



Genomics of wood-degrading fungi



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ABSTRACT

Woody plants convert the energy of the sun into lignocellulosic biomass, which is an abundant substrate for bioenergy production. Fungi, especially wood decayers from the class Agaricomycetes, have evolved ways to degrade lignocellulose into its monomeric constituents, and understanding this process may facilitate the development of biofuels. Over the past decade genomics has become a powerful tool to study the Agaricomycetes. In 2004 the first sequenced genome of the white rot fungus *Phanerochaete chrysosporium* revealed a rich catalog of lignocellulolytic enzymes. In the decade that followed the number of genomes of Agaricomycetes grew to more than 75 and revealed a diversity of wood-decaying strategies. New technologies for high-throughput functional genomics are now needed to further study these organisms.

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1. Introduction

Recent advances in genome sequencing technologies have enabled biologists to add genomics tools to their toolkits. These next generation sequencing technologies have transformed genomics from single-genome projects led by multi-institutional consortia with multi-million dollar budgets into affordable single-lab experiments. The scope of these experiments has therefore changed from single-genome studies into multi-genome comparisons. One excellent example where these transformations made a significant impact on science and applications is the genomics of wood-degrading fungi.

Woody plants, through photosynthesis, use the sun's energy to fix vast quantities of carbon into lignocellulose, a substance that gives wood its rigidity and decay-resistance, and is one of the most abundant forms of organic carbon on Earth. Lignocellulose is a heterogeneous matrix made up of the carbohydrate polymers cellulose and hemicellulose, and the aromatic polymer lignin. It is the predominant polymeric component of living plants, and is present in forest litter and soil.

Considerable energy is stored in lignocellulose, and wood has, accordingly, been used as a fuel since ancient times. Of relevance

to our modern energy needs, when the polymeric components of lignocellulose are enzymatically broken down, chemical compounds are yielded, which, through fermentation, can be made into biofuels. Lignocellulose is thus an abundant and renewable substrate for biofuel production, and indeed, plant biomass (including lignocellulose along with algal biomass) may be the most cost-effective route for converting the sun's energy into fuels (Carroll and Somerville, 2009).

Despite its appeal as a biofuel substrate, lignocellulose is highly resistant to microbial attack, and this toughness also makes it recalcitrant to biofuel production. Wood decay fungi and biofuel production share the same initial goal: to break down lignocellulose into its monomeric constituents (primarily glucose, but also xylose, mannose, galactose, rhamnose, and arabinose). Towards this end, fungi, particularly those capable of decaying wood, have evolved a broad array of hydrolytic enzymes including cellulases, hemicellulases, and pectinases, as well as oxidative enzymes serving diverse functions including depolymerizing lignin and converting the often-toxic by-products of ligninolysis that might otherwise inhibit fungal growth. Collectively, these enzymes are known as carbohydrate-active enzymes (CAZymes), and are classified into numerous families of Glycoside Hydrolases (GHs), Glycosyl Transferases (GTs), Polysaccharide Lyases (PLs), Carbohydrate Esterases (CEs), and Auxiliary Activities (AAs) (Levasseur et al., 2013; Lombard et al., 2014). Thus, it may be that wood-decaying fungi harbor degradative capabilities that facilitate the efficient production of lignocellulose-derived biofuels.

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Most wood decay fungi belong to the fungal phylum Basidiomycota, specifically, the class Agaricomycetes (Fig. 1). Currently, genomes of 31 members of the Agaricomycetes have been sequenced and published, 26 of these by the DOE Joint Genome Institute (JGI). Over the past decade, the number of sequenced genomes in this class has grown at an increasingly rapid pace to more than 75 (Fig. 2). Wood decayers can be broadly divided into white rot fungi, which completely degrade all components of the plant cell wall; and brown rot fungi, which rapidly depolymerize cellulose, but leave lignin as a modified, mostly polymeric, residue [18363712,21261800]. Neither white rot fungi nor brown rot fungi form monophyletic groups. It has been suggested that the brown rot lifestyle has evolved several times, and that all white rot fungi share a common ancestor that was itself a white rot fungus (Floudas et al., 2012). Not all Agaricomycetes are wood decayers – for example, several members of the order Agaricales occupy other ecological niches (Fig. 1). *Laccaria bicolor* and *Piriformospora indica* both form interactions with plant roots, whereas *Coprinopsis cinerea*, *Agaricus bisporus* and *Volvariella volvacea* are saprotrophs generally growing on the non-woody substrates dung, leaf litter, and straw, respectively. A considerable diversity of lifestyles beyond wood decay is therefore found in Agaricomycetes.

The results of the past ten years of sequencing and analysis are reviewed here, from the first sequenced genome of a wood-degrading fungus, *Phanerochaete chrysosporium* (Martinez et al., 2004), to massive sequencing projects like the 1000 Fungal Genomes Project (Grigoriev et al., 2014). We discuss changes in sequencing technology during that period, and developments and challenges in the assembly and annotation of sequenced genomes.

Key genomic studies of wood decay fungi and their role in the better understanding of wood decay are summarized. Furthermore, we demonstrate how new annotation methods may improve existing genome annotations. We conclude with a discussion of the need for high-throughput functional genomics, which will allow a more in-depth understanding of wood degradation by the Agaricomycetes.

2. Transformations in sequencing technology

In the last 10 years sequencing technologies have changed dramatically, offering multiple options in throughput, accuracy, and cost for answering different biological questions. Sanger sequencing (Sanger et al., 1977) was the first platform enabling sequencing of a range of organisms including human (Lander et al., 2001), *P. chrysosporium* (Martinez et al., 2004; Vanden Wymelenberg et al., 2006), and several other plant biomass-degrading fungi (Eastwood et al., 2011; Martinez et al., 2008, 2009; Morin et al., 2012; Ohm et al., 2010; Stajich et al., 2010). A Sanger-based genome assembly was usually built from paired-end reads obtained from sequencing three types of libraries with 3 kilobasepairs (kbp), 8 kbp, and 40 kbp fosmid insert sizes. Most Sanger-sequenced wood decay fungi were assembled with Jaz (Aparicio et al., 2002) or Arachne (Batzoglou et al., 2002; Jaffe et al., 2003).

More recently an explosion in the number of alternative sequencing platforms, collectively called 'next generation sequencing' (NGS), has made genome sequencing more accessible to the research community. The technological advances of NGS have led

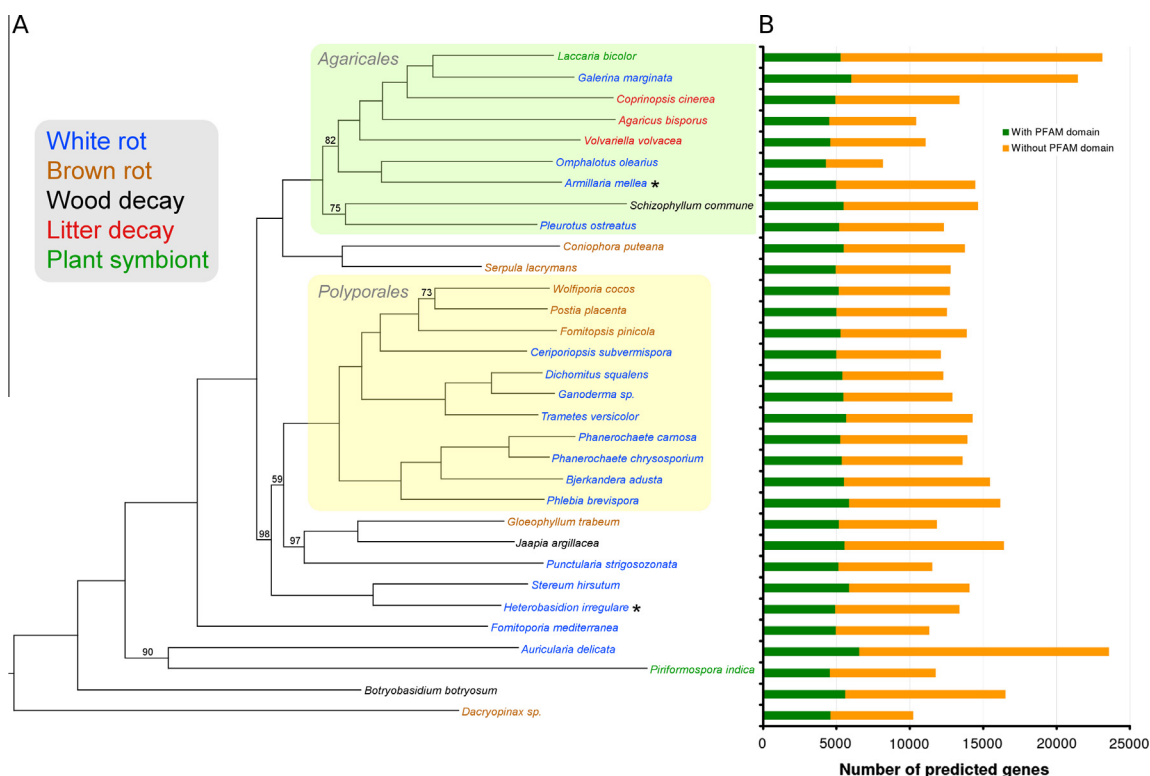


Fig. 1. (A) Phylogeny and main lifestyles of Agaricomycetes with a published genome sequence. The major orders Agaricales and Polyporales are indicated. The majority of these species are wood decayers and can be further classified as either white rot fungi (which degrade all components of the plant cell wall) or brown rot fungi (which modify lignin, but do not break it down to a large extent). *Schizophyllum commune*, *Jaapia argillacea* and *Botryobasidium botryosum* are also wood decayers, but cannot be easily classified as either white or brown rot fungi. *Coprinopsis cinerea*, *Agaricus bisporus* and *Volvariella volvacea* are saprotrophs growing on non-woody substrates. The ectomycorrhizal fungus *Laccaria bicolor* and the endophyte *Piriformospora indica* both form interactions with plant roots. Species with an asterisk (*) are predominantly plant pathogens. The genomes of *G. marginata*, *P. ostreatus*, *J. argillacea* and *B. botryosum* have been submitted for publication. See Text S1 for more details. (B) Number of predicted genes for each genome. Each bar lines up with a species from the tree in (A). The total number of genes varies per genome, but the number of genes with at least one PFAM domain is more constant. Genes without a PFAM domain outnumber those with a PFAM domain, showing that much remains to be learned about these organisms.

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