Current Research in Food Science 6 (2023) 100430

Contents lists available at ScienceDirect

Current Research in Food Science

journal homepage: www.sciencedirect.com/journal/current-research-in-food-science

Application of omics technology in the research on edible fungi

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ARTICLE INFO

Handling Editor: Professor A.G. Marangoni

Keywords:
Edible fungi
Omics technology
Genomics
Transcriptomics
Proteomics
Metabolomics

ABSTRACT

Edible fungus is a large fungus distributed all over the world and used as food and medicine. But people's understanding of edible fungi is not as much as that of ordinary crops, so people have started a number of research on edible fungi in recent years. With the development of science and technology, omics technology has gradually walked into people's vision. Omics technology has high sensitivity and wide application range, which is favored by researchers. The application of omics technology to edible fungus research is a major breakthrough, which has transferred edible fungus research from artificial cultivation to basic research. Now omics technology in edible fungi has been flexibly combined with other research methods, involving multiple studies of edible fungus, such as genetic breeding, growth and development, stress resistance, and the use of special components in edible fungus as pharmaceutical additives. It is believed that in the future, the research of edible fungi will also be brought to a deeper level with the help of omics technology. This paper introduces the application progress of modern omics technology to the study on edible fungi and mentions the application prospect of edible fungi research with the constant development of omics technology, thereby providing ideas for the follow-up in-depth research on edible fungi.

Omics technologies, include the following: genomics, which analyzes the structural composition of the whole genome of organisms; transcriptomics, which studies genes at the level of RNA; proteomics, which analyzes protein composition of organisms and its changing law; and metabolomics, which explores small molecule metabolites. These technologies have been skillfully applied to studies on animals, plants and microorganisms. With the rapid development of omics technology and its wide application to different research fields, many researchers have starting focusing on the omics research of edible fungi. Edible fungi have large fruiting bodies. Most of the discovered edible fungi belong to Basidiomycotina and Ascomycotina (Tao et al., 2019). And they have a large amount of protein, mineral elements, vitamins, and polysaccharides. They can be used for cancer prevention and anti-viral and anti-aging treatments; they have high nutritional and medicinal value (Kuang, 2020). China was the first country to cultivate edible fungi artificially, and it is where the highest number of edible fungi species grew at present. There are about 100 000 species of fungi worldwide (Kirk et al., 2008), of which more than 2300 are edible and medicinal (Boa, 2004). The following Edible fungi are being increasingly studied: *Lentinus edodes, Flammulina velutipes*, *Pleurotus eryngii*, *Agaricus bisporus*, *Ganoderma lucidum*, and *Ophiocordyceps sinensis*. In-depth molecular research on edible fungi conducted by omics technology is very important for their cultivation, breeding, and production in later stages. This paper summarizes the application and prospects of genomics, transcriptomics, proteomics, metabolomics, and multi-omics cojoint analysis in edible fungi research.

1. Application of genomics to edible fungi research

The genome simply refers to all DNA of an organism (Paterson et al., 2017). Genomics is a discipline that studies the nucleotide sequence of the complete genome of organisms, as well as the structural composition and function of genes. Genomics is also the most widely used basic science and technology in omics technology. Research directions can be

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https://doi.org/10.1016/j.crfs.2022.100430
Received 13 October 2022; Received in revised form 10 December 2022; Accepted 23 December 2022
Available online 27 December 2022

roughly divided into structural and functional genomics (Su et al., 2007). In the study of edible fungi genomics, the key genes involved in life processes are predicted by obtaining the whole genomic sequence of edible fungi, which facilitates research on the specific expression mode and molecular genetic information of the gene by using gene cloning, transgenic, gene editing, and other technologies at a later stage. Such a research direction is of great significance for research on edible fungal growth and development mechanisms, cultivation, and breeding.

1.1. Structural genomics based on whole genome sequencing

Genome sequencing underwent the development of three generations of sequencing technology. The chain termination method (Sanger et al., 1977) proposed by Sanger in 1975 is called the first generation DNA sequencing technology (FGST), which has been widely used because of its simple operation and high accuracy. This method is also used in the human genome project (Jd, 1990). In 2005, second generation DNA sequencing technology (SGS), which can sequence millions of sequences simultaneously, known as high throughput sequencing technology (HTS), was introduced. HTS is currently the most commonly used genome sequencing technology. The main sequencing platforms include 454 of Roche Company, Solexa of Illumina Company, Solid of ABI Company, and BGISEQ of BGI (Mardis, 2017). In 2014, Oxford Nanopore put forward MinION third generation DNA sequencing technology (NGS), which is based on nanopore technology. This scheme, could promote the development of genome sequencing technology again. This sequencing technology is inexpensive, simple, and portable. Moreover, it can be directly driven by laptop (Yan et al., 2020).

At present, whole genome sequencing has been completed for several edible fungi, such as *Coprinus cinereus* (Stajich et al., 2010), *L. edodes* (Lianfu et al., 2017), *Volvariella volvacea* (Bao et al., 2010), *G. lucidum* (Chen et al., 2012), *P. ostreatus* (Alfaro et al., 2016), and *F. velutipes* (Young-Jin et al., 2017). *P. nebrodensis* and *P. eryngii* are rare species of the genus *Pleurotus*. Wen Jiawei et al. (Wen, 2019) performed whole genome sequencing of *P. nebrodensis* and *P. eryngii* on the platform of PacBio RS II sequencing. The obtained genomes are 48.2 and 49.9 Mb long. Phylogenetic and epigenomic analyses were conducted for both of them, as well as for *P. ostreatus*, which has been sequenced with the whole genome published in the genus *Pleurotus*. *P. nebrodensis* can be used as an independent species in the *P. eryngii* population. Edible fungi are distributed all over the world, so the phenomenon of the same name and the same plant and different names between countries is very common. The study provides a solution to the use of genomics techniques to reclassify controversial species relationships. *V. volvacea* has a long history of cultivation in China, and its cultivation medium focuses on the agricultural waste. In 2010, Bao Dapeng et al. (Bao et al., 2010) first carried out a whole genome analysis on *V. volvacea* by using 454GS FLX sequencing technology of Roche Company and Solexa sequencing technology of Illumina Company. The genome of *V. volvacea* after integration was 36.45 Mb long. A total of 11 084 protein-coding genes were predicted, of which 5516 genes were annotated. In 2017, the Bao Dapeng team (Dapeng et al., 2013) reanalyzed the genome of *V. volvacea*, and separated many genes involved in the degradation of cellulose, hemicellulose and pectinase from *V. volvacea*. Their results provided a basis for cultivating *V. volvacea* varieties that could efficiently degrade cultivation substrates composed of agricultural wastes. With the evolution of edible fungi, the sequencing results of the genome are constantly updated, and each re-sequencing is expected to make new discoveries about the genome of edible fungi. *F. velutipes* is an edible and medicinal fungus, that can degrade lignocellulose to produce ethanol (Ryoji et al., 2009). Young-Jin Park et al. (Young-Jin et al., 2014) analyzed the genome with a total length of 35.6 Mb after obtaining the complete genome sequence of *F. velutipes*, and predicted that there were at least 12218 protein-coding genes. Further analysis showed that many highly expressed alcohol dehydrogenase genes were included. These are involved in the degradation process of lignin and carbohydrate. We can further study whether *F. velutipes* mycelia can play a role in ethanol production in the highly efficient production industry.

The sequencing technology has been applied to whole genome research on edible fungi. With technology, the size, structure, and function of the genome of edible fungi can be preliminarily analyzed. With the efforts of researchers from various countries, obtaining the basic information of different edible fungus genomes can no longer meet the needs of current research. Sequencing is gradually becoming purposeful, more in the hope of annotating the genome more. So as to obtain a large amount of functional genetic information, it lays the foundation for basic research on edible fungi. In recent years, many articles on edible fungus genomics sequencing have emerged at home and abroad, but they are all analyzed from different angles, laying the foundation for phylogenetic analysis and gene function analysis of edible fungi. And genomics technology can help identify the species characteristics of various mushrooms, facilitate the more effective use of mushrooms as food and medicinal materials, and also help to understand the structure of complex ecosystems (Anne et al., 1999).

1.2. Functional genomics based on gene function and expression

Gene cloning aims to obtain the sequence of the target gene to prepare for the later introduction of receptor cells and to study gene expression and function. Gene cloning is the most basic technology used in genome analysis. At present, many articles on gene cloning and expression in edible fungi have been published. And the focus is no longer limited to edible value, and in recent years, many edible fungi have also increased the role of edible fungi in drug research. Sun Tingting et al. (Sun et al., et al.) cloned the superoxide enzyme gene *Ah-MnSOD* in *Auricularia auricula* by using RT-PCR and studied its expression in different developmental stages. Its expression in the primordium is high. Stress resistance is inferred to be strong when *A. auricula* is in the primordium stage. On this basis, studying the expression of this gene in different growth periods of *A. auricula* under adversity stress is necessary to verify this conjecture. Yuan Xuewen et al. (Yuan et al., 2022) cloned three heme peroxidase genes *LeHPs* in *L. edodes* and analyzed their postharvest expression at different storage times. The expression of the three genes increased continuously during storage. After picking, the color of the *L. edodes* cap darkened over time. Therefore, *LeHPs* genes may be involved in regulating the browning mechanism of *L. edodes* after picking. Yin Liwei et al. (Yin and Chi, 2015) cloned the manganese peroxidase gene *He-mnp1* in *Hericium erinaceus* and studied the structure and function of the gene. *He-mnp1* is a stable hydrophilic protein that and belongs to the family of fungal heme peroxidase proteins. This protein is involved in the catalysis of the multicomponent oxidation reaction. The gene function can be further improved. The results provided guidance for screening manganese peroxidase gene engineered strains in *H. erinaceus*. Priti et al. (2022) cloned the fibrinolytic enzyme gene *CmFE* in *Cordyceps militaris* and studied the function by analyzing the degree of solubility of fibrin clots in cultures. The analysis found low homology of *CmFE* sequence with other reported fibrinolytic enzyme sequences, speculated that it may be an undiscovered novel enzyme, and performed heterologous expression and three-dimensional structure prediction on it. The discovery of this novel fibrinolytic enzyme gene has important implications for its use as a thrombolytic agent component in medicine.

In transgenic technology, gene fragments with certain characteristics are introduced into receptor cells for expression; the receptor cells possess new characteristics on the basis of the original genetic characteristics (Fang et al., 2019). Emerging gene editing technology is used to carry out the targeted modification of genes according to people's needs, such as modification or knockout (Ling and Zhao, 2018). Researchers have obtained many improved varieties of edible fungi by using two technologies. Chen Meiyuan et al. (Chen et al., 2009) transferred thermotolerance-related gene *028-1* obtained from *A. bisporus* into the non-thermotolerant strain 8213, and the thermo-tolerance of the

obtained transgenic strain was significantly improved. The study confirmed that there is no strictly meaningful plasmid in the mushroom, and that it can mediate the transformation of foreign genes through *A. bisporus*, which will advance genetic engineering research in the field of edible fungi. Wang Hongyun et al. (Wang et al., 2022) transferred the key cold-regulat protein *OsICE1* in rice into *L. edodes* mycelia by using *Agrobacterium tumefaciens* transformation, and the obtained transgenic *L. edodes* mycelia grew better than the control mycelia at 10 °C. Illustrating the feasibility of cloning key genes from other species into edible fungi through transgenic technology. These findings lay the foundation for molecular breeding of cold tolerant *L. edodes*. Yang Tao et al. (Yang et al., 2016) cloned the blue ray receptor gene *CmWC-1* in the *C. militaris* genome to study its function. After gene knock out, the conidia of *C. militaris*, as well as the carotene and cordycepin produced, were reduced. However, the biosynthesis of steroids became more active. Based on differential analysis with the normal *C. militaris* transcriptome, the *CmWC-1* gene could inhibit the biosynthesis of steroids to control the differentiation of mycelia.

The edible value and medicinal value of edible fungi themselves are favored by researchers at home and abroad. The application of genomics in edible fungus research helps us quickly obtain the basic information of edible fungi, so that we can analyze the genetic structure and evolution of edible fungi from the perspective of genetics and taxonomy, and provide reference for the species division of edible fungi. At the same time, with the help of mature gene cloning, transgenic and other technologies, the functional genes in the genome are edited and modified, and the artificial transformation of edible fungi is gradually realized. In the future research of edible fungi, genomics technology will be an important means for us to understand the molecular structure of edible fungi and discover the unique value of edible fungi, and it is believed that it will make a lot of contributions to the identification of edible fungus resources, variety selection and medical research.

2. Application of transcriptomics to edible fungi research

Transcriptome refers to the sum of transcripts of all genes in an organism (Victor et al., 1997). Transcriptomics technology is used to study the transcription of all genes in cells and the transcriptional regulation process invlved at the overall level (Jiang et al., 2020). This technology is also an important means to find the key genes in the metabolic process of biological organisms for subsequent gene cloning and functional verification (Tian, 2019). Research methods of transcriptomics include gene chip technology, serial analysis of gene expression (SAGE), high throughput transcriptome sequencing technology (RNA-Seq) (Li et al., 2020), and others. Method are selected or combined based on different research objectives. Among these method, RNA-Seq technology is greatly advantageous in terms of sequencing depth, price, and time to obtain results. At present, it is the most widely used method (Liu, 2020a). The researchers sequenced and assembled the transcripts with the help of a sequencing platform, comparing and screening out genes that were up-regulated and down-regulated in different environments, different tissues and at different growth and development stages. Functional annotation and clustering of differentially expressed genes were performed to explore the environmental response mechanism and growth and development mechanism of edible fungi (Fig. 1).

2.1. Study on differential transcriptome of edible fungi under different environmental treatments

Edible fungi are easily affected by environmental factors such as hormones, light, temperature, and others, during the growth process. These factors have a serious impact on primordial development, the differentiation of the fruiting body, and the coloration of mycelia after maturity (Yu et al., 2009). Researchers screened the specifically expressed genes in different treatments by using transcriptomics technology and explored the mechanism of the stress response, thereby

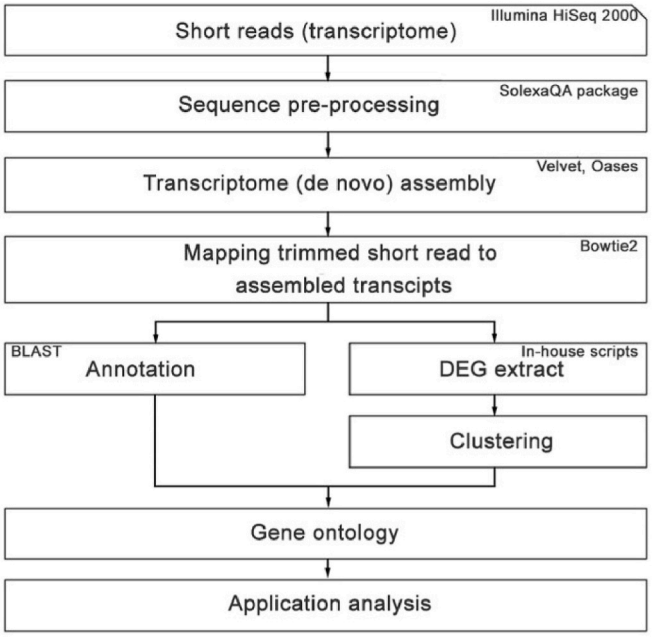

Fig. 1. Overall workflow for transcriptome assembly and RNA-seq data analysis (Song et al., 2018).

maintaining edible fungi's normal growth and development when changes occur in the external environment.

Li Yu et al. (Li et al., 2022) analyzed the impact of methyl jasmonate on the primordium of *F. velutipes* by using transcriptomics technology. Transcriptome sequencing was carried out for *F. velutipes* sprayed with methyl jasmonate and the control group (not sprayed). A total of 413 differentially expressed genes were found, including 233 upregulated genes and 180 down-regulated genes. After enrichment analysis of the metabolic pathways involved in genes, the following conclusions were drawn. Methyl jasmonate may promote the differentiation of *F. velutipes* fruiting bodies by participating in the metabolic pathways of phenylpropanoids and may promote the energy metabolism process accompanied by the primordial growth. However, the molecular mechanism of methyl jasmonate's promotion of primordial differentiation of *F. velutipes* has not been fully analyzed. But it is proposed that in actual production, spraying an appropriate amount of methyl jasmonate at the time of mushroom emergence can regulate the growth rate of edible fungi or improve the quality of edible fungi. Liu Jianyu et al. (Liu et al., 2021a) performed a transcriptome sequencing of the *F. velutipes* primordium under blue ray irradiation and dark conditions, and studied the impact of blue rays on the differentiation of the *F. velutipes* primordium. After data analysis, 168 differentially expressed genes were found, including 76 upregulated genes and 92 down-regulated genes. Further analysis showed that there were at least 10 hydrophobic protein genes and 10 membrane transporter genes, which may participate in the process of receiving blue ray and transmitting light signals and promote the formation of *F. velutipes* primordium. The paper proposed that using blue rays in the industrial cultivation of *F. velutipes* could save costs, a large number of genes that might participate in the regulation of primordium differentiation of *F. velutipes* can accumulate a plan to reduce the cost in actual production. Similar studies have been reported abroad, Jae et al. (Kim et al., 2020) compared the transcriptome of shiitake fruiting bodies under blue and dark culture conditions, screened 221 up-regulated genes and 541 down-regulated genes, and found that the cellulose and non-cellulose cell wall structures mainly involved in the morphological development of primordium and affected the development of fruiting bodies were found after gene annotation. The difference is that the study added cultivation tests and concluded that blue light mainly induced the growth of villi on the surface of fruiting bodies,

while dark conditions mainly promoted the length development of stalks. Both types of studies explore the effect of blue light on the growth and development of edible fungi, and if similar research results can be integrated and compared, it is believed that it will help to understand the mechanism of blue light in the growth and development of mushrooms, and can also contribute to improving the cultivation mode of mushrooms. Seung-il et al. (Yoo et al., 2019) studied the molecular mechanism of light-induced formation of brown films on the surface of shiitake fruiting bodies. Transcriptome sequencing was performed on mycelium with white surface in the early stage, normal brown at maturity and partial brown, and the transcriptome sequencing results were compared in pairs. Multiple differentially expressed genes related to redox process and hydrolase activity were screened, among which carbohydrate metabolism, DNA replication and cellulose binding contained a large number of upregulated genes. After analysis, it was found that the browning phenomenon in shiitake mushrooms was the result of light sensing, redox, melanin formation and other processes. Similar studies have screened many candidate genes for light-induced browning of mycelium, which is of great significance for future molecular breeding. Wang Jing et al. (Wang, 2021) extracted RNA from *P. nebrodensis* treated at 4 °C and sequenced the transcriptome by using Illumina technology. After analyzing the sequencing result, enrichment and quantitative expression analyses were performed on differentially expressed genes. The screened differentially expressed genes were enriched in oxidoreductase activity, sugar metabolism, amino acid metabolism, heme binding, and other aspects, indicating that *P. nebrodensis* responded to low temperature stress by controlling the process of substance synthesis. The growth and development of *P. nebrodensis* in low temperature environment is a multi-mechanism joint regulation process, and the synthesis function of the substances in it may be an important factor affecting the origin of Bailing side ear primordium. So when studying the growth and development mechanism of *P. nebrodensis* at low temperature, it is necessary to focus on genes related to material transport pathway, which provides theoretical basis and data support for more in-depth study of the growth and development mechanism of *P. nebrodensis* in low temperature environment. Xu Zijie et al. (Xu, 2021) set control (25 °C) and low temperature (17 °C) treatments for *P. ostreatus* to study the influencing mechanism of temperature on mycelium maturation according to the transcriptome level and physiological indexes. The analysis of the transcriptome sequencing of the two treatments showed that a total of 711 differentially expressed genes were identified from the low-temperature and control groups. With the function of heme binding, tetrapyrrole binding, and oxidoreductase activity and participation in cell transport and catabolic processes, they could respond to low temperature stress by regulating the expression of genes related to catalytic enzyme activity in *P. ostreatus*. This study narrows the scope of research to explore the emergence mechanism of *P. ostreatus*, and can cultivate high-quality *P. ostreatus* by artificially controlling its growth and development environment, which plays an important role in production practice.

It is very sensitive in the actual cultivation process of edible fungi, and it is easy to change due to the external environment. The internal mechanism that causes this change has attracted the attention of relevant researchers. Through transcriptomic analysis of edible fungus materials under different treatments, the transcriptome data before and after treatment were compared to screen out differentially expressed genes, which may participate in regulatory response to stress. The above studies can be seen that transcriptomics technology not only screens a large number of functional genes for genetically engineered edible fungi, but also provides some reliable cultivation measures for actual production. And the optimization of specific cultivation measures needs further experimental verification. In the future, the cultivation of edible fungi will encounter other environments besides hormones, temperature and light, and transcriptomics technology can also obtain more differentially expressed genes and increase gene reserves. On this basis, in addition to molecular level research such as functional verification of the screened differential genes, it is also necessary to combine transcriptomics technology with the measurement results of relevant physiological and biochemical indexes, try to jointly analyze the mechanism of edible fungi in response to stress from the transcriptome level and physiological level, and formulate appropriate cultivation measures to improve the adaptability of edible fungi in adversity in production.

2.2. Study on the differential transcriptome of edible fungi in different tissues

Studies on the differential transcriptomes between different tissues of edible fungi focus on monokaryon and dikaryon mycelia and mycelium degradation in subculture. The mycelia of edible fungi can be divided into monokaryon, dikaryon, and multinucleate mycelia. Monocaryon mycelia are formed after the germination of the basidiospores. Dikaryon mycelia are produced after the mating of two monokaryons with the affinity. The confirmation of dikaryon mycelia depends on whether there is a lock union, as determined through microscopic observation or whether there are two nuclei, as determined through the staining method. Only the determined dikaryon mycelia can produce mushrooms in the later stage to transfer edible fungi from vegetative reproduction to sexual reproduction (Li et al., 2009). Studies on differential transcriptome of monokaryon and dikaryon mycelia have been carried out in edible fungi, such as *F. velutipes*, *P. ostreatus*, and *P. eryngii*, to analyze the advantages of monokaryon and dikaryon mycelia in their growth and development. After the transcriptome sequencing of monokaryon and dikaryon mycelia of *F. velutipes*, Wang Wei et al. (Wang et al., 2015) screened a total of 3504 genes differentially expressed before and after cytoplasmic fusion. Most of the differentially expressed genes in dikaryon mycelia were involved in the synthesis of amino acids, fatty acids, and other sugars, indicating that dikaryon mycelia accumulated nutrients to provide a material basis for the formation of late primordium. However, most of the genes for regulating arginine degradation were downregulated; thus, arginine accumulation in dikaryon mycelia could better adapt to environmental changes. Liu Tianxiang (Liu, 2012) similarly performed transcriptome analysis on *P. ostreatus* monokaryon and dikaryon mycelia. Most of the differentially expressed genes screened in dikaryon and monokaryon mycelia participated in signal transduction and sugar metabolism. The dikaryon mycelia were more advantageous than the monokaryon mycelia in the growth and development of *P. ostreatus*. Shang Junjun et al. (Shang et al., 2020) studied the difference in mRNA expression in monokaryon and dikaryon mycelia of *P. eryngii* by using the Illumina HiSeq 2500 high-throughput sequencing platform. More highly expressed mRNA was found in the dikaryon mycelia with the upregulated genes; it was five times those in monokaryon strains. The role of mRNA related genes in the sexual reproduction of *P. eryngii* should be further studied. Song et al. (2018) used Illumina HiSeq platform to conduct differential transcriptomic studies on the dikaryon mycelium and mature fruiting bodies of Korean *Lentinula edodes*. 2080 differential genes were screened, including 577 upregulated genes. KEGG analysis of the differential genes was mainly concentrated in nucleic acid replication, repair and transcription, which is very important for meiosis of shiitake mushrooms during maturation. At the same time, it was also found that aspartate protease plays an important role in the maturation of fruiting bodies, and may participate in the synthesis and separation of functional substances. Most transcriptomic studies of edible fungi focus on the formation and development of fruiting bodies, ignoring the quality mixing process that most edible fungi need to go through. The above studies all focus on the nutritional reproductive process of edible fungi, and the differential transcriptome study in the monokaryon and dikaryon mycelia of edible fungi has accumulated many differentially expressed genes, which provides important clues for in-depth understanding of the sexual reproductive process of edible fungi. The aim of the follow-up work is to carry out the functional verification of differentially expressed genes to clarify the molecular mechanisms related to

sexual and asexual reproduction of edible fungi.

Mycelium degradation is a phenomenon in which edible fungi suddenly or gradually lose their vitality. Mycelium degradation can be reduced or delayed by adding nutrients to the bags, continuously improving the formula of the culture medium, and controlling the passage number of edible fungi (Gao, 2006). To study the internal mechanism of mycelium degradation, Liu Lu (Liu, 2020b) performed transcriptome sequencing of degraded and nondegraded mycelia of *Morchella esculenta* by using RNA-seq technology for the first time. A total of 1779 differentially expressed genes were obtained; these genes were involved in nucleotide metabolism and carbohydrate metabolism in the process of cell metabolism. The degradation of *M. esculenta* mycelia is actually the result of cell metabolism. Liu Xiaoxia (Liu, 2020a) studied the degradation mechanism of *V. volvacea* by using transcriptomics technology. A total of 245 differentially expressed genes were screened. These genes were involved in the process of active oxygen scavenging and substrate degradation, indicating that the expression of genes related to active oxygen scavenging and substrate degradation decreased during the subculture of *V. volvacea* strains. Nutrient synthesis and energy metabolism were inhibited, leading to strain degradation. Few studies have been conducted on the degradation mechanism of edible fungi in China, which will be an important research direction in the future. The above two studies provided gene reserves for single gene cloning in *M. esculenta* and *V. volvacea* and provided ideas for studying the degradation mechanism of mycelia in other edible fungi.

2.3. Study on the differential transcriptome of edible fungi in different growth and development periods

To understand the physiological changes and material accumulation process of edible fungi in the growth process at the transcriptome level, many scholars studied the transcript sequencing of *F. velutipes*, *P. ostreatus*, and other edible fungi in different growth and development periods, identified differentially expressed genes in different periods, and performed functional annotation to analyze their expression patterns in different growth periods. Lu Yuanping et al. (Lu et al., 2019) performed the transcriptome sequencing of the fruiting body of *A. blazei* Murill at the primordium, harvesting, and opening stages and screened differentially expressed genes related to the growth and development of the fruiting body. The genes involved in cell metabolism and DNA replication in the primordium stage were significantly upregulated, whereas the genes involved in fatty acid degradation and amino acid metabolism at the harvesting and opening stages were significantly upregulated. Li Fan et al. (Li et al., 2018) performed the transcriptome sequencing of *P. eryngii* at the mycelial, primordium, and fruiting body stages using RNA-seq technology. Differentially expressed genes were involved in carbon metabolism and amino acid metabolism at the mycelium stage. The genes encoded the key enzymes of the tricarboxylic acid cycle were all upregulated. The genes encoding the key enzymes of fatty acid metabolism at the primordium stage. The differentially expressed genes in the fruiting body stage are involved in the biosynthesis of steroids to lower the impact of the external environment on the growth of the fruiting body. The results of this study lay a foundation for the development and cloning and quality improvement of important trait functional genes in the *P. eryngii*. Lv Xiaomeng et al. (Lyu et al., 2021) analyzed the differences in the transcripts of *F. velutipes* stipes between the growth and maturation stages. The genes involved in regulating carbohydrate metabolism, amino acid metabolism, and key enzymes in the trehalose synthesis pathway during stipe growth were significantly upregulated. This finding indicated that much material and energy metabolism were involved from the growth period to the maturation period of the stipe. The specific expression of some genes during growth and maturation can improve the stress resistance of *F. velutipes*. The study also combines proteomics with the joint analysis of differential genes and differential proteins, hoping to explore the key genes and pathways affecting growth and development in *F. velutipes*, provide theoretical support for studying the regulatory mechanism of edible fungi growth and development, and promote the molecular breeding of edible fungi. Shi Xiaokun et al. (Shi et al., 2019) sequenced the transcriptome of six *A. bisporus* strains at four different growth and developmental stages (primordium, young, picking, and opening stages). They screened 13 differentially expressed genes from six strains at four stages and even thousands of highly expressed specific genes at the four stages. The main purpose of this study is to explore the genes related to the excellent characteristics of *A. bisporus* through the screening of differential genes, and to analyze the pathways related to the growth and development of fruiting bodies of *A. bisporus*. Chen Zhengqi et al. (Chen et al., 2021) performed RNA-seq sequencing of the mycelia and fruiting body of *A. auricula*. Most of the screened differentially expressed genes were involved in the transmembrane transport of cellular materials and existed in amino acid and lipid metabolism. The upregulation and down-regulation of these related genes promoted the fruiting body development of *A. auricula*. The above studies analyzed the transcriptome data of different edible fungi at different growth and developmental stages and screened the significantly upregulated and downregulated genes at different stages, thereby providing gene data for further study on their own growth and developmental mechanisms. In subsequent studies, researchers should focus on the upregulated and downregulated genes and deeply analyze their roles in the process of fruiting body development by cloning a single key gene.

The application of transcriptomics technology in edible fungus research has screened out a large number of differentially expressed genes on the basis of genomics technology, which has brought edible fungus research into a new research stage. Research at home and abroad has focused on differential transcriptomics. Starting from different environments, different tissues and different growth and development periods, and exploring the internal changes of edible fungi from the transcriptome level, leaving a large number of gene reserves for single-gene cloning. Comparison of transcriptome data between edible fungi and with other fungi makes it possible to identify conserved genes in the continuous evolution of mushrooms, which can continuously refine the reference map of mushroom formation. And help to study the evolutionary origin of mushrooms, one of the largest branches of eukaryotes, and the basis of multicellular genetic evolution.

3. Application of proteomics to edible fungi research

Genes are translated and modified after transcription before proteins are obtained. Therefore, the products of gene expression are usually proteins. Proteomics is a discipline that studies the composition, structure, function, and other aspects of all proteins in a genome or cell for qualitative and quantitative analysis on the basis of genomics and transcriptomics (Graves and Haystead, 2002). At present, most studies on the proteomics of edible fungi focus on differential proteomics, which is used to screen differentially expressed proteins of edible fungi in different environments at different growth stages and tissue morphologies (Cha et al., 2017). The research idea of differential proteomics usually consists of three parts, as follows. (1) Extract and separate the protein components from edible fungi. (2) Screening and identification of differentially expressed proteins. (3) Qualitatively analyze the structure, properties and functions of differentially expressed proteins by bioinformatics. Tris-saturated phenol law (Annamraju et al., 2008) and the TCA/acetone precipitation method (Wan et al., 2004) are usually adopted to extract the proteome of edible fungi. 2D electrophoresis (2-DE) (O'farrell, 1975) is typically used to separate the protein components. Different proteins have different molecular weights and isoelectric points. Therefore, they will appear in different positions in gel electrophoresis. This method is simple and fast with high repeatability (James, 1997). Mass spectrometry (MS) is a common method for protein identification. MS has high throughput and high resolution and includes TOF, LC-MS/MS, and HPLC (Zhen and Shi, 2011). In addition, emerging protein labeling technologies, such as iTRAQ (Wiese et al., 2007) and

TMT technologies, can be combined with chromatography and tandem mass spectrometry to conduct a proteomics study. After the separation and identification of the proteome of edible fungi, protein interaction screening, protein subcellular localization, GO functional enrichment, KEGG metabolic pathway, and cluster analysis of differentially expressed proteins were performed to reveal the biological processes involved.

3.1. Study on differential proteomics of edible fungi in different environmental treatments

Normal growing edible fungi subjected to the disturbance of temperature, plant hormones, salt, drought, and other external conditions will have corresponding responses to environmental change. Edible fungi produce specifically expressed proteins to adapt to the environment (FPAC AF et al., 2004). Therefore, researchers often treat edible fungi under different conditions and separate and identify the proteins extracted from treatment and nontreatment groups to verify the role of differentially expressed proteins in the resistance to adverse circumstances in combination with bioinformatics analysis. Thus, the resistance mechanism of edible fungi is explored. Zhu Chuanwang (Zhu, 2015) studied the effect of selenoarginine added to the cultivated material on the proteome of *P. ostreatus* fruiting body by traditional 2-DE technology combined with mass spectrometry analysis and identified 51 differentially expressed genes. Among them, 17 protein spots were significantly upregulated. Three proteins were identified, two of which were involved in the synthesis of formate dehydrogenase and aldehyde ketone reductase. The addition of selenoarginine affects the material and energy metabolism of *P. ostreatus*. The appropriate amount promotes the growth of *P. ostreatus* mycelia, whereas an excessive amount eliminates the promotion effect. Edible fungi can be sprayed with an appropriate amount of selenoarginine to promote the differentiation of fruiting bodies. This study provides an idea for studying the effects of selenium enrichment on the growth and development of other edible fungi. Wu Zhiliang (Wu, 2020) studied the changes in the proteome of the fruiting bodies of *V. volvacea* due to cold damage by using advanced iTRAQ technology, separated proteins by SDS-PAGE, and identified 332 cold damage-related proteins by LC-MS/MS mass spectrometry. After functional annotation and pathway enrichment, it was concluded that cold damage treatment could promote the production of sugar metabolism- and energy metabolism-related proteins in *V. volvacea* to cope with low temperature stress. Energy metabolism, membrane lipid metabolism, and active oxygen metabolism disorder would occur in edible fungi when cold damaged. This study aims to analyze differential proteomics of the harvested *V. volvacea* under cold stress, which makes up for the gap in the research on cold damage to fruiting bodies of fresh *V. volvacea*. Geison et al. (Cambri et al., 2016) found that the protein profile produced by *Lentinus crinitus* was more complex when using maltose and urea as cultures. In order to analyze in detail the different manifestations of cultures at the protein level, proteomic analysis was performed on mycelium in ordinary media and medium with maltose and urea added. Firstly, 98 differentially expressed proteins were isolated from protein profiles by TOP-LC-MS/MS mass spectrometry and 2-DE technology, including 25 CAZymes, 20 oxidase/reductase, 3 proteases, 5 lipases/esterase and 9 proteins with unrelated functions. The LC-MS/MS identification of the already isolated protein points yielded a total of 162 proteins. At the same time, it was found that pre-isolation of 2-DE prior to proteomic analysis increased the number of proteins identified. The differential protein contains a variety of lignocellulase and proteolytic enzymes, which can widely use the lignin in the medium to convert carbon and energy, and degrade stubborn pollutants, which has broad application prospects in industrial production. Moreover, the identified proteins are not well matched in the database, indicating that the protein secreted by Lentinus crinitus is highly complex and needs to continue to be fully annotated with its genomic information. Zhao Zhou (Zhao, 2013) analyzed the changes in proteome of *G. lucidum* mycelia under blue ray irradiation by using 2-DE protein separation technology in combination with MDLDI-TOF/MS identification technology and screened 54 differentially expressed proteins, including 32 upregulated proteins and 22 downregulated proteins. Six significantly upregulated protein spots were selected for fingerprint analysis. The 14-3-3 protein was identified from differentially expressed proteins. This protein was widely involved in multiple life processes of organisms and has been reported in studies on the stress resistance of wheat, rice, corn, and other plants. However, its specific mechanism in edible fungi has not been studied deeply. Therefore, this study explored the role of 14-3-3 protein in the stress resistance process of edible fungi. The difference in protein expression reflected the changes that occurred in edible fungi in response to environmental changes to a certain extent. Research on the changes in the proteome response to the different treatments can provide more accurate evaluation criteria for the genetic breeding of edible fungi on the basis of genomics and transcriptomics to identifify strains with excellent stress resistance.

3.2. Study on the differential proteomics of edible fungi at different developmental stages

The growth and development of edible fungi involve several processes, such as metabolism, synthesis and transport of substances, signal transduction, and pigment secretion. Researchers often start from the changes of proteome at different developmental stages to analyze the development mechanism of edible fungi fruiting bodies on the protein level. Chen Meiyuan et al. (Chen et al., 2015) analyzed the proteome of fruiting bodies of *A. bisporus* at primordium, young, harvesting, and opening stage by means of ITRAQ-MS/MS. By taking the proteome at primordium stage as the control group, a total of 1007 differentially expressed proteins were screened. The analysis results showed that the expression of the mismatch binding protein was continuously upregulated during three periods, indicating that the constant expression of mismatch binding protein was required to ensure the accuracy of DNA replication in the growth of fruiting bodies of *A. bisporus*. However, this paper only analyzed and verified the differentially expressed proteins that were significantly upregulated and downregulated. This paper also focuses on the protein that was specifically expressed during a certain period and further analyzes the molecular mechanism underlying the fruiting body development of *A. bisporus*. Wang Weike et al. (Wang et al., 2017) analyzed protein components of *P. geesteranus* strain "Taixiu5766" in mycelium growth, primordium formation, coral, and fruiting body maturity stages and identified 885 differentially expressed proteins. The proteins involved in glycolysis and the tricarboxylic acid cycle increased significantly with the progression of the growth period. If changes occurred in the two pathways, then such changes would have a very important impact on the growth and development of *P. geesteranus*. The HSP70 protein was found to be involved. This protein has attracted more attention in the study on the stress resistance of plants. Many studies have shown that the overexpression of HSP70 protein can improve the high-temperature tolerance of plants (Jonathan et al., 2008). This protein also plays an important role in the high-temperature tolerance process of edible fungi, which can be further verified. Liu et al. (2021b) studied differential proteomics of *C. militaris* in four stages, such as mycelium, primordium, and fruit bodies at the growth stage and fruit bodies at the mature stage. Taking the proteome at the mycelium stage as the control, the differential proteins at the primordium stage were found to be involved in organic nitrogen compound synthesis, AMP synthesis, active oxygen accumulation, and other processes. This finding indicated that cordycepin had begun to accumulate during primordium formation and could be regulated by oxidation reactions during primordium development. These findings provided ideas for exploring the regulation mechanism of cordycepin in biosynthesis. Norasfaliza et al. (Rahmad et al., 2014) used 2D-DIGE technology to conduct differential proteomic studies on mycelium, primordium and fruiting bodies of *Termitomyces heimii*. A total of 271

differential protein points were identified, and 19 protein points were identified after fingerprint analysis, which were involved in carbohydrate metabolism, energy metabolism, amino acid metabolism and response to environmental stress. It shows that most of the protein is retained during growth and development. Differential proteomics in different tissues of edible fungi was studied to identify out many proteins specifically expressed in different tissues. These proteins play roles in the growth of mycelia and development of fruiting bodies of edible fungi, thereby providing a foundation for further study on the growth and development mechanism of edible fungi.

3.3. Study on differential proteomics of edible fungi in different tissue morphologies

Few studies have been conducted on differential proteomics in different tissue morphologies. Studies have focusd on fertile/non fertile mycelia, homokaryotic/heterokaryotic mycelium of edible fungi, and the same tissue of different edible fungi. Studying the affinity of mycelia through proteomics is of great significance for breeding research on edible fungi. Liu Yongnan (Liu, 2015) analyzed the proteome of sterile primary and fertile secondary mycelia of *F. velutipes* by using iTRAQ combined with LC-MS/MS technology. A total of 468 differentially expressed proteins were obtained. The expressions levels of catalase and superoxide dismutase in the fertile secondary mycelia were lower than those in the sterile primary mycelia, indicating that the sterile primary mycelia were more prone to senescence and degradation. In this paper, three technical repeats were adopted in the study on differential proteomics to map the amino acid synthesis pathway and glycolysis pathway of differential proteins. Bioinformatics global analysis was carried out on experimental data. Therefore, the results were more accurate and specific. Liu Jingyu et al. (Liu et al., 2012) analyzed the homokaryon and heterokaryon mycelia proteome of *V. volvacea* for the first time by using iTRAQ technology combined with LC-MS/MS technology. A total of 1039 differential proteins were identified. Differentially expressed proteins were concentrated in the cytoplasm and cell membrane. With their ability to resist oxidation and regulate enzyme activity, they were involved in material transport, cell apoptosis, carbohydrate metabolism, and other pathways. In this study, the new protein labeling technology iTRAQ combined with tandem chromatography/mass spectrometry was used to isolate the *V. volvacea* proteome efficiently. Therefore, this new technology can also be applied to proteomics research on other edible fungi. Studies have shown that Angiotensin converting enzyme (ACE) can be isolated from mushrooms, and this substance plays an important role in the treatment and prevention of hypertension (Chang and Miles, 2004). Lau et al. (2012) used RPHPLC technology to conduct proteomic studies on antihypertensive-related proteins in different countries' mushrooms, *Agaricus bisporus*, *F. velutipes*, *L. edodes*, Hericium erinaceus, Pleurotus citrinopileatus, Pleurotus cystidiosus, Pleurotus flabellatus, Pleurotus florida and Pleurotus sajor-caju. After comparative analysis, it was found that in 9 kinds of mushrooms was found *P. cystidiosus* and *A. bisporus* contain high levels of antihypertensive protein. It is speculated that the main reason why these two mushrooms can have high ACE may be the protein with a molecular weight of 3–10 KDa. In the course of this study, it was found that the screened ACE inhibitory proteins had different characteristics, indicating that the amino acid arrangement order and protein structure may affect the inhibition of ACE enzymes. If the specific mechanism of action can be clarified, it will cause great repercussions in the field of edible fungi and medicine. Kiyotaka et al. (Horie et al., 2008) analyzed differences in the proteins of fruiting bodies of two edible fungi, namely, *Sparassis crispa* and *H. erinaceus*, by using 2-DE technology. Twenty-one coexisting expressed proteins were identified, most of which belonged to 14-3-3 and stepin family proteins. The 14-3-3 proteins generally exist in eukaryotes and are involved in signal transduction of cells, whereas some members of the stepin family proteins are related to tumorigenesis. This may be the main reason why edible fungi can improve human health. However, this proteomics study only involved the fruiting body stage. On this basis, if the mycelium and other developmental stages are added, then proteomics studies on the whole growth and developmental stages of *S. crispa* and *H. erinaceus* can be performed completely.

With the development of biochemical technology in recent years, proteomics research has gradually become an important technology to develop the various values of edible fungi after genome and transcriptome, especially for edible fungi with medical application potential. At the same time, proteomics technology is also constantly updated, and the accuracy and detection range are constantly improving. Compared with other fungi, proteomics has not been used much in the study of edible fungi, but it has been able to involve functional protein content, mushroom development stage, cell wall protein in the development process, the effect of emulsifiers on mycelium growth and mushroom medicinal properties. The challenge in future research is to flexibly combine proteomics with other omics techniques to become one of the important technical means for edible fungus research.

4. Application of metabolomics technology to edible fungi research

Metabolomics is a new discipline that emerged after the introduction of genomics, transcriptomics, and proteomics (Tang and Wang, 2006). The concept of metabolomics was proposed by Nicholson in 1999 when he was studying the urine of rats (Nicholson et al., 1999). Based on many studies, metabolomics is the quantitative and qualitative analysis of all metabolites produced by an organism or cell (Royston, 2004). Metabolomics can most intuitively reflect the change law of an organism in a certain process. Studies on metabolomics have been carried out in animals, plants, and microorganisms on a large scale, including sample extraction, metabolite separation and analysis, data processing and analysis, and result description (Xia et al., 2009). Metabolite samples are usually extracted with water and organic solvent. Then, other components are removed from the extracted sample by solid-phase microextraction (SPME), solid-phase extraction (SPE), and affinity chromatography (Qiu and Huang, 2004). Metabolites in samples with impurities are usually separated and analyzed by GC-MS, LC-MS, CE-MS, NMR, and FTIR/MS (Lu and Liang, 2008). The data obtained from analysis should be analyzed by chemometrics (hierarchical cluster and principal component analyses) to solve and analyze the structure and function of metabolites in combination with the metabolome databases and websites, such as MassBank, PubChem, KEGG, LIGAND, and BRENDA ADDIN NE.Ref.{F57C1A22-5DE8-4619-8AC1-426E28300618} (Zhao et al., 2011). Studies on metabolome in edible fungi need to be carried out on the basis of genomics, transcriptomics, and proteomics. Therefore, the application of metabolomics technology to edible fungi research is relatively infrequent and involves the metabolic pathway of bioactive substances and differential metabolomics.

4.1. Application of metabolomics to the research on bioactive substances in edible fungi

The edible and medicinal values of edible fungi come from the fact that they contain a large number of special bioactive substances, such as polysaccharides, alkaloids, terpenoids, sterols, and proteins. They have good health care functions (Xiang, 2021). Park et al. (Yu et al., 2017) analyzed the nontarget metabolites of the cap and stipe of brown and white beech mushroom strains by GC-TOF-MS and UHPLC-MS/MS, respectively. The cap containing a large quantity of amino acids controlled the taste and nutrition of the mushroom. The brown strain contained a large amount of hypsiprenol, which could be used as a sign to distinguish different strains of beech mushroom. The innovation of this study was that a new standard for the classification of beech mushrooms was added. Zhao et al. (2022) analyzed the nontarget metabolites of the unique components contained in *M. esculenta* by using UPLC-Q-TOF-MS technology. Apoferritin and sideromycin were found

in *M. esculenta*. Yu Fu et al. (2022) analyzed the metabolites produced by harvested dried mushrooms by using LC-MS/MS technology and tried to explain their browning mechanism. The browning pigment produced was from L-dopamine. The synthesis pathway of dopa melanin and the metabolism pathway of phenyl C compounds in the mushrooms were the main reasons for browning, which could be prevented by inhibiting the activity of phenoloxidase and enhancing antioxidants. Jin et al. (Mingliang et al., 2019) orally fed rats the mycelium polysaccharide of *G. lucidum* to identify its produced metabolites by means of GC-TOF/MS technology. The differential metabolites were related to pyrimidine, glutamate, and mannose metabolism. These metabolic processes were involved in the improvement of intestinal immune function and the regulation of intestinal microbiota. The mycelium polysaccharide of *G. lucidum* could be used as an additive to improve intestinal health.

The unique bioactive substances contained in edible fungi have been favored by researchers. After screening the bioactive substances in edible fungi and their metabolic pathways using metabolomics, the contents of important active substances in edible fungi can be improved by molecular technology. It is useful for the research of new drugs or lead compounds in the medical field. The difficulty of this research is that there is less information on the purification of biologically active secondary metabolites and related secondary metabolism and regulation, and if the metabolites produced by mushrooms can be systematically and comprehensively analyzed with the help of metabolomics technology, it will be very helpful for future pharmacological research and drug applications.

4.2. Application of differential metabolomics to edible fungi research

Jiang et al. (Ai-Liang et al., 2019) analyzed the metabolomics of *G. lucidum* treated by MeJA for 24 h by means of GC-MS and LC-MS to study the mechanism underlying MeJA's effect on the metabolism of *G. lucidum*. MeJA treatment led to the transfer of energy metabolism from basic metabolism to secondary metabolism in *G. lucidum* cells, inhibited energy supply and protein synthesis, and promoted the occurrence of secondary metabolism, thereby confirming that MeJA was involved in promoting the synthesis of ganoderic acid. Satria et al. (Dedi et al., 2019) divided *G. lucidum* into eight stages according to its morphology. Metabolites of *G. lucidum* at different stages were analyzed by using GC-MS and LC-MS. Nontargeted metabonomic analysis showed that the main metabolites of *G. lucidum* at different stages were related to the morphology of *G. lucidum.* The labeled metabolites screened by this research provide an effective clue for the subsequent comprehensive analysis of targeted metabolites of *G. lucidum*. Sato et al. (2017) analyzed the metabolomics of two different species of *Grifola frondosa* under different culture conditions by using GE-MS technology. The strain with a higher production efficiency contained more organic acids and chitin, but fewer amino acids. The content of nitrogen compounds in the metabolites might affect the production efficiency of *G. frondosa*. Li Kangle (Li, 2012) studied differences in the metabolomics of mycelia in 32 different entomopathogenic and edible fungi by means of HPLC-MS technology. The active ingredients of *O. sinensis,* namely cordycepin and adenosine, also exist in other fungi, and there might be some undiscovered small molecular substances in *O. sinensis* and *C. militaris*. If relevant research could be carried out, their pharmacological effects might be further explained. Chen Chao (Chen, 2017) examined the metabolites of nondegraded and degraded strains of *V. volvacea* by means of HPLC-MS metabolomics technology. The reduction of luteolin-3′, 7-di-O-glucoside might lead to the degradation of the strain. Li Jing (Li, 2016) analyzed the metabolome of the fruiting bodies and mycelia of *Antrodia cinnamomea* under different cultivation methods. The differences occurred in the amino acid synthesis and metabolism, carbon metabolism, and sugar metabolism pathway. This study result can be used to optimize the production techniques of *A. cinnamomea* and improve its quality and yield.

Metabolomics research can be divided into targeted and nontargeted research according to different research objects. Most studies on edible fungi are nontargeted. Many metabolic markers have been screened. In subsequent studies, the metabolic network and production mechanism of these markers can be analyzed by using targeted metabolomics technology, and the complete regulatory network map of material and energy metabolism of edible fungi can be gradually drawn. Both domestic and foreign studies are very concerned about the medicinal value of mushrooms, and the research of metabolomes is mostly carried out around this purpose. In addition to analyzing the basic properties of metabolites in mushrooms, the isolation of metabolites is also a difficult task.

5. Application of multi-omics cojoint technology to edible fungi research

Genomics, transcriptomics, proteomics, and metabolomics are all used to study the physiological and biochemical changes and production mechanisms of edible fungi at different levels. Whole genome sequencing technology makes the genome sequence of edible fungi transparent. Transcriptome sequencing technology can be used to screen out differentially expressed genes in edible fungi. Proteome sequencing technology has been determined to play an important role in the growth and development of edible fungi. Metabolome sequencing technology can be used to analyze the metabolic pathway of substances in edible fungi. Further intensive research found that these technologies are used to conduct studies on different levels. However, there are relations among them as a whole. Studies on the first development of the three omics are progressive according to the transmission order of genetic information from DNA and RNA to protein. Study on the metabolome, which has been finally developed, directly reflect the material changes of organisms in the process of genetic information transmission. The research results of omics technologies are mutually corroborative. A single omics analysis technology can no longer meet the needs of current research. Researchers hope to fully explain the causes, processes, and results of changes in substances inside and outside the organism. These would require the integration of multiple omics technologies, the use of bioinformatics to dig deep into the major omics data, and analyzing results from multiple angles and levels (Fig. 2).

In practical application, multi-omics data are large. Thus performing data analysis is difficult. Therefore, its applications to edible fungi are relatively few. Zhao Xu (Zhao, 2019) explained the mechanism underlying the response of *L. edodes* to high-temperature stress by analyzing the different physiological and biochemical reactions of two different strains of *L. edodes* under high temperature stress conditions. On this basis, the cultivation conditions could be optimized to reduce the impact of high temperature on the production of *L. edodes*. Li Tingting (Li, 2020) comprehensively analyzed the changes in the synthetic pathway of polysaccharides in *Phellinus linteus* before and after atmospheric room temperature plasma (ARTP) mutagenesis based on genomics, transcriptomics, and proteomics. ARTP technology could improve the biosynthetic metabolism mechanism of polysaccharides in *P. linteus*. α-Trehalose hydrolase was involved in the regulation of polysaccharide anabolism. However, obtaining the testing materials was difficult, and there was no research object for comparison in the genome analysis. Therefore, no other polysaccharide-related synthesis genes were identified before and after mutagenesis. Yu Fei (Yu, 2020) analyzed the interaction between *Russula griseocarnosa* collected in the field and its rhizospheric microorganism based on genomics, transcriptomics, and metabolomics. They studied the genetic evolution of *R. griseocarnosa*, the formation process of symbiotic system, and the coevolutionary relationship with its rhizospheric microorganism. The genome of *R. griseocarnosa* was officially published in this study. However, because a pure culture of *R. griseocarnosa* has not yet been obtained, there are certain limitations in relevant omics research. Liu Zhengjie (Liu, 2020c) performed basic research on a rare species, *Floccularia luteovirens*, under artificial planting conditions. Bioactive substances were developed, and

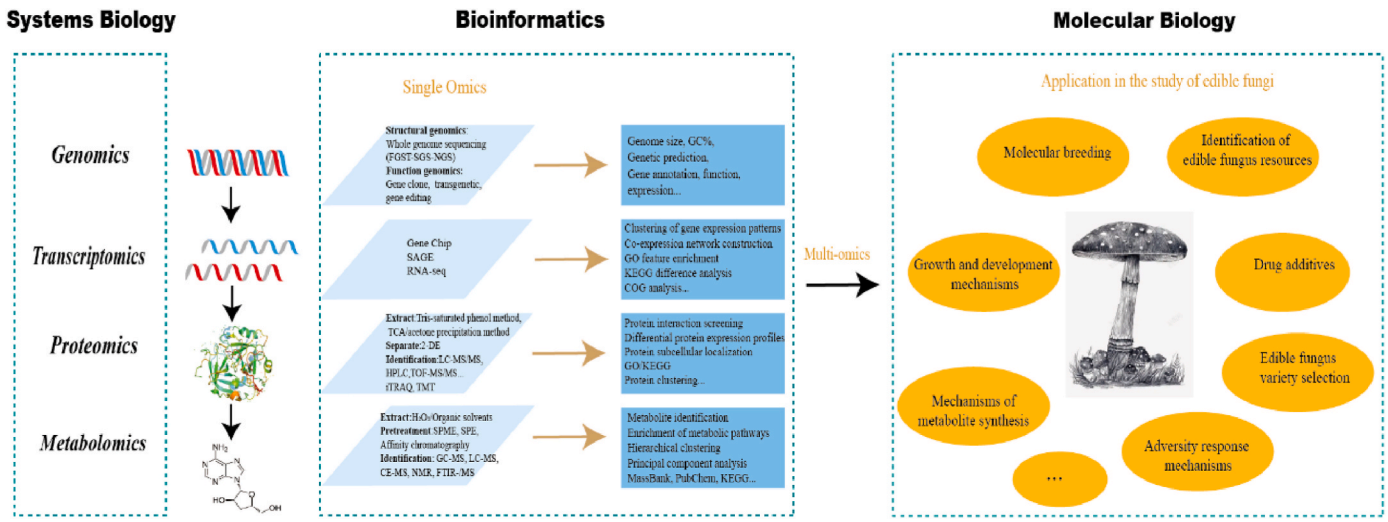

Fig. 2. The idea and application of multi-omics technology in edible fungus research.

the genetic and molecular mechanisms of fruiting body development were determined by using genomics and transcriptomics technologies. The artificial cultivation of fruiting bodies of *F. luteovirens* was not realized, but the genome and transcriptome data of *F. luteovirens* in four stages were reported for the first time. The results promoted research on *F. luteovirens* and provided ideas for protecting rare edible fungi, such as *F. luteovirens*, from resource depletion. Mushroom virus X (MVX) is a collective name for a variety of viruses found on the mushroom in European countries such as the United Kingdom in the early days, affecting the commercial traits of the mushroom (Rao et al., 2007). Eoin et al. (O'connor et al., 2021) performed mushroom emergence tests on early MVX treatment, late MVX treatment and non-MVX treated bisporus mushrooms, and transcriptome and proteome analysis of harvested fruiting bodies. This study controlled the processing node time of MVX and analyzed the differences in transcriptome and proteome between the fruiting bodies of the treatment group and the control group, so as to study how MVX affects the growth and development of the mushroom bisporus. It was found that when a strain is infected with MVX virus, not only at the molecular level, but also at the reduced yield, abnormal phenotype, and browning of fruiting bodies. Some multi-omics studies account for less in the field of omics technology, but the advantages of its comprehensive analysis have always attracted people's attention. Follow-up should overcome the difficulties in the research and vigorously apply multi-omics in the study of edible fungi.

6. Conclusions

The wide application of omics technology to the field of life science has made omics a research hotspot. Many different omics technologies have been combined for scientific research in the field of edible fungi. In genomics research on edible fungi, whole genome sequencing and gene editing technology has been adopted to analyze the genome data of different species, the result of which can provide a reference for genetics and taxonomy research. In transcriptomics and proteomics research, sequencing technology is adopted to analyze different expressions of genes and proteins in different tissues of edible fungi under different treatments and to perform subsequent molecular research by reserving a large quantity of gene data and protein data. In metabolomics research, the special bioactive substances produced in the growth and development of edible fungi are analyzed, along with their anabolic pathways. Omics research on edible fungi is the only way to comprehensively understand their molecular mechanism. The application of omics technology in edible fungus research involves the systematic biology and molecular biology of edible fungi, in which data are mainly processed and analyzed by bioinformatics methods. The impact of various stresses on the growth and development of edible fungi can be analyzed. Based on this, the cultivation conditions are optimized for different species of edible fungi. A more comprehensive study of the various aspects of edible fungi can be conducted by combining multiple omics. The analysis of previous omics studies on edible fungi shows that the global edible fungi resources are very rich, but the types of edible fungi involved in the study are limited. Researchers have focused on *L. edodes*, *V. volvacea*, *F. velutipes*, *G. lucidum* and other common edible fungi. This finding indicates that a large gap still exists in edible fungi omics research. Most of the omics technologies applied to edible fungi research remain in single omics research. Few studies have combined two or three omics technologies. Therefore, multiple omics technologies can be integrated to make omics research on edible fungi more specific and reliable. Omics technology itself is constantly developing and omics research on edible fungi is also constantly deepening.

The edible value and medicinal value of mushrooms themselves have always attracted much attention, so the future omics research of mushrooms will mainly focus on these two points. In food processing, people hope to continuously improve the taste of mushrooms, so it is necessary to artificially change the traits of fruiting bodies to obtain good commercial traits, obtain high-yield strains through molecular breeding and genetic breeding, and still grow and develop normally to form fruiting bodies when encountering adverse environments. In terms of drug treatment, it is necessary to explore the type and content of bioactive substances contained in mushrooms themselves, and hope to artificially increase the content of their biological activities, and extract them as pharmaceutical additives to treat diseases. None of these studies are overnight, but require step-by-step puzzles to be solved. Omics techniques will play a very important role in these studies. In the future, the omics research of edible fungi will continue to increase, and more and more problems will be encountered, especially the advantages of omics technology will be effectively combined with other research methods. We need to continuously innovate on the basis of previous studies to open a broader prospect for edible fungi research.

Funding

This work was supported by Gansu Provincial Youth Science and Technology Fund Program (No.20JR5RA064), Scientific and Technological Innovation Talents of Sichuan Province (No.2022JDRC0034), Central Public-interest Scientific Institution Basal Research Fund (No. S2022007) and Local Financial Funds of National Agricultural Science and Technology Center, Chengdu (No.NASC2021KR06).

CRediT authorship contribution statement

Luping Cao: Conceptualization, Methodology, Writing – original draft. **Qin Zhang:** Writing – review & editing, Visualization. **Renyun Miao:** Investigation, Writing – review & editing. **Junbin Lin:** Investigation, Writing – review & editing. **Rencai Feng:** Investigation, Writing – review & editing. **Yanqing Ni:** Investigation, Writing – review & editing. **Wensheng Li:** Investigation, Writing – review & editing. **Delong Yang:** Supervision, Project administration, Funding acquisition. **Xu Zhao:** Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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