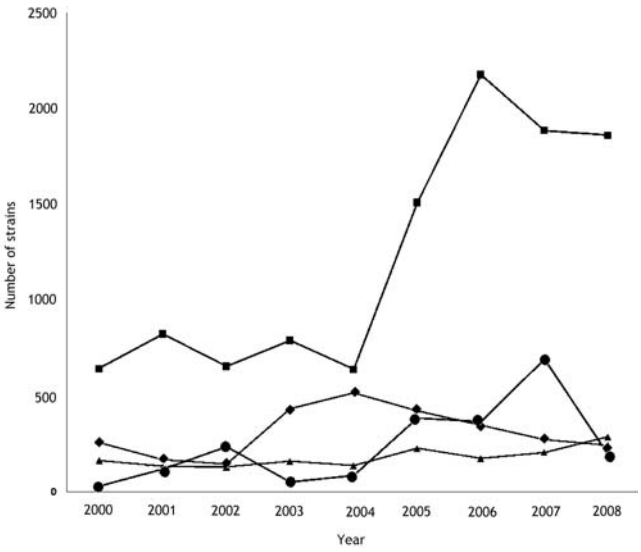


**Figure 2.** Numbers of strains distributed over the past nine years. (■) *Neurospora* strains, (▲) *Aspergillus* strains, (●) other fungal strains, and (♦) plasmids and other molecular clones.

**Table 4.** Breakdown of strain distribution

| | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 |
|---|---|---|---|---|---|---|---|
| *Neurospora* | 656 | 791 | 640 | 1509 | 2174[a] | 1874[a] | 1859[a] |
| *Aspergillus* | 133 | 163 | 141 | 230 | 176 | 211 | 289 |
| Other strains | 236 | 55 | 87 | 386 | 368 | 370 | 197 |
| All strains (foreign)[b] | 1025 (541) | 1009 (301) | 868 (431) | 2125 (1169) | 2718[a] (1266) | 2455[a] (1145) | 2354 (1113) |
| Plasmids | 146 | 435 | 519 | 425 | 349 | 263 | 245 |
| Cloned cDNA | 10 | 35 | 0 | 8 | 0 | 0 | 0 |
| DNA | NA[c] | NA[c] | NA[c] | NA[c] | 13 | 12 | 3 |

[a]This does not include 3936 *N. crassa* KO strains sent as arrayed mutants in 96-well format in 2006, 27 000 in 2007 and 28 000 in 2008.
[b]The number of strains sent to foreign destinations is shown in parentheses.
[c]DNA samples were not available prior to 2006.

The FGSC is a unique resource for research on filamentous fungi. It occupies a central position that gives it a unique perspective on trends in genetics research. This is seen in the way material distribution rises in a growing economy and falls as research efforts are scaled back when the economy falls. For example, distribution to commercial clients fell from an all-time high of 71 orders in 1999 to a low of 21 in 2002, mirroring the economic downturn experienced in 2002. The FGSC also has a geographical perspective on research trends. We distribute materials to countries from South Africa to Iceland, and changes in requests reflect expansion of research in different countries.

The FGSC distributes materials without regard for the ability to pay. We ask modest fees for strains and offer fee waivers for researchers who do not have support. We do not distribute strains to private individuals and ship only to academic or recognized commercial addresses.

The importance of holding resources without regard to their apparent usefulness is exhibited by the distribution patterns of strains of *N. crassa* carrying the *os-2* lesion. These strains were requested relatively infrequently until they were shown to be resistant to fungicides, at which point they became among the most widely requested strains in the collection (McCluskey and Plamann 2008). If the FGSC was required to de-accession materials that are now held as archival materials, we would lose the ability to respond to changes in knowledge. Many strains that have anonymous mutations, such as temperature-sensitive or morphological mutations, have increased value once the actual open reading frame is identified. These strains offer insight that deletion mutants likely cannot.

While strains can be useful to many different researchers, being able to find strains is a necessary prerequisite to ordering strains. In this regard, there have been a number of efforts towards making strain catalogues available over the internet. Recently, investigators at the University of Gent have launched a meta-index called *straininfo.net*. This site allows access to strain databases from a number of collections including the FGSC as well as the American Type Culture Collection and many others. The FGSC catalogue is also online at *www.fgsc.net*.

There are many collections of fungi in the US and around the world. Most emphasize the diversity of fungi, or at least the diversity of either a geographical or biological subset of all fungi. There are no other collections that emphasize the genetics of filamentous fungi. In this regard, the FGSC is unique. However, because the FGSC also holds large numbers of wild-collected isolates, it resembles in some ways a type collection, albeit one with a narrow focus. Another area where we resemble a type collection is in holding strains that have had their genome sequenced. The FGSC holds over 25 such isolates and has agreed to take on additional strains as they are sequenced. While this is valuable for the FGSC, it also imposes particular challenges. Many fungi are regulated by different government agencies. Plant pathogens are regulated by the US Department of Agriculture (USDA) animal and plant health inspection service. Genetically engineered plant pathogens are regulated by the USDA biotechnology regulatory service. Some human pathogens are regulated by the US Centers for Disease Control and Prevention and some fungi, such as *Magnaporthe*, are regulated by the US Department of State, Bureau of Industry and Security. *Magnaporthe* cannot be exported from the US because it was at one point developed as a biological weapon. This exemplifies the increasingly byzantine regulatory environment in which we operate. Shipping regulations continually evolve, as do import restrictions. Individual countries have different restrictions based on their own needs and conditions. The FGSC has always maintained that recipients must provide any appropriate permits prior to shipping materials but, in some cases, import or customs officers at the destination require additional payments, making the importation of biological materials prohibitive. Scientist-to-scientist exchanges may circumvent these obstacles, but any publication citing the source of materials may be *de facto* admission of violation of regulations pertaining to the organisms in question.

Collections such as the FGSC have a great responsibility to preserve the biological resources of the current generation for future researchers. Whether in a type collection with tremendous breadth, or in a genetic collection emphasizing one or two specific areas, the value of materials increases as they are used and characterized by multiple researchers. Collections allow this material to span generations and facilitate the translation from basic research to industrial or pharmaceutical applications.

## Acknowledgements

This material is based upon work supported by the National Science Foundation under Grant No. DBI-0742713.

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*MS received 21 July 2009; accepted 23 November 2009*

*e*Publication: 29 January 2010

Corresponding editor: DURGADAS P KASBEKAR