Current Overview of Breeding and Genomic Studies of White Button Mushroom (*Agaricus bisporus*)

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Abstract

Agaricus bisporus is a popular edible mushroom that is cultivated worldwide. *Agaricus bisporus* is the model fungus which acts as an important component of the human diet for over 200 years. Repetitive DNA elements are ubiquitous constituents of eukaryotic genomes and the availability of whole genome sequence leads to draw a picture of the genome-wide distribution of genes of interest. This also provides insights into potential mechanisms of genome arrangement and their expression pattern. The genomic data played an important role in assessing the evolution, adaptation of mushrooms and will enhance the scope of future genetic improvements of *A. bisporus*. Several microsatellites appeared widely and distributed over the whole genome sequence of *A. bisporus*. Molecular markers techniques help the researchers for accurate identification and differentiation of cultivars/strains of white button mushroom. These markers were developed by mining the genome sequence and an efficient technique for the identification of *A. bisporus* cultivars and have adequate potential to facilitate the marker-assisted breeding in the future.

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14.1 Introduction

Agaricus bisporus (Lange) Imbach (white button mushroom) is an extensively cultivated edible mushroom throughout world. *Agaricus bisporus* is a widely cultivated mushroom known for its significant economic value and abundant nutritional and medicinal attributes (Beelman et al. 2003). White button mushroom (*Agaricus bisporus*) is considered one of the most widely consumed and popular edible mushrooms, not only for delicious taste but also for its rich nutrition and medicinal value. This mushroom is one of the best source of vitamins, dietary fibre, protein, minerals, amino acids and bioactive compounds (Khan et al. 2014). Business related to edible mushrooms is estimated around US$42 billion per annum (Prescott et al. 2018). Besides consumption of fruit bodies of *Agaricus bisporus*, the spent substrate generated after cultivation of *A. bisporus* has been utilized for treatment of textile effluents decolourization (Singh et al. 2012) and bioremediation of 4 structurally different azo dyes (Ahlawat and Singh 2009). The white-rot fungi, viz., *Schizophyllum commune* and *Pezizomycotina* sp. Exhibit in the spent waste of this mushroom has also reported to decolourize the structurally different textile dyes (Singh and Chauhan 2017). The two strains of *Agaricus bisporus* (U3 and S11) were screened for their mycelia growth in petri plates for decolourization against 9 structurally different textile dyes (Singh et al. 2013; Singh 2014). The present chapter will highlights the advancement made in the field of, molecular breeding, improvement in germplasm and genomics pertaining to *A. bisporus*.

14.2 Genome Sequencing of *Agaricus bisporus*

The whole genome of white button mushroom (*Agaricus bisporus* var. *bisporus* ARP23) was sequenced and assembled with genome sequencing platform, viz., Illumina and PacBio sequencing technology. Morin et al. in 2012 sequenced and published the genome of *A. bisporus*. The two genomes H-97 and JB137-s8 have sizes of 30.4 and 32.8 Mb with 10,438 and 11,289 protein-coding genes estimated and reported. The fruiting ability of *A. bisporus* var. *burnettii* at 25 °C in have been reported by combination of QTL mapping, transcript analyses and candidate gene studies to unravel the genetic and molecular mechanisms. Numerous candidate genes have been identified and are analysed for potential targets and for functional analysis. The *A. bisporus* genome contains a full set of genes for polysaccharide-degrading enzymes similar to other fungi growing on plant wastes or wood, and two Mn peroxidases for lignin breakdown. Motifs pertaining to genome-sequenced soil-inhabiting or lignocellulosic fungi occurs at a higher rate in genomes of *A. bisporus*

which are 4.2 and 3.1 times more frequent in JB137-s8 and H97 (Morin et al. 2012). The combination of various factors, viz., physiology, genome composition and transcriptional regulation, does not allow *A. bisporus* to be considered as white-rot or brown-rot fungi. This edible fungi is well adopted to humic-rich environments and is the only genome-sequenced organism with this adaptation; it is therefore the 'type organism' or model species for this environment (Morin et al. 2012). In past several researchers have identified many genes and ESTs associated with mushroom growth and development both while attached to the mycelium and harvested mushroom fruit bodies (De Groot et al. 1997; Ospina-Giraldo et al. 2000; Eastwood et al. 2001). Analysis of the A. *bisporus* genome suggested that some of the regulatory switches are shared with other *Agaricus* species, while others are clade specific (Morin et al. 2012).

14.3 Expression of Genes and Their Linkage with White Button Mushroom

The overexpression of *c2h2* in *A. bisporus* mushroom results in faster production of mushrooms due to faster mycelia run in the cultivation substrates. The c2h2 gene is also involved in faster pin head formation and fruit body development. The c2h2 orthologue of *Agaricus bisporus* was overexpressed and forming basidiomycete using *Agrobacterium*-mediated transformation. Several important parameters, like morphology, cap formation rate and total number and biomass of mushrooms, were not affected by overexpression of c2h2. The crop of mushroom strain having c2h2 overexpression picked 1 day earlier as compared to control. The gene c2h2 impacts timing of mushroom formation at an early stage of development, making its encoding gene a target for breeding of commercial button mushroom strains (Pelkmans et al. 2016).

In another study, the expression of carbohydrate active enzyme (CAZyme)-encoding genes in compost casing layer and fruit body development during commercial cultivation of *A. bisporus* suggested a clear tissue-type related regulatory system (Patyshakuliyeva et al. 2013). Sufficient diversity of CAZy genes has been expressed in compost-grown mycelium which is related to the degradation of plant biomass components, while fruiting bodies mainly expressed CAZy genes which synthesized and modified the cell wall of this edible fungi. Differences were also visible at the metabolic level as the compost-grown mycelium-expressed genes of a wide variety of sugar catabolic pathways, while in the fruiting body, only glycolysis-related genes were expressed (Patyshakuliyeva et al. 2013). This showed the diversity of sugars released by the CAZymes is being converted simultaneously by *white button mushroom*, but in fruiting bodies only glucose and derivatives of glucose, such as trehalose or sorbitol and mannitol, are converted into fungal biomass. Other monosaccharides or other sugar alcohols could not be traced in the fruiting bodies which suggested that only these compounds are transported into the fruiting body from the mycelium of *A. bisporus*. This suggested that sugar transport to the fruiting

Table 14.1 Different types of genes encoding for necessary traits in *A. bisporus*

S. N.	Name of genes	Traits	Name of authors
1.	PPO and PAL genes *AbPPO1, AbPPO2, AbPPO3, AbPPO4, AbPPO5, AbPPO6, AbPAL1* and *AbPAL2*	Browning development	Xiaochen Qian et al. (2021)
3.	Cys2His2 (c2h2) zinc finger protein gene	c2h2 gene of *Schizophyllum commune* overexpressed for fruit bodies formation/earliness in *A. bisporus*	Pelkmans et al. (2016)
4.	Urea	Encoding urease in *A. bisporus*	Matthijs et al. (2006); Wagemaker et al. (2005)
5.	Riboflavin-aldehyde-forming enzyme (raf) gene	Transcriptional regulation of the raf gene during *A. bisporus* morphogenesis	Sreenivasaprasad et al. (2006)
6.	hom2 (homeodomain gene)	hom2 gene of *Schizophyllum commune* overexpressed in *A. bisporus*	Ohm et al. (2011)
7.	Gat1	Played a role in expansion of the fruiting body	Pelkmans et al. (2016); Ohm et al. (2011)
8.	Carbohydrate active enzyme (CAZyme)	Played a role in carbohydrate utilization by *A. bisporus*	Patyshakuliyeva et al. (2013)
9.	Heat shock protein (HSP70) gene	High temperature tolerance genes	Hao et al. (2021)
10.	Para-aminobenzoic acid (PABA) synthase	–	Lu et al. (2014)

body is not solely an osmotically driven process but involves either specific transporters or carrier proteins.

Comparative transcriptomics of mycelium grown on casing soil, defined medium and compost revealed genes encoding enzymes involved in pectin, cellulose, xylan and protein degradation are highly expressed in cultivation substrates. There is need to intregrate the output pertaining to mapping of quantative trait loci (QTL), transcript analysis and expression of candidate genes will make the genetic and molecular mechanism more understable. The specific growing temperature may be easily optimized and identified for cultivation of white button mushroom at industrial scale. Several candidate genes have been also identified and are potential targets for further functional analysis. Heat shock protein (HSP70) is high temperature tolerance genes of *A. bisporus* may release the high temperature tolerance varieties (Table 14.1).

14.4 Pangenome Genes of *Agaricus bisporus*

Pangenome is defined as the union of all genes observed across all strains/isolates of a species. A study was conducted for *A. bisporus* species and pangenome was constructed using the synteny-dependent PanOCT method implemented in Pangloss with the default parameters (Fouts et al. 2012; McCarthy and Fitzpatrick 2019a, b). PanOCT clusters homologous sequences into synthetic orthologous clusters (SOCs) based on BLAST score ratio (BSR) assessment of sequence similarity and on proportions of relative synteny (conserved gene neighbourhood, CGN) among the orthologues (Fouts et al. 2012; Rasko et al. 2005).

14.5 Gene Editing in *Agaricus bisporus*

Researcher from Penn state university engineered the common white button mushroom (*Agaricus bisporus*) to resist browning. They targeted the family of genes that encodes polyphenol oxidase (PPO) that causes browning. Yang et al. knocked out one of 6 PPO genes which ultimately led to reducing the 30% of enzyme's activity. Man-made gene editing techniques include zinc-finger nuclease (ZFN), transcription activator-like effector nuclease (TALEN) systems and recently developed hottest tool, CRISPR-Cas9. Yang et al. 2000 applied the CRISPR/Cas9 tool to edit the white button mushroom (*Agaricus bisporus*). This genome editing tool does not contain any foreign DNA from pests, viruses, fungi and bacteria. Mushroom that reduce browning are beneficial because they keep their colour for longer period when silenced which enhanced their shelf life. In September, 2015, Penn state university filed the provisional patent application for the protection of this innovative technology.

14.6 Molecular Markers Developed from Genome Sequences

DNA-based molecular markers developed in last two decades for *A. bisporus* are used to analyses and identification of important agronomic traits. Several simple sequence repeat (SSR) markers were also developed by mining the genome sequences of *A. bisporus* (Table 14.2). SSRs, also known as microsatellites or short tandem repeats (STRs), constituted from DNA sequences of length one to six base pairs (bp) (Jany et al. 2006; Dettori et al. 2015). These markers are multiallelic and co-dominant in nature and are considered more informative than other markers (Selkoe and Toonen 2006). These markers are frequently in use and have been used successfully in past for genetic studies and varietal identification of *A. bisporus* (Foulongne-Oriol et al. 2009, 2011; Rokni et al. 2015; Fu et al. 2016; Wang et al. 2016). In similar study, Wang et al. (2019) has identified 3134 SSRs markers and out of these 1644 are distributed in the intergenic regions and 1490 were reported from gene models. A total of 17 polymorphic primer pairs were produced and SSR fingerprints were constructed for all the commercial genotypes. The

Table 14.2 Different types of molecular markers used to study the *A. bisporus*

S. N.	Type of molecular marker/traits	Name of mushroom/strain	Name of authors
1.	SNPs	Linkage analysis in *A. bisporus*	Foulongne-Oriol (2012); Gao et al. (2015, 2016); Sonnenberg et al. (2016)
2.	RAPD	To identify button mushroom cultivars	Moore et al. (2001)
3.	Restriction fragment length polymorphism (RFLP)	To elucidate the life cycle of *A. bisporus*, to genotype commercial and wild lines and to generate the first linkage map	Summerbell et al. (1989); Loftus et al. (1988); Kerrigan et al. (1993)
4.	SSR	Demonstrated that microsatellite markers were more powerful to generate linkage maps for *A. bisporus*.	Foulongne-Oriol et al. (2009)
5.	Inter-simple sequence repeat marker (ISSR)	*A. bisporus* for strain differentiation	Barroso et al. (2000); Guan et al. (2008)
6.	Directed amplification of microsatellite-region DNA (DAMD)	*A. bisporus* for strain differentiation	Barroso et al. (2000); Guan et al. (2008)

variation in the number of repeats among genotypes and deletion or insertion of base pairs leads to showing polymorphism (Feng et al. 2016).

Mining of more and more SSR markers from the whole genome sequences may generate more accurate and informative SSR markers and these supposed to be more cost-effective than the markers developed by others methods (Zhao et al. 2012; Du et al. 2013; Chen et al. 2015). The aim of the above-mentioned study was to determine the SSR profile in the whole genome sequences of *A. bisporus* and develop a set of SSR markers for testing different genotypes of *A. bisporus*. Several researchers have already used the SSRs markers to study the genetic diversity, strain identification, genetic mapping and population structure of different fungi (Goodwin et al. 2007; Albertin et al. 2014; Masneuf-Pomarede et al. 2016). Similarly, ISSR markers provide an efficient alternate for identification of homokaryons and suggest these markers be considered as new tools for the survey of *Agaricus* species (Barroso et al. 2000; Guan et al. 2008). Others molecular markers, viz., directed amplification of microsatellite-region DNA (DAMD) and inter-simple sequence repeat marker (ISSR), are based on the amplification of a genomic region between two copies of a microsatellite sequence by using a single primer defined on the repeated motif. They were successfully developed in *A. bisporus* for differentiation of genotypes (Barroso et al. 2000; Guan et al. 2008).

Molecular markers provide an efficient technique for the identification of *A. bisporus* cultivars and this study will also facilitate the molecular identification and marker-assisted breeding of other mushrooms in the future.

After the publication of the whole genome sequence of *Agaricus bisporus* (Morin et al. 2012; Sonnenberg et al. 2016), SNP markers were designed and used because they appear to be very useful in generating linkage maps (Gao et al. 2015, 2016) and to study the precise location of meiotic crossovers (Sonnenberg et al. 2016).

14.7 Conclusion

Breeding programmes exploiting the variability in *Agaricus* germplasm with the aim to develop varieties, which may fulfil the broader objectives, such as resistance to disease, adaptation to climate changes or response to cultural conditions. Molecular markers are key tools to support and speed up the breeding programmes. There is need to develop more and more markers in *A. bisporus* for marker-assisted selection, linkage mapping, and strain fingerprinting and population diversity analysis. Presently, SSR markers are being utilized as an efficient and reliable technical support for the protection of mushroom varieties. Wild germplasm resources generally exhibit better genetic diversity and carry superior traits compared to commercial lines, which should be exploited and utilized to develop new varieties with improved agronomic and quality traits of button mushrooms. The SSR markers described in this study will lead to protect the breeders' rights of mushroom varieties, and they will also enhance the activities related to marker-assisted selection in future breeding practices. As co-dominant markers, SSRs are interesting for various genetic studies because they display a high level of heterozygosity and transferability; they are then key tools for genotyping individuals from natural populations or from a collection of cultivated strains. Sequencing the genome of *A. bisporus* has opened the way to understand the transcriptomics analysis & expression pattern of the specific strains towards cultivation substrates over the time. Post-genomic study needs to focus on solving the problem of wet bubble and dry bubble diseases in *Agaricus bisporus*. There is need to develop more and more strains of biotic and abiotic resistance in near future.

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