## 1 Introduction

Filamentous fungi are of considerable socioeconomic importance, being both vital as industrial tools of enzyme and antibiotic production ([Santos and Linardi, 2004](#_ENREF_28); [Ward et al., 2004](#_ENREF_35)[Goto et al., 1996](#_ENREF_13); [Roze et al., 2007](#_ENREF_27)) and as pests of crops ([Bosmans, 2009](#_ENREF_2)). In addition, fungi are used as model organisms in fundamental research, such as on the effect of sex and recombination ([Bruggeman et al., 2003](#_ENREF_3); [Leslie and Klein, 1996](#_ENREF_16)) and the dynamics of adaptation ([Schoustra et al., 2009](#_ENREF_31)). Despite their significance, we know little about the population biology of individual fungal colonies. Chiefly important for this understanding is the development of population growth models for filamentous fungi ([Nielsen, 1992](#_ENREF_24)). Current models on fungal growth focus on directly describing biomass or product formation involved in particular industrial processes without regard to the underlying population growth driving the system [e.g. ([Mitchell et al., 2004](#_ENREF_22))].

**References**

Adams, T.H., Wieser, J.K., and Yu, J.-H., 1998. Asexual Sporulation in *Aspergillus nidulans*. Microbiology and Molecular Biology Reveiws 62, 35–54.

Bosmans, S., 2009. On the evolution of pesticide resistance in *Phytophtora infestans*: an experimental evolution approach. PhD Thesis, Wageningen University, Wageningen.

Bruggeman, J., Debets, A.J.M., Wijngaarden, P.J., de Visser, J.A.G.M., and Hoekstra, R.F., 2003. Sex slows down the accumulation of deleterious mutations in the homothallic fungus *Aspergillus nidulans*. Genetics 164, 479-485.

Buchanan, R.L., Whiting, R.C., and Damert, W.C., 1997. When simple is good enough: comaprison of the Gompertz, Baranyi, and three phase linear models for fitting bacterial growth curves. Food Microbiology 14, 313-326.

Clark, T.A., and Anderson, J.B., 2004. Dikaryons of the basidiomycete fungus *Schizophyllum commune*: evolution in long-term culture. Genetics 167, 1663-1675.

Clutterbuck, A.J., 1994. Mutants of *Aspergillus nidulans* deficient in nuclear migration during hyphal growth and conidiation. Microbiology 140, 1169.

De Crecy, E., Jaronski, S., Lyons, B., Lyons, T., and Keyhani, N., 2009. Directed evolution of a filamentous fungus for thermotolerance. BMC Biotechnology 9.

Edelstein, L., and Segel, L.A., 1983. Growth and metabolism in mycelial fungi. Journal of Theoretical Biology 104.

Elander, R., 2003. Industrial production of beta-lactam antibiotics. Applied and Environmental Biotechnology 61, 385-392.

Elena, S.F., and Lenski, R.E., 2003. Evolution experiments with microorganisms: the dynamics and genetic bases of adaptation. Nature Reviews Genetics 4, 457-469.

Ferrer, J., Prats, C., Lopez, D., and Vives-Rego, J., 2009. Mathematical modelling methodologies in predictive food microbiology: a SWOT analysis. International Journal of Food Microbiology 134, 2-8.

Fitzsimmons, J., Schoustra, S.E., Kerr, J., and Kassen, R., 2010. Population consequences of mutational events: effects of antibiotic resistance on the *r/K* trade-off. Evolutionary Ecology 24, 227-236.

Gifford, D.R., De Visser, J.A.G.M., and Wahl, L.M., 2012. Model and test in a fungus of the probability that beneficial mutations survive drift. Biology Letters, doi: 10.1098/rsbl.2012.0310.

Goto, T., Wicklow, D., and Yto, Y., 1996. Aflatoxin and cyclopiazonic acid production by a scelrotium-producting *Aspergillus tamarii* strain. Applied and Environmental Microbiology 62, 4036-4038.

Hamidi-Esfahani, Z., Hejazi, P., Shojaosadati, S., Hoogschagen, M., Vasheghani-Farahani, E., and Rinzema, A., 2007. A tow-phase kinetic model for fungal growth in solid state cultivation. Biochemical Engineering Journal 36, 100-107.

Isaac, P.K., 1963. Abnormally divergent sectors in cultures of filamentous fungi. Nature 200, 382-383.

Leslie, J.F., and Klein, K.K., 1996. Female Fertility and Mating Type Effects on Effective Population Size and Evolution in Filamentous Fungi. Genetics 144, 557-567.

Lew, R., 2011. How does a hypha grow? The biophysics of pressurized growth in fungi. Nature Reviews Microbiology, 509-518.

Matcham, S., Jordan, B., and Wood, D., 1985. Estimation of fungal biomass in a solid state substrate by three independent models. Appl. Environ. Microbiol. 21, 108-112.

McKellar, R.C., 1997. A heterogeneous population model for the analysis of bacterial growth kinetics. International Journal of Food Microbiology 36, 179-186.

McMeekin, T., Bowman, J., McQuestin, J., Mellefont, L., Ross, T., and Tamplin, M., 2008. The future of predictive microbiology: strategic reseach, innovative applications and great expectations. International Journal of Food Microbiology 128, 2-9.

Mims, C., Richardson, E., and Timberlake, W., 1988. Ultrastructural analysis of conidiophore development in the fungus *Aspergillus nidulans* using freeze-substitution. Protoplasma 144, 132-141.

Mitchell, D., Von Meien, O., Krieger, N., and Dalsenter, F., 2004. A review of recent developments in modeling of microbial growth kinetics and intraparticle phenomena in solid-state fermentation. Biochemical Engineering Journal 17, 15-26.

Momany, M., and Taylor, I., 2000. Landmarks in the early duplication cycles of *Aspergillus fumigatus* and *Aspergillus nidulans*: polarity germ tube emergence and septation. Microbiology 146, 3279.

Nielsen, J., 1992. Modelling the growth of filamentous fungi. Advances in Biochemistry Engineering and Biotechnology 46, 187-223.

Polizeli, M., Rizzatti, A., Monti, R., Terenzi, H., Jorge, J., and Amorim, D., 2005. Xylanases from fungi: properties and industrial applications. Applied Microbiology and Biotechnology 67, 577-591.

Pontecorvo, G., and Gemmell, A.R., 1944. Colonies of *Penicillium notatum* and other moulds as models for the study of population genetics. Nature 154, 532-534.

Roze, L., Beaudry, R., Arthur, A., Calvo, A., and Linz, J., 2007. Aspergillus volatiles regul;ate aflatoxin synthesis and asexual sporulation in *Aspergillus parasiticus*. Applied and Environmental Microbiology 67, 577-591.

Santos, V., and Linardi, V., 2004. Biodegradation of phenol by a filamentous fungus isolated from industrial effluents - identification and degradation potential. Process Biochemistry 39, 1001-1006.

Schoustra, S.E., 2004. Reducing the cost of antibiotic resistance. Experimental evolution in the filamentous fungus *Aspergillus nidulans*, Wageningen.

Schoustra, S.E., Slakhorst, M., Debets, A.J.M., and Hoekstra, R.F., 2005. Comparing artificial and natural selection in rate of adaptation of genetic stress in *Aspergillus nidulans*. Journal of Evolutionary Biology 18, 771-778.

Schoustra, S.E., Bataillon, T., Gifford, D.R., and Kassen, R., 2009. The Properties of Adaptive Walks in Evolving Populations of Fungus. PLOS Biology 7, e1000250.

Schoustra, S.E., Rundle, H.D., Dali, R., and Kassen, R., 2010. Fitness-Associated Sexual Reproduction in a Filamentous Fungus. Current Biology 20, 1350–1355.

Timberlake, W., 1991. Temporal and spatial controls of Aspergillus development. Current Opinion in Genetics and Development 1, 351-357.

Vargaz-Perez, I., Sanchez, O., Kawasaki, L., Georgellis, D., and Aguirre, J., 2007. Response regulators srra and sska are central components of a phosphorelay system involved in stress signal transduction and asexual sporulation in *Aspergillus nidulans*. Eukaryotic Cell 6, 1570.

Ward, M., Lin, C., Victoria, D., Fox, B., Fox, J., Wong, D., Meerman, H., Pucci, J., Fong, R., Heng, M., Tsurushita, N., Gieswein, C., Park, M., and Wang, H., 2004. Characterization of humanized antibodies secreted by *Aspergillus niger*. Applied and Environmental Microbiology 70, 2567-2576.

Wolkow, T., Harris, S., and Hamer, J., 1996. Cytokinesis in *Aspergillus nidulans* is controlled by size, nuclear positioning and mitosis. Journal of Cell Science 109, 2179.

Zwietering, M.H., Jongenburger, I., Rombouts, F.M., and Van t Riet, K., 1990. Modeling of the bacterial growth curve. Applied and Environmental Microbiology 56, 1875.