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Heat Stress Induces Apoptotic-Like Cell Death in Two *Pleurotus* Species

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Abstract High temperature is an important environmental factor that affects the growth and development of most edible fungi, however, the mechanism(s) for resistance to high temperature remains elusive. Nitric oxide is known to be able to effectively alleviate oxidative damage and plays an important role in the regulation of trehalose accumulation during heat stress in mycelia of *Pleurotus eryngii* var. *tuoliensis*. In this paper, we investigated whether heat stress can activate apoptosis-like cell death in mycelia of *Pleurotus*. Two *Pleurotus* species were used to detect morphological features characteristic of apoptosis including nuclear condensation, reactive oxygen species accumulation, and DNA fragmentation when exposed to heat stress (42 °C). The results showed that these classical apoptosis markers were apparent in *Pleurotus* strains after heat treatment. The heat-induced apoptosis-like cell death in *Pleurotus* was further probed using oligomycin and *N*-acetylcysteine, both of which were shown to block processes leading to apoptosis. This is the first report that apoptosis-like cell death occurs in *Pleurotus* species as a result of abiotic stress, and that this process can be inhibited with chemicals that block mitochondrial-induced apoptotic pathways and/or with ROS-scavenging compounds.

Introduction

Pleurotus species (Basidiomycota, Agaricales) are worldwide-distributed white-rot fungi often responsible for causing hardwood decay in terrestrial ecosystems [30]. Many *Pleurotus* fungi have been widely cultivated in China for use in the bioconversion of lignocellulosic substrates into high-value nutritional and medicinal supplements [3, 24]. Little, however, is known concerning the mechanisms by which the fungus responds to heat stress, and thus far there have been few reports examining susceptibility to heat stress and link to autophagy and programmed cell death (PCD).

PCD represents a highly conserved cellular suicide program that contributes to normal growth and development in multicellular organisms. It is associated with maintenance of cell homeostasis, removal of damaged cells, and in the mediating responses to biotic and abiotic stresses [9]. Although PCD is well recognized in higher metazoans, it appears to occur in all living organisms, including plants, fungi, and bacteria [11, 17, 23]. Indeed, a number of recent reports have focused on PCD in yeasts and filamentous fungi, especially in *Saccharomyces cerevisiae* and *Aspergillus nidulans* [5, 7, 10, 16]. Many environmental factors can induce filamentous fungal apoptosis-like cell death. These include oxidative, osmotic, heat, and ultraviolet-irradiation stress [29]. However, research on apoptosis-like cell death in mushrooms, particularly in *Pleurotus* fungi, is limited, and knowledge concerning apoptotic pathways and regulatory elements remains partial.

Heat stress is known to inhibit mycelial growth, impair fruiting body formation, ultimately affecting the quality of mushroom [2]. Our previous research found that nitric oxide (NO) could effectively alleviate oxidative damage and plays an important role in the regulation of trehalose accumulation during heat stress in mycelia of *P. eryngii* var. *tuoliensis* [14, 15]. In this study, it was investigated whether heat could act via other response mechanisms to

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