



Heat stress in macrofungi: effects and response mechanisms

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Abstract

Temperature is one of the key factors that affects the growth and development of macrofungi. Heat stress not only negatively affects the morphology and growth rate of macrofungi, but also destroys cell structures and influences cell metabolism. Due to loosed structure of cell walls and increased membrane fluidity, which caused by heat stress, the outflow of intracellular nutrients makes macrofungi more vulnerable to invasion by pathogens. Macrofungi accumulate reactive oxygen species (ROS), Ca²⁺, and nitric oxide (NO) when heat-stressed, which transmit and amplify the heat stimulation signal through intracellular signal transduction pathways. Through regulation of some transcription factors including heat response factors (HSFs), POZCP26 and MYB, macrofungi respond to heat stress by different mechanisms. In this paper, we present mechanisms used by macrofungi to adapt and survive under heat stress conditions, including antioxidant defense systems that eliminate the excess ROS, increase in trehalose levels that prevent enzymes and proteins deformation, and stabilize cell structures and heat shock proteins (HSPs) that repair damaged proteins and synthesis of auxins, which increase the activity of antioxidant enzymes. All of these help macrofungi resist and adapt to heat stress.

Key points

- The effects of heat stress on macrofungal growth and development were described.
- The respond mechanisms to heat stress in macrofungi were summarized.
- The further research directions of heat stress in macrofungi were discussed.

Keywords Heat stress · Macrofungi · Growth · Development · Signal transduction · Response mechanisms

Introduction

Macrofungi, also known as mushrooms and truffles, are defined as a kind of fungi with well-developed hyphae that usually can form large fruiting bodies (Turlo 2014). Some macrofungi have high nutritional value; they are rich in proteins, polysaccharides, vitamins, and minerals (Sun et al. 2020). And some contain triterpenoids, flavonoids, and phenolic compounds, etc. which make them have a wide range of medicinal value, such as anti-tumor, antioxidant, antiviral, and immunomodulatory (Kalaras et al. 2017). However, during growth and development,

macrofungi may encounter unsuitable environmental factors, which seriously affect their yields and qualities (Belletini et al. 2019; He et al. 2020; Pavlík et al. 2020).

Temperature is one of the main environmental factors that may unexpectedly disrupt macrofungi growth and development (Andrew et al. 2018; Büntgen et al. 2012; Larson et al. 2016). In the mycelial stage, optimal temperature is beneficial to the continuous growth and nutrient accumulation of vegetative mycelia (Deshaware et al. 2021; Wan Mahari et al. 2020; Zervakis et al. 2001). Excessive temperatures can cause heat stress, which not only affects the mycelial growth rate, but also disrupts cell structures and cell metabolism and increases the probability of infection by pathogenic microorganisms (Liu et al. 2017a; Qiu et al. 2018b). The quality of mycelial growth is closely related to the formation of primordia and production efficiency of fruiting bodies (Foulongne-Oriol et al. 2014; Salmones et al. 2018). In the fruiting body stage, heat stress may cause mass deaths of young fruiting bodies and even reduce the production significantly (Chang

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et al. 2021). Therefore, studying growth and development changes in response to heat stress and revealing the heat-resistant mechanisms are important for avoiding heat damage and improving the heat tolerance of macrofungi.

There are more and more studies on heat stress in macrofungi, but the underlying mechanisms for them to respond to heat stress are not systematically described. As a reference, here we review the effects of heat stress on the morphology, cell structure, and metabolism of macrofungi and summarize recent progress in understanding the response mechanisms of macrofungi to heat stress. At the same time, future research directions are also discussed.

Effects of heat stress on macrofungal growth and development

Effect on mycelial and fruiting body morphology

Under normal growth conditions, aerial hyphae grow rapidly and vigorously. However, aerial hyphae become loose and wilted after heat stress, which readily deform and fracture (Hoa and Wang 2015; Yan et al. 2020). During the recovery stage from heat stress, hyphae usually form obvious heat shock loops (Fig. 1, our unpublished work). At a temperature of 30 °C, hyphae of *Cantharellus cibarius* even stop

growing (Deshaware et al. 2021). Furthermore, continuous increase of temperature may lead to the increase of aerobic respiration. Because of the restriction of air circulation and the enhancement of aerobic respiration, dissolved oxygen in cultured bag decreases, and the activity of anaerobic respiration enzymes increases. At 34 °C, which is far lower than the maximum growth temperature of 38 °C and lethal temperature of 41 °C, the inhibition of anaerobic respiratory metabolites, and low energy-saving efficiency can cause “spawn-burning” syndrome in *Pleurotus eryngii* (Zhang et al. 2016a). Heat stress have been shown to darken the color of ectomycorrhizal fungus *Tuber borchii* and weaken its survival ability on host roots (Leonardi et al. 2017). During fruiting, excessive temperature may cause a longer stipe and a thinner, smaller cap (Foulongne-Oriol et al. 2014; Halbwachs and Simmel 2018). Some reddish spinules may appear on the top of *Cordyceps militaris* fruiting bodies under heat stress (Zhang et al. 2018). All of these features lead to the deterioration of macrofungal morphology. What's more, extreme temperatures and long stress periods can cause a reduction in hyphal branching, which is not conducive for the formation of fruiting body primordia, and cause mass deaths of young fruiting bodies, or secondary non-fruiting, and in some cases even no production at all (Chang et al. 2021; Hoa and Wang 2015; Kang et al. 2013).

Effect on cell structure

Heat stress can destroy the cell wall of *Pleurotus ostreatus*, leading to chitin deposition and loose structure, thus destroying the first protective barrier of cells (Qiu et al. 2018a). It may cause a reduction in the content of unsaturated fats by changing the fatty acid composition of cell membrane, which affects the fluidity of the cell membrane (Li et al. 2020; Liu et al. 2017b). Moreover, changes to the plasma membrane fluidity and permeability increase the outflow of intracellular electrolytes (Awasthi et al. 2015). The increase of mycelial extracellular metabolites and the outflow of intracellular nutrients can accelerate mycelial growth and spore germination of pathogenic fungi, thus causing apoptosis-like cell death in *P. eryngii* and *P. ostreatus* (Liu et al. 2017a; Qiu et al. 2018b). In addition, heat stress also causes secondary and tertiary structural changes to some enzymes, even inactivation in severe cases, resulting in nuclear condensation, mitochondrial dysfunction, and DNA fragmentation (Prasad et al. 2016; Yan et al. 2020; Zhou et al. 2017).

Effects on cell metabolism

Microorganisms typically respond to stress by undergoing metabolic changes. The activities of various proteins involved in metabolism were found to be downregulated in *P. ostreatus* when placed under heat stress (Zou et al. 2018). The metabolic pathways which include tricarboxylic acid

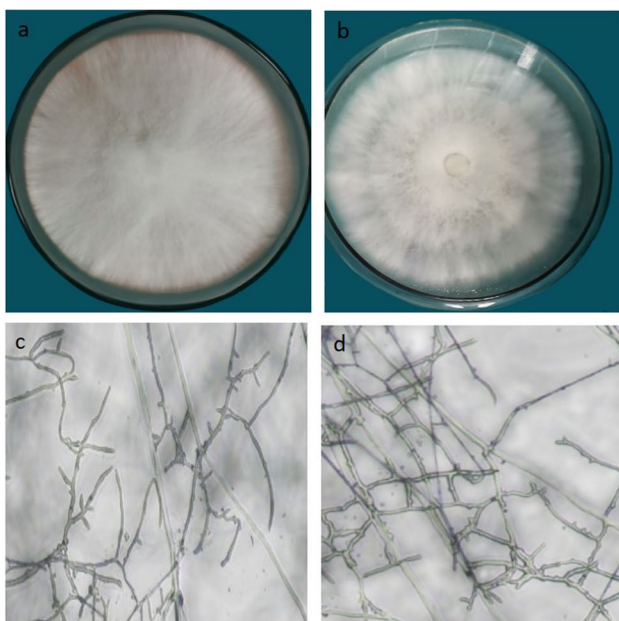


Fig. 1 Effect of heat stress on apparent and microscopic morphology of *Pleurotus tuber-regium*. **a** The mycelium is thick and powerful when grew at 32 °C for 7 days. **b** The mycelium is thin with obvious heat shock circles when grew at 32 °C for 4 days, stressed at 40 °C for 10 h, and then at 32 °C for 3 days. **c** Micrograph of mycelium grew at 32 °C, the hyphae had more branches. **d** Micrograph of mycelium stressed at 40 °C for 10 h, the hyphae twined, and branches decreased

cycle, glucose metabolism, sphingolipid metabolism, and some amino acid metabolism may change significantly under heat stress. During the early stages of exposure to heat stress, intermediate metabolites that are part of glycolysis and the tricarboxylic acid cycle were observed to decrease in *Lentinula edodes*, resulting in carbon starvation, which stunted growth and development of *L. edodes* (Zhao et al. 2018). To maintain an energy balance, cells need more energy, which involves conversion of glycogen to glucose. Those typical energy supply pathways such as glycolysis, tricarboxylic acid cycle, and the pentose phosphate pathway may be activated to cope with heat stress (Tan et al. 2018a). Heat stress can promote the continuous degradation of proteins and increase the content of amino acids, such as valine, phenylalanine, and tyrosine, which contributes to the stability of the cell wall under heat stress (Krah et al. 2021; Wang et al. 2018b). Heat stress can promote the synthesis of ganoderic acid and increase the content of polysaccharides (Tan et al. 2018b; Tian et al. 2019). All of these processes suggest that appropriate heat stress is beneficial for macrofungi to accumulate nutrients, and such stress can be used to improve the accumulation of particular metabolites in cells. However, long-term exposure to heat stress increases the content of FMN, FAD, NADP, riboflavin, and nicotinic acid, indicating that electron transfer ability and the redox state of cells are negatively affected by heat stress (Yan et al. 2020). Furthermore, under heat stress, the accelerated respiration rate of macrofungi can cause accumulation of reactive oxygen species (ROS). Elevated concentrations of ROS may disrupt redox homeostasis and cause oxidative stress damage, such as membrane peroxidation, and even facilitate apoptosis (Song et al. 2014; Xu et al. 2021c; Zhang et al. 2016a). Therefore, it is necessary to study the response mechanisms of macrofungi to heat stress.

Intracellular heat signal transduction systems in macrofungi

Under heat stress, macrofungi show certain physiological changes in cell structure and metabolism. Therefore, macrofungi are probably able to perceive stress signals. Studies in plants have found that the cell membrane is highly influenced by temperature and thus may act as a potential cellular thermoreceptor (Los and Murata 2004; Vu et al. 2019). In bacteria, higher temperatures cause greater disorder in lipid arrangement, and the cell membrane becomes thinner. Sensors located in the transmembrane region register changes in cell membrane thickness, which activates the corresponding kinase activity. The destruction of the helix between transmembrane segment and intracellular domain is mechanically used to transfer temperature-dependent conformational changes from the transmembrane to the intracellular domain (Inda et al. 2014). Then the thermal signal

transmitted through intracellular signal transduction systems (Krah et al. 2021). However, research on thermal sensors in macrofungi have not been reported. Current studies have reported mainly on the signal transduction of ROS, Ca^{2+} , and nitric oxide (NO) during heat stress (Chen et al. 2017; Liu et al. 2018b). Some transcription factors in macrofungi, such as heat response factors (HSFs), POZCP26, and MYB have been reported to transmit signals and regulate the expression of a variety of genes in response to heat stress (Hou et al. 2020b; Vihervaara et al. 2018; Wang et al. 2018a).

ROS signaling

ROS is a by-product of all aerobic respiration. Its production is not only a sign of stress damage degree to organism, but also a signal molecule involved in secondary metabolism biosynthesis and response to environmental stimuli (Li et al. 2015; Liang et al. 2015). The accumulation of ROS, a typical signaling molecule of all organisms, in several macrofungal mycelia under heat stress has been reported recently (Lei et al. 2019; Liu et al. 2018a). For example, heat stress has been shown to increase the fluidity of the *Ganoderma lucidum* membrane, which activates NADPH oxidase (NOx) to produce ROS. The increase of intracellular ROS can activate the antioxidant defense system of *G. lucidum* to alleviate oxidative damage caused by heat stress (Shi et al. 2015). Furthermore, an increase in ROS production activates the Ca^{2+} signaling pathway and stimulates heat shock proteins (HSPs) expression under mild heat stress (Zuo et al. 2015; Liu et al. 2018c).

Ca^{2+} signaling

As the second messenger connecting extracellular environment and intracellular physiological activities, Ca^{2+} is a key messenger in the growth and development of fungi and plays a crucial role in stress signal transduction (Juvvadi et al. 2014; Zhu et al. 2019). The intracellular-free Ca^{2+} concentration in heat-tolerant *P. ostreatus* and *G. lucidum* has been found to be relatively high (Yao et al. 2019; Zhang et al. 2016b). An increase in the fluidity of the plasma membrane following heat stress causes the temporary opening of specific calcium channels and triggers Ca^{2+} flow into cells (Liu et al. 2017c). Meanwhile, high temperature stress stimulates inositol phospholipid metabolism of cells. GTPases activate phosphatidylinositol kinase (PIK), which phosphorylates phosphatidylinositol (PI) into PI-4,5-bisphosphate [PI(4,5)P₂]. PI(4,5)P₂ can act as a precursor to inositol 1,4,5-trisphosphate (IP₃) and triggers the rapid accumulation of IP₃ and the release of intracellular calcium pool (Liu et al. 2006, 2018d; Tang et al. 2007). After Ca^{2+} influx into cells, they bind to the EF-hand binding domains of calmodulin (CaM) to activating specific CaM- and kinase-dependent signaling pathways and interact with DNA-binding proteins to regulate

their activities (Kameshita et al. 2007; Kamthan et al. 2015). Ca^{2+} entering into mitochondria, it may be accompanied by the hyperpolarization of mitochondrial intima and the increase in ROS production, which can directly or indirectly regulate ROS production and HSP synthesis through respiratory burst homologous proteins (Liu et al. 2018c; Pathak and Trebak 2018; Yao et al. 2019; Zhang 2016b). In addition, the synergistic effect of Ca^{2+} and NO can regulate the biosynthesis of ganoderic acid under high temperature stress (Chen et al. 2017).

NO signaling

Nitric oxide regulates the activity of antioxidant enzymes through protein modification and helps cells to proliferate and resist heat stress (Napoli et al. 2013; Xuan et al. 2010). Heat stress promotes the NO synthase (NOS) oxidation of L-arginine with NADPH and O_2 as substrates to produce NO (Liu et al. 2018c). The stress signal is further transmitted to downstream response factors by activating guanylate cyclase and increasing cGMP levels (Loshchinina and Nikitina 2016). The addition of the NOS inhibitor nitro-L-arginine methyl ester inhibits the production of NO and increases the content of malondialdehyde in *P. eryngii* mycelium, which suggests that NO effectively alleviates oxidative damage caused by heat stress (Kong et al. 2012a). NO enhances the activity of antioxidant enzymes, eliminates harmful ROS, and maintains cellular redox homeostasis; at the same time, it can regulate the protective effects of carotenoids (neutralizing free radicals) (Parankusam et al. 2017). By inhibiting the protein and gene expression of aconitase (ACO), NO can stimulate the expression of alternating oxidase (AOX), thereby reducing oxidative damage of *P. ostreatus* (Hou et al. 2020a; Kleschyov 2017). Moreover, NO participates in the accumulation of intracellular trehalose and stimulates the DNA-binding activity of heat-stimulated HSF and the accumulation of HSP18.2 by regulating the expression of *AtCaM3* (Kong et al. 2012b; Xuan et al. 2010).

Transcription factors

Transcription factors (TFs) are trans-acting factors that can combine with specific DNA sequences to control gene expression, so as to ensure the effective life activities of an organism at a specific time or in a specific cell (Latchman 1997; Pelkmans et al. 2017). Currently, HSFs are master transcription factors affecting the response of macrofungi to heat stress. Under heat stress, Ca^{2+} , ROS, and NO can interdependently change the activity of HSF by activating multiple signaling pathways through post-translational modification (Li et al. 2018; Liu et al. 2018b). When macrofungi are exposed to heat stress, HSFs transform from an inactive monomeric state to an active trimeric state, and

activated HSFs recognize the heat shock element region upstream of heat stress genes, which leads to an increase in transcription and accumulation of heat-stimulated gene products (Liu and Chen 2015; Tiwari et al. 2015; Vihervaara et al. 2018). When stress is relieved or HSPs accumulate to a particular level, HSFs adopt an inactivate state and switch off transcription of HSPs (Taipale et al. 2010). PoZCP26 as a transcription factor have double zinc-finger transcription domain in *P. ostreatus* that positively regulates heat stress tolerance and post-stress recovery of mycelium (Hou et al. 2020b). As one of the largest family of transcription factors in eukaryotes, the *MYB* gene family exhibits extremely high expression levels after heat stress, which regulates a variety of genes in response to environmental changes and helps mycelium to resist heat stress (Wang et al. 2018a). Currently, there is limited research on transcription factors in macrofungi that response to heat stress, which hampers research examining heat stress signaling pathways. Therefore, the role of transcription factors in protecting macrofungi from heat stress requires further study.

Heat stress response in macrofungi

Antioxidant defense system

Antioxidant enzymes play an important role in the whole growth and development of macrofungi (Orban et al. 2021). It is found that oxidative stress is often associated with heat stress and can directly induce cell damage after heat stress (Liu et al. 2019). Therefore, macrofungi response to heat stress usually causes an increase in cell oxidative scavenging capacity. Glutathione peroxidase (GPX) regulates the level of ROS in *G. lucidum*, affects the Ca^{2+} content in the cytoplasm, and regulates Ca^{2+} signaling pathway-related genes involved in the regulating heat stress, thereby reducing heat damage (Li et al. 2015). The activities of catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) in *G. lucidum* mycelium were found to increase after heat treatment (Liu et al. 2018c). CAT is the primary enzyme that scavenges for ROS and alleviates oxidative damage under heat stress; however, different stress temperatures and stress durations cause different expressions of CAT-encoded genes (Wang et al. 2017). Moreover, Vitamin C (Vc) and N-acetylcysteine also reduce ROS content in *G. lucidum* following heat stress (Liu et al. 2018d).

Synthesis and metabolism of trehalose

High concentrations of trehalose can prevent denaturation and inactivation of enzymes and proteins under stress, reduce protein aggregation, and stabilize cells (Arastoo et al. 2018; Jain and Roy 2008). Numerous studies have shown

that the trehalose contents in macrofungi increased under heat stress (Lei et al. 2019; Liu et al. 2016, 2019; Meng et al. 2015). The accumulation of intracellular trehalose induces a decrease in lipoxygenase (Lox) activity, by reducing the accumulation of H_2O_2 and O^{2-} . Trehalose has been shown to partially alleviate oxidative damage of membranes and promote the recovery of *P. pulmonarius* mycelia growth following heat stress (Liu et al. 2019). Currently, there are three viewpoints on the molecular mechanism of trehalose alleviating oxidative damage induced by heat stress: (i) trehalose activates the total antioxidant reduction system (Rohman et al. 2019); (ii) trehalose acts directly on the glycolysis pathway and pentose phosphate pathway to restore mitochondrial dysfunction (Yan et al. 2020); and (iii) trehalose activates the nuclear factor erythrocyte type 2-associated factor (Nrf2) mediating the antioxidant pathway (Mizunoe et al. 2018). NADPH is a central cofactor in the antioxidant system of glutathione and thioredoxin/peroxygenase and a product of the pentose phosphate pathway; thus, the pentose phosphate pathway is considered to be the main pathway in trehalose response to heat stress (Boone et al. 2017; Matsumoto et al. 2018).

However, addition of trehalose cannot completely repair growth defects caused by the deletion of the trehalose 6 phosphate synthase (TPS) gene, suggesting that TPS rather than trehalose may be responsible for protecting fungi from heat stress (Gibney et al. 2015). TPS stimulates trehalose biosynthesis and maintains the ATP level to ensure energy homeostasis. However, it has been shown that the products of TPS protein itself may also help *Pleurotus tuoliensis* tolerate heat stress (Petitjean et al. 2015; Wu et al. 2018).

Expression of heat shock proteins

As molecular chaperones, HSPs prevent protein aggregation, remove denatured proteins, help damaged proteins fold, and play a key role in response to adversity stress (Clerico et al. 2015; Mogk et al. 2015). According to the mode of action, HSPs are divided into inducible and constitutive types. Inducible HSPs have a protective effect on cells and are only synthesized when cells are stimulated by external factors, whereas constitutive HSPs are mainly involved in cell differentiation processes and are synthesized at all stages of growth and development (Kurahashi et al. 2014; Treseder and Lennon 2015). Proteomic and transcriptomic studies have shown that the expression of HSPs in macrofungi is significantly upregulated under heat stress (Krah et al. 2021; Liu et al. 2020; Tan et al. 2018a; Zou et al. 2018). The small HSP gene *LeDnaJ* silent mutant of *L. edodes* was defective in mycelial growth under heat stress (Wang et al. 2018a). Xu et al. (2020) cloned an Hsp70 (A0A369K2K3) gene *hmHsp70* of *Hypsizygus marmoreus* into tobacco; the transgenic tobacco displayed enhanced resistance to a lethal

temperature. These observations indicate that HSPs play an important role in macrofungal heat stress response.

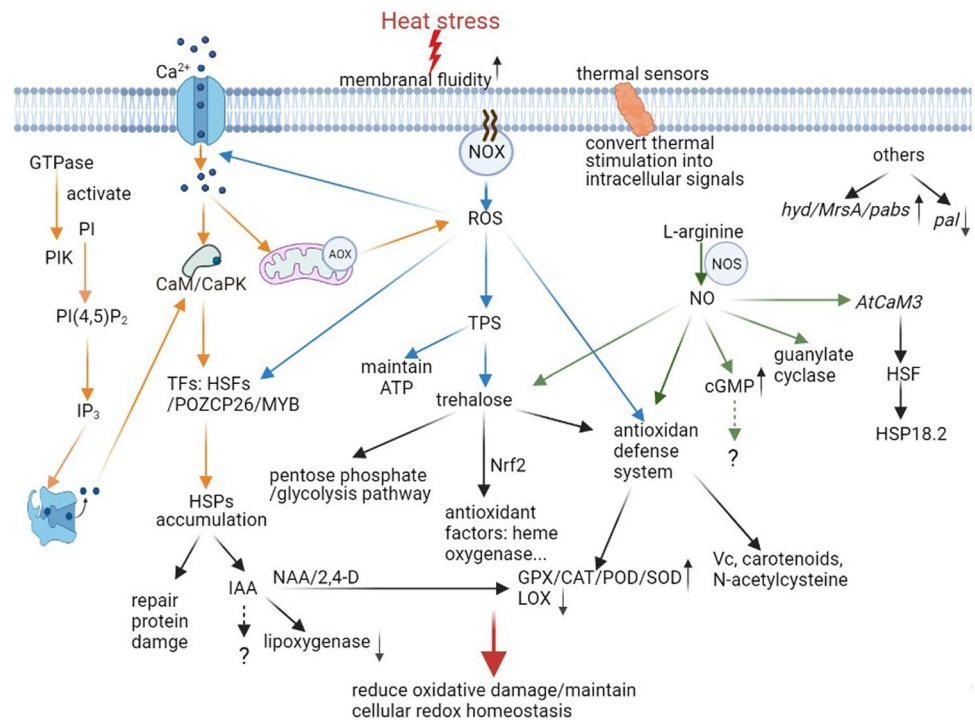
Synthesis of auxins

Exogenous addition of indoleacetic acid (IAA), auxin analogue α -naphthylacetic acid (NAA) and 2, 4-dichlorophenylacetic acid (2, 4-D) to *L. edodes* was shown to inhibit the production of O^{2-} , reduce the activity of lipoxygenase, and maintain the activity of POD under heat stress, thus reducing heat injury (Zhou et al. 2018). Proteomic and transcriptomic studies by Wang et al. (2018b) indicated that IAA improves the heat tolerance of *L. edodes* through regulation of the tryptophan pathway. Ma et al. (2018) found that the synthesis gene of anthranilate synthase may regulate mycelial heat resistance by affecting the IAA content in *L. edodes*. Yeast two-hybrid and bimolecular fluorescence complementation showed that LeDnaJ07 may also be involved in the regulation of IAA biosynthesis and resistance to heat stress by interacting with LetrpE (Wang et al. 2020). However, suitable concentration of IAA restores the mycelial growth of heat sensitive strain after heat stress, while excessive concentration of IAA inhibits the recovery ability of mycelial growth (Wang et al. 2018c). Furthermore, exogenous salicylic acid improves the heat tolerance of mycelium, and an increase of salicylic acid under heat stress may represent a defense mechanism of *P. ostreatus* (Yan et al. 2020). However, the mechanisms of these auxins under heat stress require further investigation.

Other heat-related genes

In addition to the heat stress response mentioned above, some additional genes also participate in these responses of macrofungi. Yin et al. (2015) found that overexpression of methionine sulfoxide reductase A gene (*MsrA*) enhanced the thermal tolerance of *P. ostreatus*. Xin et al. (2016) reported that the gene *hydI* of *L. edodes* played an important role in the response to heat stress. The work of Andreu et al. (2021) confirmed that efficient expression of hydrophobins of HFBI and DewA on the cell surface of *Saccharomyces cerevisiae* increased resistance to several adverse conditions including heat and osmotic stress. In *P. ostreatus*, 40 hydrophobin genes were screened by genome and transcriptome sequencing and functional characterized; meanwhile, a microRNA (Po-MiR-1) may perform its physiological function through negative regulation of its target hydrophobin gene *POH1* (Xu et al. 2021a, b). Under heat stress, the expression of para-aminobenzoic acid (PABA) synthase gene *Pabs* increased, which enhanced thermotolerance of *Agaricus bisporus* by removing H_2O_2 and elevating defense-related proteins (Lu et al. 2014). In addition, the results of a heat stress test showed that the RNAi strains of phenylalanine

Fig. 2 Main heat stress response mechanisms in macrofungi. The orange lines indicate the Ca^{2+} signaling, and the blue lines indicate the ROS signaling, the green lines indicate the NO signaling; the black line shows heat stress response pathways, and the red lines represent the result of these response mechanisms. The dotted line and question mark indicate the unknown mechanism



ammonia lyase gene *pal 1* enhanced mycelial tolerance to heat stress, and *pal 2* RNAi strains enhanced mycelial resistance to H_2O_2 , which confirmed that *pal* may negatively regulate the heat stress response of *P. ostreatus* through different regulatory processes (Hou et al. 2019).

Summary and prospect

Cultivation of high-yield and high-quality macrofungi remains a hot research topic because of the high economic value these macrofungi offer. Temperature is a key factor affecting the growth and development of macrofungi. Heat stress have been shown that affects the morphology of macrofungi and damages cell structure and metabolism. Damage to the cell structure and the outflow of metabolites increase the vulnerability of macrofungi to the invasion of pathogenic microorganisms and induce cell apoptosis. Signal transduction pathways in macrofungi involving ROS, Ca^{2+} , NO, and transcription factors have been found to participate in intracellular heat stress signal transductions. Macrofungi respond to heat stress in many ways. Antioxidant defense systems eliminate excessive accumulation of ROS caused by heat stress; the synthesis and metabolism of trehalose prevent the denaturation of enzymes and proteins under heat stress and stabilize the structure of cells; HSPs repair protein damage; auxin synthesis improves the activity of antioxidant enzymes. All of these processes combine to increase macrofungi resistance and adaption to heat stress (Fig. 2).

Although researchers have studied extensively how macrofungi respond to heat stress, the mechanisms of response to heat stress in macrofungi remain unresolved, and there are many areas that require further investigation. Firstly, thermal sensors in macrofungi have not been identified, and the intracellular heat signal transduction systems are not fully understood. There are possibly other heat-signaling pathways that have not been discovered. Secondly, current researches focus mostly on the mycelial stage. It remains to be verified whether heat-resistant substances that improve heat resistance in the mycelial stage play a role in the growth and development of the fruiting body. Thirdly, the specific mechanism and potential relationship between signal transduction and response pathways have not been clarified. In addition, the temperature limit of beneficial or harmful effects on macrofungi requires further investigation. Understanding these issues in greater detail will promote the economic value of macrofungi.

Author contribution All authors contributed to this study. LL and AM had the ideas for the article and performed the literature search and data analysis. LL wrote the manuscript. SZ, JW, XS, and AM critically reviewed the manuscript.

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Declarations

Ethics approval This article does not contain any studies with human participants or animals performed by any of the authors.

Conflict of interest The authors declare no competing interests.

Disclaimer The views stated here are ours and ours only. We apologize if we failed to mention other significant research from other mechanisms of macrofungi in response to heat stress and if our interpretation of the data is not accepted by other researchers.

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