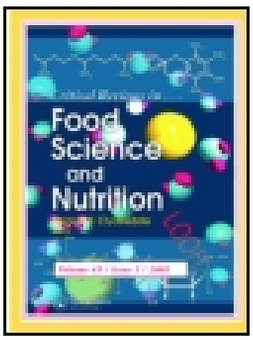

Critical Reviews in Food Science and Nutrition

ISSN: 1040-8398 (Print) 1549-7852 (Online) Journal homepage: http://www.tandfonline.com/loi/bfsn20

The Impact of the Postharvest Environment on the Viability and Virulence of Decay Fungi

Jia Liu, Yuan Sui, Michael Wisniewski, Zhigang Xie, Yiqing Liu, Yuming You, Xiaojing Zhang, Zhiqiang Sun, Wenhua Li, Yan Li & Qi Wang

To cite this article: Jia Liu, Yuan Sui, Michael Wisniewski, Zhigang Xie, Yiqing Liu, Yuming You, Xiaojing Zhang, Zhiqiang Sun, Wenhua Li, Yan Li & Qi Wang (2017): The Impact of the Postharvest Environment on the Viability and Virulence of Decay Fungi, Critical Reviews in Food Science and Nutrition, DOI: 10.1080/10408398.2017.1279122

To link to this article: http://dx.doi.org/10.1080/10408398.2017.1279122

The Impact of the Postharvest Environment on the Viability and Virulence of Decay Fungi

Jia Liu[1], Yuan Sui[1,*], Michael Wisniewski[2], Zhigang Xie[1], Yiqing Liu[1], Yuming You[1], Xiaojing Zhang[3], Zhiqiang Sun[3], Wenhua Li[3], Yan Li[4], Qi Wang[4]

[1]Chongqing Key Laboratory of Economic Plant Biotechnology, College of Forestry & Life Science/Institute of Special Plants, College of Materials and Chemical Engineering, Chongqing University of Arts and Sciences, Yongchuan 402160, China

[2]U.S. Department of Agriculture - Agricultural Research Service (USDA-ARS), 2217 Wiltshire 11 Road, Kearneysville, WV 25430, USA

[3]Yantai Lvyun Biotechnology Co. Ltd, Yantai 264003, China

[4]Key Laboratory of Plant Pathology, Ministry of Agriculture, Department of Plant Pathology, China Agricultural University, Beijing 100193, China

*Corresponding author at Institute of Special Plants, Chongqing University of Arts and Sciences, Yongchuan 402160, China.

Tel.: +86-23-49682178; E-mail: suiyuan-mine@163.com

Abstract

Postharvest decay of fruits, vegetables, and grains by fungal pathogens causes significant economic losses. Infected produce presents a potential health risk since some decay fungi produce mycotoxins that are hazardous to human health. Infections are the result of the interplay between host resistance and pathogen virulence. Both of these processes, however, are significantly impacted by environmental factors, such as temperature, UV, oxidative stress and

water activity. In the present review, the impact of various physical postharvest treatments (e.g., heat and UV) on the viability and virulence of postharvest pathogens is reviewed and discussed. Oxidative injury, protein impairment, and cell wall degradation have all been proposed as the mechanisms by which these abiotic stresses reduce fungal viability and pathogenicity. The response of decay fungi to pH and the ability of pathogens to modulate the pH of the host environment also affect pathogenicity. The effects of the manipulation of the postharvest environment by ethylene, natural edible coatings, and controlled atmosphere storage on fungal viability are also discussed. Lastly, avenues of future research are proposed.

Keywords**:** Heat stress, manipulated environment, oxidative stress, pathogen viability, pH, stress response

Introduction

Postharvest decay of fruits, vegetables, and grains by phytopathogens, especially fungal pathogens, causes significant economic losses. Some decay fungi also produce mycotoxins that represent a risk to human health, especially in processed foods meant for children. Worldwide concern about food safety, as well as environmental protection, has provided the incentive for researchers to identify effective, ecofriendly methods for the management of postharvest fungal diseases (Gatto et al., 2011; Liu et al., 2013; Sui et al., 2016; Romanazzi et al., 2017). Characterizing the response of plant hosts to fungal pathogens has been a major research focus with the goal of better understanding resistance and virulence mechanisms so that new management approaches could be developed (Mbengue et al., 2016). The two principal components of this interaction are both impacted by temperature, pH, UV, oxidative stress, etc. (Imahori, 2011). The impact of such factors on postharvest pathosystems, especially the physiology and virulence of postharvest fungal pathogens, still requires much study.

Temperature is a key determinant in the success or failure of both microbial invasion and host evasion (Willi et al., 2011; Cheng et al., 2013). The pH of the microenvironment is another major factor that can significantly impact the physiology and virulence of pathogenic fungi. Within the larger context of fungal and environmental interactions, fungi have developed a complex regulatory system to sense and respond to changes in pH (Peñalva et al., 2008; Lebretonet al., 2014). The infection process by some pathogens is initiated and supported by the secretion of organic acids or ammonia that locally acidify or alkalinize host tissues when establishing an infection (Alkan et al., 2013). An oxidative burst, during which large quantities of reactive oxygen species (ROS), mainly hydrogen peroxide and hydroxyl radicals, are

generated by the host, represents one of the earliest host defense mechanisms triggered by the attempted invasion of a pathogen (Nanda et al., 2010). The resulting oxidative microenvironment may also have a direct effect on pathogen viability and virulence (Yang et al., 2016). Therefore, characterizing the response of fungal pathogens to temperature, pH, and oxidative stress is essential for understanding the physiological mechanisms responsible for virulence.

Tiwari et al. (2015) reviewed the role of heat-shock proteins (Hsps) in the cellular function and biology of fungi. Expression of Hsp60, Hsp90, Hsp104, Hsp30, and Hsp10 proteins increased in fungi exposed to heat stress. In contrast, expression of Hsp12 protein was induced in response to cold stress and Hsp30, Hsp70, and Hsp90 proteins were induced in response to pH stress. Another stress-related gene in fungi is *Fgk3*, a glycogen synthase kinase, whose expression was reported to be essential to development, pathogenesis, and stress adaptation (cold, heat, H_2O_2, and salt) in the wheat scab fungus, *Fusarium graminearum* (Qin et al., 2015). Conidia produced by *CsVosA* knockout mutants (Δ*CsVosA*) of the fungal cereal pathogen, *Cochliobolus sativus,* lacked the ability to synthesize trehalose and exhibited a significant reduction in viability, less pigmentation, and had a significantly reduced tolerance to heat, oxidative, and ion stress (Wang et al., 2015). Cervantes-Chávez et al. (2016) also reported that trehalose was required for stress tolerance (e.g., oxidative, heat, acid, ionic and osmotic stress) and virulence of *Ustilago maydis*, a basidiomycete pathogen of corn.

The present review provides a general overview of the response of postharvest fungal pathogens to various abiotic (e.g., heat, pH, and oxidative) stresses and environmental stresses brought about by the manipulation of the postharvest environment, such as exposure to ethylene,

controlled atmosphere, and natural edible coatings (Figure 1). Table 1 provides a comprehensive listing of the literature on this subject.

Response to heat stress

Extreme temperatures (high and low) are one of the major environmental stresses experienced by fungi. In fact, various heat treatments (hot water dipping/rinsing/brushing, vapor heat, hot air, etc.) are applied to harvested produce as a method of controlling postharvest diseases, improving storage quality, or as part of the normal processing needed to dry wet fruit and the various waxes that are applied (Lurie and Pedreschi, 2014). Heat treatments can have a direct inhibitory/lethal effect on fungal spores depending on the treatment dose (temperature and duration) and also an indirect effect brought about by stimulating host defense systems (Sui et al., 2016). Cervantes-Chávez et al. (2016), reported that the synthesis of trehalose was crucial to the induction and development of heat stress tolerance in *U. maydis* and the ability of this pathogen to maintain high levels of spore germination at elevated temperatures. *Trehalose-6-phosphate synthase* (*TPS1*) and *neutral trehalase* (*NTH1*) genes are involved in the biosynthesis of trehalose in *Botrytis cinerea* (Doehlemann et al., 2006) and *Aspergillus niger* (Svanström and Melin, 2013), and are induced in response to heat stress.

ROS-generating systems are activated when fungi are exposed to heat stress, leading to the accumulation of undesirable amounts of intracellular ROS. The rate of cyanide-resistant respiration also increases in a temperature/time-dependent manner. These changes result in an increase in the production of storage carbohydrates and an increase in the level of proteins and lipids that suffer oxidative damage. If oxidative damage is sufficiently high, a reduction or

complete loss of spore and/or mycelial viability can occur (Gessler et al., 2007; Abrashev et al., 2008). The inhibitory effect of heat treatments on spore viability and/or hyphal growth has been reported for many postharvest fungal pathogens. Hot water treatment (45 ^{o}C for 10 min) effectively inhibited spore germination and germ tube elongation in *Penicillium expansum* and *B. cinerea* (Chen et al., 2015). The loss in viability was attributed to the accumulation of intracellular ROS and its negative impact on proteins (Chen et al., 2015). Heat-induced ROS accumulation in *B. cinerea* was attributed to an increase in the expression of *NADPH oxidase*, a gene that encodes a critical membrane-bound enzyme in the plasma membrane that is part of the cellular redox system (Zhao et al., 2014).

Mitochondrial respiration is responsible for the production of a major portion of intracellular ROS in fungal pathogens in response to heat stress. For example, in *Monilinia fructicola* (Liu et al., 2012) and *Fusarium oxysporum* (Sui et al., 2014), two common postharvest pathogens, heat stress triggers the collapse of mitochondrial membrane potential, the accumulation of ROS, a decrease in intracellular ATP, and an increase in protein impairment. These effects result in a significant reduction in their viability. Even though comprehensive physiological studies have been reported on the response of several model fungi, like yeasts, to heat stress (Li et al., 2010b), the identification of specific stress response signaling pathways and genes involved in heat stress tolerance still remain to be elucidated.

Response to pH

Changes in the pH of the microenviroment surrounding fungi can have a significant impact on the infection process, including both spore germination and mycelial development (Manteau et

al., 2003). The effect of various pH values on spore germination of *P. expansum* was determined by culturing spores in a medium whose pH was adjusted to pH 2.0, 5.0, or 8.0. Results indicated that pH values of 2.0 or 8.0 inhibited spore germination causing a change in the intracellular pH of the fungus. A proteomic analysis also indicated that protein synthesis and folding were impaired at these pH values (Li et al., 2010a). More recently, pH has been shown to affect the production of patulin, a mycotoxin, in *P. expansum* by regulating the expression of genes involved in patulin synthesis (Zong et al., 2015; Tannous et al., 2016). Manteau et al. (2003) reported that varying levels of several putative virulence factors, such as extracellular polysaccharides, oxalic acid, aspartic acid proteases, polygalacturonase, and laccase, were secreted by *B. cinerea* at different pH values, ranging from 2.0 to 7.0. Li et al. (2012) demonstrated that the composition of the secretome of *B. cinerea* varied considerably when the fungus was exposed to a range of pH between 4.0 and 6.0. At pH 4.0, more proteins related to proteolysis were induced, whereas most of the proteins induced at pH 6 were cell-wall-degrading enzymes. These findings indicate that *B. cinerea* adjusts the protein profile of its secretome in response to different pH values.

Pathogens may also enhance their virulence by locally modulating the pH of the microenvironment within the host. This mechanism ensures that genes encoding cell-wall-degrading extracellular enzymes are expressed and their products are secreted at a pH that is optimal for their activity (Prusky et al., 2004 & 2014). D-gluconic acid accumulation can modulate patulin synthesis in *P. expansum* by inducing the expression of the transcription factor, *PACC*, which regulates the expression of pathogenicity factors that contribute to host-tissue colonization (Barad et al., 2014). *Colletotrichum gloeosporioides* in avocado, *C. coccodes* in

tomato, and *C. acutatum* in apple, exhibit an accumulation of ammonia in infected host tissues when pH increases from 7.5 to 8, ensuring an optimal pH value for the activity of a pectatelyase that functions in degrading host cell walls. Ammonia secretion was a virulence factor that raised the pH in the microenvironment surrounding the fungus and thus increased the pathogenicity of *Colletotrichum* sp. (Prusky et al., 2001). External pH and different nitrogen sources have also been reported to affect the level of secretion of pectatelyase by *C. gloeosporioides* (Drori et al., 2003). Bi et al. (2015) recently reported that the regulation of environmental pH by small molecules secreted by various fungi can modulate pathogenicity. They demonstrated that *C. gloeosporioides*, *P. expansum*, *Aspergillus nidulans*, and *F. oxysporum* secrete small pH-affecting molecules which impact and regulate either acidic or alkaline colonizing strategies. Acidification is induced under carbon excess (≥175 mM sucrose, the most abundant sugar in fruits). In contrast, alkalinization occurred under conditions of carbon deprivation (≤ 15 mM sucrose).

Response to oxidative stress

The application of oxidative compounds, such as ozone (Whangchai et al., 2006; Gabler et al., 2010; Crowe et al., 2012) or chlorine (Chen and Zhu, 2011; Crowe et al., 2012), are commonly used as disinfectants during the postharvest handling of produce to manage fungal decay and lower microbial counts. Knowledge of how fungal pathogens respond to oxidative stress will not only reveal the molecular mechanisms involved in ROS signaling in host-pathogen interactions (Yang et al., 2016), but also guide the efficient and novel use of existing and new oxidative treatments. Qin et al. (2011) reported that complex III of the mitochondrial respiratory chain

contributes to intracellular ROS generation by mitochondria in *P. expansum* subjected to oxidative (H_2O_2) stress. The excessive accumulation of ROS caused oxidative damage to mitochondrial proteins and led to the collapse of the mitochondrial membrane potential. ATP synthase was also involved in the response of *P. expansum* to oxidative stress. Collectively, oxidative stress results in mitochondrial impairment due to a functional alteration of oxidative stress-sensitive proteins. Recently, a balanced redox status, maintained by the thioredoxin system, was found to be essential for the development and pathogenesis of *B. cinerea* (Viefhues et al., 2014). Additionally, a glutathione peroxidase 3 (*AaGPx3*) was found to be a component of the complex signaling network that plays an essential role in the detoxification of cellular stresses induced by ROS, as well as playing an essential role in the pathogenesis of *A. alternata* in citrus (Yang et al., 2016).

Response to UV radiation and water activity

UV irradiation of harvested produce is a method to control decay and extend shelf-life that is increasing in use. Current research on this topic is mainly focused on host response. Few studies have examined the physiological and molecular response of fungal pathogens to UV. It was found that conidial germination and mycelial growth of the grape powdery mildew fungus *Uncinula necator* was affected by UV-B radiation (Willocquet et al., 1996). Specifically regarding postharvest fungi, Marquenie et al. (2002) reported that spores of *B. cinerea* did not survive a UV-C treatment of 1 J/cm^2, and that *Monilinia fructigena* conidia were even more sensitive, with a UV-C treatment of 0.50 J/cm^2 completely inactivating spores. Furthermore, Janisiewicz et al. (2016) recently found that UV-C irradiation of *B. cinerea* could effectively kill

this fungus if a dark period followed the treatment. The addition of a 4-h dark period after exposing *B. cinerea* conidia on agar media to 12.36 J/m^2 resulted in nearly 100% lethality.

Water activity (a_w) in host tissues can affect pathogen physiology but its impact is dependent on the prevailing environmental conditions. Therefore, it is important to understand the response of pathogenic fungi to a_w. The effect of a_w on mycotoxin production and growth has been investigated in *Aspergillus* and *Penicillium* (Northolt et al., 1979; Parra et al., 2004; Tassou et al., 2007; Garcia et al., 2011). Tannous et al. (2016) reported a significant decrease in both the growth rate and patulin production of *P. expansum* when the a_w was lowered from 0.99 to 0.85 (Tannous et al., 2016).

Response to environmental manipulations

Exogenous ethylene is a common postharvest practice used to induce ripening. Thus, it represents a manipulation of the environment of both the harvested produce and any pathogens that are present. El-Kazzaz et al. (1983) investigated the effect of 1, 10, 100, and 10^3 µL/L ethylene on spore germination of *A. alternata, B. cinerea, C. gloeosporioides, M. fructicola, P. expansum, P. digitatum, P. italicum, Rhizopus stolonifer,* and *Thielaviopsis paradoxa*. They found that ethylene stimulated germination of *P. expansum, P. digitatum, P. italicum* and *T. paradoxa,* and germ tube elongation of *A. alternata, C. gloeosporioides, M. fructicola, P. digitatum, P. italicum,* and *R. stolonifer*. Additionally, ethylene production by harvested produce often increases once infected by a pathogen. Tomato fruits inoculated with *B.cinerea* exhibited a rapid increase in ethylene production, and higher ACC synthase and lipoxygenase activity, relative to non-inoculated fruits. The addition of an ethylene absorbent to storage containers

inhibited *B. cinerea* infection of inoculated tomatoes, and significantly reduced infection-related enzyme activity. These findings indicate that disease development is positively related to ethylene production (Tian et al., 2002). Although numerous studies have been conducted on the role of ethylene in ripening, the response of decay fungi to ethylene needs to be further investigated at the molecular level.

Treatments, such as controlled atmosphere and natural edible coatings, are also used to extend the storage life of fruit. Controlled atmospheres (CA, 5% O_2+10% CO_2, and 8% O_2+10% CO_2) effectively controlled the growth of mesophilic, aerobic bacteria, psychrotrophs, *Pseudomonas* spp., yeasts, and molds (*Penicillium* spp.) on sweet cherries during 15 days of storage (Serradilla et al., 2013). In addition, the effect of CA enriched with monoxide (CO) was examined by El-Goorani and Sommer (1979), who found that CA (2.3% O_2+5% CO_2) + 9% CO could effectively inhibit the growth of postharvest fungal pathogens such as *M. fructicola*, *P. expansum*, *P.digitatum, P. italicum,* and *Whetzelinia sclerotiorum* both *in vitro* and *in vivo*.

Natural edible coatings with antifungal properties, like chitosan, have been extensively studied in recent years. Irkin and Guldas (2014) reported that a chitosan coating on red table grape and fresh-cut honey melon effectively inhibited *Fusarium* rot caused by *F. oxysporum*. Likewise, the inhibitory effects of a chitosan coating on *A. niger* and *R. stolonifer*, as well as the naturally-occurring fungi, on table grape have been documented (de Oliveira et al., 2014). Similar results on the effect of chitosan coating on fungal decay have been obtained with other fruits, such as citrus (Chien et al., 2007), avocado (Bill et al., 2014), and jujube (Zhang et al., 2014). The mechanism by which chitosan inhibits fungi appears to be related to the interaction of chitosan with the negatively charged residues of macromolecules exposed on the surface of

fungal cells that changes the permeability of the plasma membrane, and/or a negative alteration in fungal metabolism (Romanazzi et al., 2017).

In order to increase decay control, integrated methods have been used on harvested produce rather than a single treatment. Using this principle, coatings composed of chitosan with *Mentha* essential oils (Guerra et al., 2015), *Aloe vera* with ascorbic acid coatings (Sogvar et al., 2016), and locust bean gum-based edible coatings with biocontrol yeasts (Parafati et al., 2016), have all been used to manage postharvest pathogens of cherry tomato, strawberry, and mandarin.

Conclusions and future prospects

Considerable research has been conducted on the development of alternative approaches to managing postharvest diseases that do not rely on the use of synthetic chemical fungicides. The majority of these alternative approaches to managing postharvest decay, however, have been developed using an empirical approach. Although a considerable number of studies have been reported on the response of harvested produce to a variety of abiotic and biotic stresses, studies on the effect of environmental and other abiotic stresses on the physiology, pathogenicity, and viability of decay fungi are still lacking. Increased knowledge of the molecular and biochemical processes involved in the response of fungi to environmental stress will inevitably provide a better understanding of virulence and pathogenicity. This need should provide incentives for future research on this topic, especially as it relates to the management of postharvest decays of fruits, vegetables, and grains.

Acknowledgements

This work was supported by National Natural Science Foundation of China (31501688 and 31670688), the project of Chongqing Education Commission (KJ1711275), the project sponsored by the Scientific Research Foundation for the Returned Overseas Chinese Scholars, State Education Ministry to Yuan Sui, and the project of Chongqing Science & Technology Commission (cstc2016jcyjA1769). We greatly appreciate the many contributions published on the subject of this review, and apologize to the investigators whose specific studies were not be cited due to space limitations but whose work framed the issues and ideas that are discussed.

References

Abrashev, R.I., Pashova, S.B., Stefanova, L.N., Vassilev, S.V., Dolashka-Angelova, P.A., and Angelova, M.B. (2008). Heat-shock-induced oxidative stress and antioxidant response in *Aspergillus niger* 26. *Can. J. Microbiol.* **54:** 977-983.

Alkan, N., Espeso, E.A., and Prusky, D. (2013). Virulence regulation of phytopathogenic fungi by pH. *Antioxid. Redox Signal.* **19:** 1012-1025.

Barad, S., Horowitz, S.B., Kobiler, I., Sherman, A., andPrusky, D. (2014). Accumulation of the mycotoxin patulinin the presence of gluconic acid contributesto pathogenicity of *Penicillium expansum*. *Mol. Plant Microbe Interact.* **27:** 66-77.

Bi, F., Barad, S., Ment, D., Luria, N., Dubey, A., Casado, V., Glam, N., Mínguez, J.D., Espeso, E.A., Fluhr, R., andPrusky, D. (2015). Carbon regulation of environmental pH by secreted small molecules that modulate pathogenicity in phytopathogenic fungi. *Mol. Plant Pathol.* **17:** 1178-1195.

Bill, M., Sivakumar, D., Korsten, L., and Thompson, A.K. (2014). The efficacy of combined application of edible coatings and thyme oil in inducing resistance components in avocado (*Persea americana* Mill.) against anthracnose during post-harvest storage. *Crop Prot.* **64:** 159-167.

Caracuel, Z., Roncero, M.I., Espeso, E.A., González-Verdejo, C.I., García-Maceira, F.I., and Di Pietro, A. (2003). The pH signalling transcription factor PacC controls virulence in the plant pathogen *Fusarium oxysporum*. *Mol. Microbiol.* **48:** 765-779.

Casals, C., Teixidó, N., Viñas, I., Silvera, E., Lamarca, N., and Usall, J. (2010). Combination of hot water, *Bacillus subtilis* CPA-8 and sodium bicarbonate treatments to control postharvest brown rot on peaches and nectarines. *Eur. J. Plant Pathol.* **128:** 51-63.

Cervantes-Chávez, J.A., Valdés-Santiago, L., Bakkeren, G., Hurtado-Santiago, E., León-Ramírez, C.G., Esquivel-Naranjo, E.U., Landeros-Jaime, F., Rodríguez-Aza, Y., and Ruiz-Herrera, J. (2016). Trehalose is required for stress resistance and virulence of the Basidiomycota plant pathogen *Ustilago maydis*. *Microbiology* **162:** 1009-1022.

Chen, H., Cheng, Z., Wisniewski, M., Liu, Y., and Liu, J. (2015). Ecofriendly hot water treatment reduces postharvest decay and elicits defense response in kiwifruit. *Environ. Sci. Pollut. Res.* **22:** 15037-15045.

Chen, Z., and Zhu, C. (2011). Combined effects of aqueous chlorine dioxide and ultrasonic treatments on postharvest storage quality of plum fruit (*Prunussalicina*L.). *Postharvest Biol. Technol.* **61:** 117-123.

Cheng, C., Gao, X., Feng, B., Sheen, J., Shan, L., and He, P. (2013). Plant immune response to pathogens differs with changing temperatures. *Nat. Commun.* **4:** 2530.

Chien, P.J., Sheu, F., and Lin, H.R. (2007). Coating citrus (*Murcott tangor*) fruit with low molecular weight chitosan increases postharvest quality and shelf life. *Food Chem.* **100:** 1160-1164.

Crowe, K.M., Bushway, A., and Davis-Dentici, K. (2012). Impact of postharvest treatments, chlorine and ozone, coupled with low-temperature frozen storage on the antimicrobial quality of lowbush blueberries (*Vaccinium angustifolium*). *LWT-Food Sci. Technol.* **47:** 213-215.

de Oliveira, C.E.V., Magnani, M., de Sales, C.V., de Souza Pontes, A.L., Campos-Takaki, G.M., Stamford, T.C.M., and de Souza, E.L. (2014). Effects of post-harvest treatment using chitosan from *Mucor circinelloides* on fungal pathogenicity and quality of table grapes during storage. *Food Microbiol.* **44:** 211-219.

Doehlemann, G., Berndt, P., and Hahn, M. (2006). Trehalose metabolism is important for heat stress tolerance and spore germination of *Botrytis cinerea*. *Microbiology* **152:** 2625-2634.

Drori, N., Kramer-Haimovich, H., Rollins, J., Dinoor, A., Okon, Y., Pines, O., and Prusky, D. (2003). External pH and nitrogen source affect secretion of pectatelyase by *Colletotrichum gloeosporioides*. *Appl. Environ. Microbiol.* **69:** 3258-3262.

El-Goorani, M.A., and Sommer, N.F. (1979). Suppression of postharvest plant pathogenic fungi by carbon monoxide. *Phytopathology* **69:** 834-838.

El-kazzaz, M.K., Sommer, N.F., and Kader, A.A. (1983). Ethylene effects on in vitro and in vivo growth of certain postharvest fruit-infecting fungi. *Phytopathology* **73:** 998-1001.

Eshel, D., Miyara, I., Ailing, T., Dinoor, A., and Prusky, D. (2002). pH regulates endoglucanase expression and virulence of *Alternaria alternata* in persimmon fruit. *Mol. Plant Microbe Interact.* **15:** 774-779.

Gabler, F.M., Mercier, J., Jiménez, J.I., and Smilanick, J.L. (2010). Integration of continuous biofumigation with *Muscodor albus* with pre-cooling fumigation with ozone or sulfur dioxide to control postharvest gray mold of table grapes. *Postharvest Biol. Technol.* **55:** 78-84.

Garcia, D., Ramos, A.J., Sanchis, V., and Marín, S. (2011). Modelling the effect of temperature and water activity in the growth boundaries of *Aspergillus ochraceus* and *Aspergillus parasiticus*. *Food Microbiol.* **28:** 406-417.

Gatto, M.A., Ippolito, A., Linsalata, V., Cascarano, N.A., Nigro, F., Vanadia, S., and Venere, D.D. (2011). Activity of extracts from wild edible herbs against postharvest fungal diseases of fruit and vegetables. *Postharvest Biol. Technol.* **61:** 72-82.

Gessler, N.N., Aver'yanov, A.A., and Belozerskaya, T.A. (2007). Reactive oxygen species in regulation of fungal development. *Biochemistry* **72:** 1091-1109.

Guerra, I.C.D., de Oliveira, P.D.L., de Souza Pontes, A.L., Lúcio, A.S.S.C., Tavares, J.F., Barbosa-Filho, J.M., Madruga, M.S., and de Souza, E.L. (2015). Coatings comprising chitosan and *Mentha piperita* L. or *Mentha* × *villosa* Huds essential oils to prevent common postharvest mold infections and maintain the quality of cherry tomato fruit. *Int. J. Food Microbiol.* **214:** 168-178.

Imahori, Y. (2011). Postharvest stress treatments in fruits and vegetables. **In:** Abiotic stress responses in plants. pp 347-358. Ahmad, P., and Prasad, M.N.V., Eds., Springer, New York.

Irkin, R., and Gulda, M. (2013). Chitosan coating of red table grapes and fresh-cut honey melons to inhibit *Fusarium oxysporum* growth. *J. Food Process. Preserv.* **38:** 1948-1956.

Janisiewicz, W.J., Takeda, F., Glenn, D.M., Camp, M.J., and Jurick II, W.M. (2016). Dark period following UV-C treatment enhances killing of *Botrytis cinerea* conidia and controls gray mold of strawberries. *Phytopathology***106:** 386-394.

Jemric, T., Ivic, D., Fruk, G., Matijas, H.S., Cvjetkovic, B., Bupic, M., and Pavkovic. B. (2011). Reduction of postharvest decay of peach and nectarine caused by *Monilinia laxa* using hot water dipping. *Food Bioprocess Technol.* **4:** 149-154.

Karabulut, O.A., Cohen, L., Wiess, B., Daus, A., Lurie, S., and Droby, S. (2002). Control of brown rot and blue mold of peach and nectarine by short hot water brushing and yeast antagonists. *Postharvest Biol. Technol.* **24:** 103-111.

Lebreton, L., Daval, S., Guillerm-Erckelboudt, A.Y., Gracianne, C., Gazengel, K., and Sarniguet, A. (2014). Sensitivity to pH and ability to modify ambient pH of the take-all fungus *Gaeumannomyces graminis* var. *tritici*. *Plant Pathol.* **63:** 117-128.

Li, B., Lai, T., Qin, G., and Tian, S. (2010a). Ambient pH stress inhibits spore germination of *Penicillium expansum* by impairing protein synthesis and folding: a proteomic-based study. *J. Proteome Res.* **9:** 298-307.

Li, H., Wang, H.L., Du, J., Du, G., Zhan, J.C., and Huang, W.D. (2010b). Trehalose protects wine yeast against oxidation under thermal stress. *World J. Microbiol. Biotechnol.* **26:** 969-976.

Li, B., Wang, W., Zong, Y., Qin, G., and Tian, S. (2012). Exploring pathogenic mechanisms of *Botrytis cinerea* secretome under different ambient pH based on comparative proteomic analysis. *J. Proteome Res.* **11:** 4249-4260.

Liu, J., Sui, Y., Wisniewski, M., Droby, S., and Liu, Y. (2013). Review: utilization of antagonistic yeasts to manage postharvest fungal disease of fruit. *Int. J. Food Microbiol.* **167:** 153-160.

Liu, J., Sui, Y., Wisniewski, M., Droby, S.,Tian, S., Norelli, J., and Hershkovitz, V. (2012). Effect of heat treatment on inhibition of *Monilinia fructicola* and induction of disease resistance in peach fruit. *Postharvest Biol. Technol.* **65:** 61-68.

Lurie, S., and Pedreschi, R. (2014). Fundamental aspects of postharvest heat treatments. *Hortic. Res.* **1:** 14030.

Manteau, S., Abouna, S., Lambert, B., and Legendre, L. (2003). Differential regulation by ambient pH of putative virulence factor secretion by the phytopathogenic fungus *Botrytis cinerea*. *FEMS Microbiol. Ecol.* **43:** 359-366.

Margosan, D.A., Smilanick, J.L., Simmons, G.F., and Henson, D.J. (1997). Combination of hot water and ethanol to control postharvest decay of peaches and nectarines. *Plant Dis.* **81:** 1405-1409.

Marquenie, D., Lammertyn, J., Geeraerd, A.H., Soontjens, C., Van Impe, J.F., Nicolaï, B.M., and Michiels, C.W. (2002). Inactivation of conidia of *Botrytis cinerea* and *Monilinia fructigena* using UV-C and heat treatment. *Int. J. Food Microbiol.* **74:** 27-35.

Maxin, P., Weber, R.W.S., Pederson, H.L., and Williams, M. (2012). Hot-water dipping of apples to control *Penicillium expansum*, *Neonectria galligena* and *Botrytis cinerea*: effects of temperature on spore germination and fruit rots. *Euro. J. Hort. Sci.* **77:** S1-S9.

Mbengue, M., Navaud, O., Peyraud, R., Barascud, M., Badet, T., Vincent, R., Barbacci, A., and Raffaele, S. (2016). Emerging Trends in molecular interactions between plants and the broad host range fungal pathogens *Botrytis cinerea* and *Sclerotinia sclerotiorum*. *Front. Plant Sci.***7:** 422.

Nanda, A.K., Andrio, E., Marino, D., Pauly, N., and Dunand, C. (2010). Reactive oxygen species during plant-microorganism early interactions. *J. Integr. Plant Biol.* **52:** 195-204.

Northolt, M.D., Van Egmond, H.P., and Paulsch, W.E. (1979). Ochratoxin A production by some fungal species in relation to water activity and temperature. *J. Food Prot.* **42:** 485-490.

Parafati, L., Vitale, A., Restuccia, C., and Cirvilleri, G. (2016). The effect of locust bean gum (LBG)-based edible coatings carrying biocontrol yeasts against *Penicillium digitatum* and *Penicillium italicum* causal agents of postharvest decay of mandarin fruit. *Food Microbiol.* **58:** 87-94.

Parra, R., and Magan, N. (2004). Modelling the effect of temperature and water activity on growth of *Aspergillus niger* strains and applications for food spoilage moulds. *J. Appl. Microbiol.* **97:** 429-438.

Peñalva, M.A., Tilburn, J., Bignell, E., and Arst, H.J. (2008). Ambient pH gene regulation in fungi: making connections. *Trends Microbiol.* **16:** 291-300.

Prusky, D.,Barad, S., Luria, N., and Ment, D. (2014). pH modulation of host environment, a mechanism modulating fungal attack in postharvest pathogen interactions. **In:** Post-harvest Pathology. pp 11-25. Prusky, D., and Gullino, M.L., Eds., Springer International Publishing, Switzerland.

Prusky, D.,McEvoy, J.L., Leverentz, B., and Conway, W.S. (2001). Local modulation of host pH by *Colletotrichum* species as a mechanism to increase virulence. *Mol. Plant Microbe Interact.* **14:**1105-1113.

Prusky, D., McEvoy, J.L., Saftner, R., Conway, W.S., and Jones, R. (2004). Relationship between host acidification and virulence of *Penicillium* spp. on apple and citrus fruit. *Phytopathology* **94:**44-51.

Qin, G., Liu, J., Li, B., and Tian, S. (2011). Hydrogen peroxide acts on sensitive mitochondrial proteins to induce death of a fungal pathogen revealed by proteomic analysis. *PLoS One* **6:** e21945.

Qin, J., Wang, G., Jiang, C., Xu, J.R., and Wang, C. (2015). Fgk3 glycogen synthase kinase is important for development, pathogenesis, and stress responses in *Fusarium graminearum*. *Sci. Rep.* **5:** 8504.

Rollins, J.A., and Dickman, M.B. (2001). pH signaling in *Sclerotinia sclerotiorum*: identification of a pacC/RIM1 homolog. *Appl.Environ.Microbiol.* **67:**75-81.

Romanazzi, G., Feliziani, E., Baños, S.B., and Sivakumar, D. (2017). Shelf life extension of fresh fruit and vegetables by chitosan treatment. *Crit. Rev. Food Sci.Nutr.***57:**579-601.

Serradilla, M.J., Villalobos, M. del C., Hernández, A., Martín, A., Lozano, M., and Córdoba, M. de G. (2013). Study of microbiological quality of controlled atmosphere packaged 'Ambrunés' sweet cherries and subsequent shelf-life.*Int. J. Food Microbiol.* **166:** 85-92.

Sogvar, O.B., Saba, M.K., and Emamifa, A. (2016). *Aloe vera* and ascorbic acid coatings maintain postharvest quality and reduce microbial load of strawberry fruit. *Postharvest Biol. Technol.* **114:** 29-35.

Spadoni, A., Neri, F., Bertolini, P., and Mari, M. (2013). Control of Monilinia rots on fruit naturally infected by hot water treatment in commercial trials. *Postharvest Biol. Technol.* **86:** 280-284.

Sui, Y., Droby, S., Zhang, D., Wang, W., and Liu, Y. (2014). Reduction of Fusarium rot and maintenance of fruit quality in melon using ecofriendly hot water treatment. *Environ. Sci. Pollut. Res.* **21:** 13956-13963.

Sui, Y., Wisniewski, M., Droby, S., Norelli, J., and Liu, J. (2016). Recent advances and current status of the use of heat treatments in postharvest disease management systems: Is it time to turn up the heat? *Trends Food Sci. Tech.* **51:** 34-40.

Svanström, Å., and Melin, P. (2013). Intracellular trehalase activity is required for development, germination and heat-stress resistance of *Aspergillus niger* conidia. *Res.Microbiol.* **164:** 91-99.

Tassou, C.C., Panagou, E.Z., Natskoulis,P., and Magan, N. (2007). Modelling the effect of temperature and water activity on the growth of two ochratoxigenic strains of *Aspergillus carbonarius* from Greek wine grapes. *J. Appl. Microbiol.* **103:** 2267-2276.

Tannous, J., Atoui, A., El Khoury, A., Francis, Z., Oswald, I.P., Puel, O., and Lteif, R. (2015). A study on the physicochemical parameters for *Penicillium expansum* growth and patulin production: effect of temperature, pH, and water activity. *Food Sci. Nutri.***4:** 611-622.

Tian, S., Luo, Y., Gong, Q., and Liu, H. (2002). Effect of fungal infection on ethylene production, acc synthase and lipoxygenase activity in tomato fruits. *Acta Phytopathol. Sin.* **32:** 159-164.

Tiwari, S., Thakur, R., and Shankar, J. (2015). Role of heat-shock proteins in cellular function and in the biology of fungi. *Biotechnol. Res. Int.* **2015:** 132635.

Viefhues, A., Heller, J., Temme, N., and Tudzynski, P. (2014). Redox systems in *Botrytis cinerea*: impact on development and virulence. *Mol. Plant Microbe Interact.* **27:** 858-874.

Wang, R., Leng, Y., and Zhong, S. (2015). The regulatory gene *VosA* affects conidiogenesis and is involved in virulence of the fungal cereal pathogen *Cochliobolus sativus*. *Fungal Biol.* **119:** 884-900.

Whangchai, K., Saengnil, K., and Uthaibutra, J. (2006). Effect of ozone in combination with some organic acids on the control of postharvest decay and pericarp browning of longan fruit. *Crop Prot.* **25:** 821-825.

Willi, Y., Frank, A., Heinzelmann, R., Kälin, A., Spalinger, L., and Ceresini, P.C. (2011). The adaptive potential of a plant pathogenic fungus, *Rhizoctonia solani* AG-3, under heat and fungicide stress. *Genetica* **139:** 903.

Willocquet, L., Colombet, D., Rougier, M., Fargues, J., and Clerjeau, M. (1996). Effects of radiation, especially ultraviolet B, on conidial germination and mycelial growth of grape powdery mildew. *Eur. J. Plant Pathol.* **102:** 441-449.

Yang, S.L., Yu, P.L., and Chung, K.R. (2016). The glutathione peroxidase-mediated reactive oxygen species resistance, fungicide sensitivity and cell wall construction in the citrus fungal pathogen *Alternaria alternata*. *Environ.Microbiol.* **18:** 923-935.

Zhang, H., Wang, L., Zheng, X., and Dong, Y. (2007). Effect of yeast antagonist in combination with heat treatment on postharvest blue mold decay and *Rhizopus* decay of peaches. *Int. J. Food Microbiol.* **49:** 308-313.

Zhang, H., Wang, S., Huang, X., Dong, Y., and Zheng, X. (2008). Integrated control of postharvest blue mold decay of pears with hot water treatment and *Rhodotorula glutinis*. *Postharvest Biol.Technol.* **49:** 308-313.

Zhang, S., Yu, Y., Xiao, C., Wang, X., and Lei, Y. (2014). Effect of ultraviolet irradiation combined with chitosan coating on preservation of jujube under ambient temperature. *LWT-Food Sci. Technol.* **57:** 749-754.

Zhao, W., Wisniewski, M., Wang, W., Liu, J., and Liu, Y. (2014). Heat-induced oxidative injury contributes to inhibition of *Botrytis cinerea* spore germination and growth. *World J.Microbiol.Biotechnol.* **30:** 951-957.

Zong, Y., Li, B., and Tian, S. (2015). Effects of carbon, nitrogen and ambient pH on patulin production and related gene expression in *Penicillium expansum*. *Int. J. Food Microbiol.* **206:** 102-108.

Table 1. Representative studies of postharvest fungal pathogens in response to difference environmental factors.

Environmental factor	Exposure intensity/duration	Pathogen	Reference
Temperature	32-70 ^{o}C (3 min)	*Penicilliumexpansum*, *Botrytis cinerea* *Neonectriagalligena*, *Neofabraea alba*	Maxin et al., 2012
	43 ^{o}C (10-30 min)	*B. cinerea*	Zhao et al., 2014
	40 ^{o}C (5 or 10 min)	*Moniliniafructicola*	Liu et al., 2012
	40-48 ^{o}C (6 or 12 min)	*Monilinialaxa*	Jemric et al., 2011
	46 or 50 °C (1-8 min)	*M. fructicola*, *Rhizopusstolonifer*	Margosan et al., 1997
	46 °C (5-20 min)	*P. expansum*	Zhang et al., 2008

	37 °C (2 d)	*P. expansum, R. stolonifer*	Zhang et al., 2007
	45-60 °C (1-10 min)	*Moniliniafructigena, M. laxa, M. fructicola*	Spadoni et al., 2013
	35-48 °C (3-20 min)	*B. cinerea, M. fructigena*	Marquenie et al., 2002
	55-70 °C (20-60 s)	*M. laxa*	Casals et al., 2010
	50-60 °C (10-40 s)	*P. expansum, M. fructicola*	Karabulut et al., 2002
	52 °C (2.5 min)	*R. stolonifer, M. fructicola*	Bake and Smith Jr., 1970
	4-30 °C (2 weeks)	*P. expansum*	Tannous et al., 2015
	45 °C (10 min)	*P. expansum, B. cinerea*	Chen et al., 2015
pH	pH 2 or 8 (5 or	*P. expansum*	Li et al., 2010a

	10 h)		
	pH 3-8 (48 h)	*P. expansum*	Zong et al., 2015
	pH 2.5-7 (7 d)	*P. expansum*	Tannous et al., 2016
	pH 4 or 6 (12-72 h)	*B. cinerea*	Li et al., 2012
	pH 2-7 (7 d)	*B. cinerea*	Manteau et al., 2003
	pH 4 or 6 (12 h)	*Colletotrichumgloeosporioides*	Drori et al., 2003
	pH 4-8 (12 h)	*Fusariumoxysporum*	Caracuel et al., 2003
	pH 3-7 (4 d)	*Sclerotiniasclerotiorum*	Rollins and Dickman, 2001
	pH 4-7 (5 d)	*Alternariaalternata*	Eshel et al., 2002

Oxidative stress	10-30 mM H_2O_2 (1 h)	*P. expansum*	Qin et al., 2011
	5-20 mM H_2O_2 (3 d)	*B. cinerea*	Viefhues et al., 2014
	5 mM H_2O_2 (4-7 d)	*A. alternate*	Yang et al., 2016
UV-C	0.01 to 1.50 J/cm^2	*B. cinerea, M. fructigena*	Marquenie et al., 2002
	12.36 J/cm^2	*B. cinerea*	Janisiewicz et al., 2016
Water activity	a_w 0.85, 0.90 and 0.95 (2 weeks)	*P. expansum*	Tannous et al., 2016
Ethylene	1, 10 and 100 µL/L of air	*A. alternate, B.cinerea, C.gloeosporioides,*	El-kazzaz et al.,1983

		M.fructicola, P. expansum, P.digitatum, P. italicum, R.stolonifer, Thielaviopsisparadoxa	
Controlledatmospheres	5% O_2+10% CO_2, 8% O_2+10% CO_2	*Penicillium* spp.	Serradilla et al., 2013
Natural edible coating	1.5% chitosan 0.4% chitosan+2.5 µL/L *Mentha piperita* L. essential oil+1.25 µL/L *Mentha × villosa* Huds essential oil	*F. oxysporum* *A. niger, B. cinerea, P. expansum,R. stolonifer*	Irkin and Guldas, 2014 Guerra et al., 2015

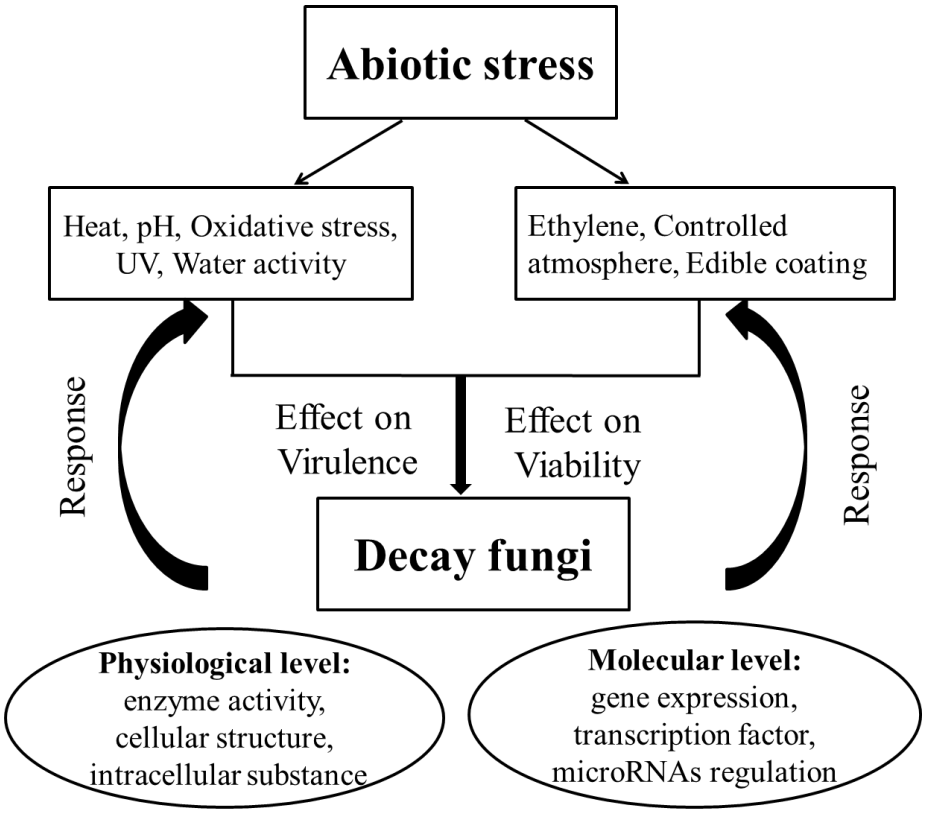

Figure 1. Diagram of responses of postharvest decay fungi to abiotic stress.