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REVIEW

Factors affecting mushroom *Pleurotus* spp.

Marcelo Barba Bellettini ^{a,*}, Fernanda Assumpção Fiorda ^a,
Helayne Aparecida Maieves ^a, Gerson Lopes Teixeira ^a, Suelen Ávila ^a,
Polyanna Silveira Hornung ^a, Agenor Maccari Júnior ^b, Rosemary Hoffmann Ribani ^a

^a Federal University of Paraná, Department of Chemical Engineering, Graduate Program in Food Engineering, PO Box 19011, Zip Code: 81531-980 Curitiba, Paraná State, Brazil

^b Federal University of Paraná, Department of Agronomy, PO Box 19011, Zip Code: 80035-060 Curitiba, Paraná State, Brazil

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Abstract *Pleurotus* genus is one of most extensively studied white-rot fungi due to its exceptional ligninolytic properties. It is an edible mushroom and it also has several biological effects, as it contains important bioactive molecules. In basidiomycete fungi, lignocellulolytic enzymes are affected by many typical fermentation factors, such as medium composition, ratio of carbon to nitrogen, pH, temperature, air composition, etc. The survival and multiplication of mushrooms is related to a number of factors, which may act separately or have interactive effects among them. Out that understanding challenges in handling *Pleurotus* species mushroom requires a fundamental understanding of their physical, chemical, biological and enzymatic properties. This review presents a practical checklist of available intrinsic and extrinsic factors, providing useful synthetic information that may help different users. An in-depth understanding of the technical features is needed for an appropriate and efficient production of *Pleurotus* spp.

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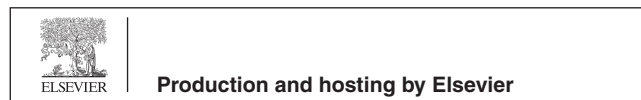
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* Corresponding author.

E-mail address: marcelobeletini@yahoo.com.br (M.B. Bellettini).

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1. Introduction

Over 200 species of mushrooms have long been used as functional foods around the world (Kalac̆, 2013), but only about 35 species have been commercially cultivated (Aida et al., 2009; Xu et al., 2011). They are a rich source of nutrients, particularly proteins, minerals as well as vitamins B, C and D (Panjikkaran and Mathew, 2013). Mushrooms contain 20–35% of protein (dry weight), are low in lipids and contain all the nine essential amino acids (Kalac̆, 2009). Mushrooms are delicacy food items praised for their characteristic texture when biting and enjoyable flavor. They have received overwhelming attention from food and pharmaceutical researchers due their bioactive constituents (Sheu et al., 2007; Mariga et al., 2014). These bio-molecules, such as phenolic compounds, terpenes, steroids and polysaccharides, have various biological activities (Shang et al., 2015). Mushrooms may have health-promoting benefits due to a multitude of compounds with antifungal activity (Ye et al., 1999), antigenotoxicity (Wang et al., 2005), antioxidation (Roupas et al., 2012), antiproliferative (Zhou et al., 2013), anti-tumorigenic (Kim et al., 2015b), antihyperlipidemic activity (Opletal et al., 1997), anti-hypertensive, anti-nociceptive, immunostimulation (Vaz et al., 2011), hypocholesterolaemic/anti-atherogenic properties (Han et al., 2011), stress-reducing properties and are also good for diabetic patients (Akata et al., 2012). Mushrooms are generally low in saturated fats and high in fiber and protein, and may reduce harmful blood cholesterol and act as an appetite suppressant. (Kim et al., 2011).

The mushrooms of the genus *Pleurotus* rank second in the world mushroom market and is the most popular mushroom in China. The *Pleurotus* spp. of the class basidiomycetes belongs to a group known as “white rot fungi” (Tsujiyama and Ueno, 2013) as they produce a white mycelium and are generally cultivated on non-composted lignocellulosic substrates (Savoie et al., 2007) in which various kinds of *Pleurotus* are commercially cultivated and have considerable economic value, including *P. ostreatus* (oyster mushroom), *P. eryngii* (king oyster or Cardoncello), *P. pulmonarius* (phenix mushroom), *P. djamor* (pink oyster mushroom), *P. sajor-caju*

(indian oyster), *P. cystidiosus* (abalone oyster), *P. citrinopieatus* (golden oyster mushroom) and *P. cornucopiae* (Pérez-Martínez et al., 2015; Knop et al., 2015; Zhang et al., 2016). *Pleurotus* species require a short growth time, compared to other mushrooms. Its fruiting body is not often attacked by diseases and pests and it can be grown in a simple and cheap way, with high yield, wider substrate utilization, sporelessness, wide temperature and chemical tolerance, as well as environmental bioremediation. It is an edible mushroom and also has several biological effects, as it contains important bioactive molecules (Yang et al., 2013b). *P. ostreatus* is characterized by high water content and low calorific value (1510 kJ kg⁻¹ edible parts), making it suitable for inclusion into calorie-controlled diets (Jaworska and Bernás, 2009). The pileus of *P. ostreatus* are valued not only for their taste but also for their nutritional qualities, especially in vegetarian diets.

Pleurotus spp. is one of most extensively studied white-rot fungi for its exceptional ligninolytic properties (Philippoussis et al., 2001; Olivieri et al., 2006; Li and Shah, 2016). This genus cleavages cellulose, hemicellulose and lignin from wood, whereas brown rot fungi only cleavage cellulose and hemicellulose (Machado et al., 2016). In basidiomycete fungi, extracellular laccases are constitutively produced in small amounts and the lignocellulolytic enzymes are affected by many typical fermentation factors, such as medium composition, pH, temperature, aeration rate, etc (Ahmed et al., 2013; Cogorni et al., 2014; Velioglu and Urek, 2015). Mushroom survival and multiplication are related to a number of factors, which may act individually or have interactive effects among them. Chemical composition, water activity, ratio of carbon to nitrogen, minerals, surfactant, pH, moisture, sources of nitrogen, particle size, and amount of inoculum, antimicrobial agents and the presence of interactions between microorganisms are considered as chemical, physical and biological factors that are linked to mushroom production (Eira, 2003). The main environmental factors encompass temperature, humidity, luminosity and air composition of the surrounding substrate, such as concentration of oxygen and carbon dioxide (AMGA, 2004). This review presents a practical checklist of available intrinsic and extrinsic factors, providing useful synthetic information that

may help different users. This study may be widely used by researchers, practitioners, professionals, handlers and others involved in farming and agro-food industry.

2. Effects of intrinsic factors

2.1. Composition of substrates

Substrates used in mushrooms cultivation have effect on chemical, functional and sensorial characteristics of mushrooms (Oyetayo and Ariyo, 2013). *Pleurotus* spp. is a saprophyte, and it extracts its nutrients from the substrate (grasses, wood and agricultural residues) through its mycelium, obtaining substances necessary for its development, such as carbon, nitrogen, vitamins and minerals (Urban, 2004). Agro-industrial waste is produced in huge amounts, and it becomes an interesting substrate, due its commercial exploitation as well as associated environmental problems (Cui et al. 2007; Silva et al., 2012b). They also can add value to low-cost products as agro-waste (Ahmed et al., 2013; Dahmardeh, 2013). Many studies have been conducted to test the ability of *Pleurotus* spp. to grow on different agro wastes, such as rice straw, wheat straw and cotton wastes (Hussain et al., 2002; Pant et al., 2006), olive mill waste, pine needles (Kalmis et al., 2008; Ruiz-Rodriguez et al., 2010; Al-Momany and Ananbeh, 2011), corn straw (Dias et al., 2003), thatch grass (Fanadzo et al., 2010), palm oil (Rizki and Tamai, 2011), weed plants (Das and Mukherjee, 2007), chopped office papers, cardboard, and plant fibers (Mandeel et al., 2005), sawdust, banana leaves, (Reddy et al., 2003) leaf of hazelnut (Yildiz et al., 1997), palm leaves (Alananbeh et al., 2014), tomato tuff (Ananbeh and Almomany, 2008), fruit pulp and peel, coffee pulp, sugarcane residues (Li et al., 2001; Eira, 2003; Ragunathan and Swaminathan, 2003; Moda et al., 2005), weed plants (Khatun et al., 2007), biogas residual slurry manure (Banik and Nandi, 2004), and jute waste products (Basak et al., 1996). A mixture of agro-wastes can be interesting. According to Owaid et al. (2015), productivity and biological efficiency were increased in some mixtures when compared with wheat straw alone, because of a variation in the capability of such substrates to aid the nutritional and environmental requirements and difference in cellulose, hemicellulose and lignin contents (Kuhad et al., 1997). The low contamination might have occurred due to a high substrate quality. Therefore, it is important to keep the dry substrate in dry conditions. When contaminants, such as green molds, as *Trichoderma* or *Aspergillus*, are scarce in the substrate, they do not offer a competence for the mycelium of *Pleurotus* which quickly colonizes it. The proportion of inoculum of *Pleurotus* against contaminants is much higher (Mejía and Albertó, 2013).

The use of different types of substrate by fungus will depend on its capacity to secrete enzymes such as oxidative (ligninase, laccase, manganese peroxidase) and hydrolytic (cellulase, xylanase and tannase) enzymes which are involved in utilizing lignocellulosic substrates (Rossi et al., 2001; Donini et al., 2009; Luz et al. 2012). Singh et al. (2008) and Singh and Singh (2012) reported that *P. sapidus* mushrooms produce extracellular enzymes that affect the increase in its nutritional value. Mushrooms degrade the substrate through enzyme production, and the first sign of mushroom growth is seen after 2 to 3 days of inoculation (Patel et al., 2009). Polyphenol

oxidases, plant cell wall, lytic enzymes and microbial cell wall lytic enzymes have been identified in axenic as well as non-axenic cultures of various strains of *Pleurotus* spp. *P. ostreatus* (Jacq.: Fr.) Kumm and *P. pulmonarius* (Fr.) also produces manganese peroxidases and its activities increase during vegetative growth, and decreases during sporocarp enlargement (Velázquez-Cedeño et al., 2002). In general, a higher laccase activity is obtained during substrate colonization than during reproductive stages. Production of manganese peroxidase enzyme is similar to laccase, presenting high levels during the colonization stage (Savoie et al., 2007). A decrease in manganese peroxidase activity is observed during primordia formation and fructification and a new increase is obtained during the post-harvest stage.

According to Mukhopadhyay et al. (2002) and Curvetto et al. (2002), in fungus growth and development, both quality and quantity aspects (biological productivity and efficiency), are closely linked to nutrient type and growth conditions. For example, wheat straw was found to be superior over other types of agro-waste in colonization and production rates (Philippoussis et al., 2001; Pant et al., 2006; Fanadzo et al., 2010). The substrate has a direct influence on mineral composition, because the hyphae of fungi is in contact with the compound and it withdraws its essential elements. It can also accumulate toxic metals such as lead, mercury and arsenic. Variations were found in protein and other nutrient contents in mushroom fruiting bodies when grown on different agro-wastes (Michael et al., 2011). For that, it is important to know the chemical composition of substrates before making its use in mushroom cultivation (Patil et al., 2010). Biotin and thiamine are recommended vitamins to be incorporated into the substrate (Chang and Miles, 2004).

2.2. Sources of nitrogen

There are several parameters that affect the enzyme production; however, its nitrogen source is a major factor (Singh et al., 2008). Nitrogen is important in protein, nucleic acid, purine, pyrimidine and polysaccharide synthesis (Drozdowski et al., 2010; Abdullah et al., 2015) constituents of the cell wall of many fungi, which are composed of β (1-4)-linked unit of N-acetylglucosamine (Miles and Chang, 1997) and may be added in the form of ammonium nitrate or organic nitrogen (Chang and Miles, 2004; Gil-Ramírez et al., 2013). Nitrate is a nitrogen source for mushrooms (Martinez-Espinosa et al., 2011). Efficient nitrate use requires an active enzyme system, composed of nitrate reductase, nitrite reductase and hydroxylamine reductase, which can catalyze the following metabolic processes: $\text{NO}_3^- \rightarrow \text{NO}_2^- \rightarrow \text{NH}_2\text{OH} \rightarrow \text{glutamate}$. Therefore, nitrate uptake and use are essential to amino acid synthesis and other metabolic changes (Bóbits et al., 2015).

Pleurotus genus is essentially cellulolytic (Silva et al., 2012a), however, there are fungi that grow on substrates with low nitrogen content in the range from 0.03% to 1.0% (Machado et al., 2016). Ortega et al. (1992), in their studies with *Pleurotus* spp. cultured on bagasse supplemented, described a nitrogen increase in mushrooms related to the amount present in the initial substrate plus the nitrogen amount present in the inoculum, indicating a possible fixation of this element by mushrooms. Sturion and Oetterer (1995) also observed a nitrogen increase in the residual substrate,

which ranged from 4% to 37% in the cultivation of *Pleurotus* spp. on different substrates, suggesting the possibility that this genus fixes nitrogen, or the presence of fixing bacteria associated with the mushroom. Li et al. (2015) reported that the increase in perilla stalks content on the substrate promoted higher antioxidant activity in *P. ostreatus*. Both organic or inorganic compounds, such as ammonium chloride, ammonium sulfate, ammonium phosphate dibasic, ammonium nitrate, sodium nitrate, potassium nitrate, ammonium acetate, ammonium tartrate, urea, hydrolyzed proteins, amino acids and yeast extract, have been added to the culture medium in concentrations of nitrogen, ranging from 0.012% to 0.11%. They can be used as a nitrogen source for the mushrooms (Lima et al., 1975). Neelam et al. (2013) also reported that ammonium chloride supported mycelium growth in *P. florida* and *P. ostreatus* better than sodium nitrate and calcium nitrate because nitrate ions have been implicated in the inhibitory effect of some basidiomycetes, which may be difficult to transport across the fungal membrane, where it can promote growth. Hoa and Wang (2015) related that the mycelium growth in oyster mushroom *P. cystidiosus* and *P. ostreatus* also increased with the concentration of ammonium chloride from 0.01% to 0.05% and 0.03% to 0.09%.

According to Zhang et al. (2002) protein content in *P. sajor-caju* fruiting bodies can range from 26.3% to 36.7%, but Rangunathan and Swaminathan (2003) reported that these values may be higher, ranging from 25.6% to 44.3%. Therefore, the type of substrate used for the cultivation of *Pleurotus* spp. probably influences the nutritional composition of the fruiting bodies. The crude protein content of fruiting bodies seems to be related to the nitrogen content in the gross starting substrate, combined or supplemented with sharps and/or agricultural fertilizers. The increase in basidiocarp protein content results in low lipid content. Supplementation with nitrogen can increase crop productivity, but to a certain level, as high nitrogen values can inhibit fruiting of mushrooms *Pleurotus* sp. "Florida" (Silva et al., 2007). According to these authors, there was growth inhibition when *P. ostreatus* was cultivated in hydrolyzed sugarcane bagasse without added nitrogen, or when addition of different nitrogen sources resulted in levels greater than or equal to 1.5% nitrogen, based on dry matter. The low nitrogen level can stimulate ligninolytic enzyme production, whereas a high nitrogen level represses it.

Among the most used cultivation supplements, cereal brans are sources of organic nitrogen (N₂), necessary to the growth of the mycelium mass, which may interfere in productiveness and biological efficiency of the fungus. The quantity and the kind of bran may vary according to the species or the strain under development as well as the growth stage (Donini et al., 2009). Different supplements were used to enhance oyster mushroom production including cottonseed hull (Fanadzo et al., 2010), soya bean (Upadhyay et al., 2002), wheat bran (Yildiz et al., 2002; Al-Momany and Ananbeh, 2011), olive mill waste (Ruiz-Rodriguez et al., 2010), rice bran and maize powder (Alam et al., 2010). According to Singh et al. (2011), Locci et al. (2008) and Machado et al. (2016) on *P. eryngii*, *P. ostreatus* and *Lentinus edodes* growth, respectively, the wheat bran is the most suitable for starchy compound of lignocellulosic mushrooms growth in solid-state fermentation. Wang et al. (2001) upon researching the cultivation of *P. ostreatus* found that the supplementation of the barley straw

substrate with wheat bran up to a 45% ratio promoted an increase in biological efficiency of the mushroom. Dias et al. (2003) verified that *P. sajor-caju* cultivated in pure corn straw substrate with 10% of wheat bran supplement raised this value to 83%. Wheat straw also was used to cultivate *P. ostreatus*, *P. pulmonarius*, *P. djamor* (Ruán-Soto et al., 2006; Lechner et al., 2004) and *P. eryngii* (Philippoussis et al., 2001). During *Pleurotus* spp. mycelium growth, wheat bran elemental composition decreases in its carbon content and increases in nitrogen and oxygen content, suggesting a preferential degradation by the fungal mycelium for certain polysaccharides than the others, and accumulation of proteins in the substrate (Locci et al., 2008; Alananbeh et al., 2014). This could be attributed to the ability of the supplement to promote different enzymes (cellulose (s), hemicellulase (s), and laccases) secretion, which are important in the degradation of cellulose, hemicelluloses and lignin, respectively (Rajarathnam et al., 1986). El-Batal et al. (2015) also reported that wheat bran has high yield of laccase and abundant source for hydroxycinnamic acids, particularly ferulic and p-coumaric acids, which are known to stimulate laccase production.

The control and monitoring of nitrate levels in different food products are an essential matter. For mushrooms, in general, nitrate distribution along the fruiting body is equal, but in mushroom caps samples, high levels of nitrate in *P. ostreatus* were found. No essential differences were found among the various species or samples produced by means of different conservation technologies (mushrooms in own juice, natural or marinated products). Accumulation of nitrate was not found in fruiting bodies of cultivated mushrooms (Bóbcics et al., 2015).

2.3. Ratio of carbon to nitrogen (C/N)

Mushroom production has been supplementing culture substrates with starchy organic or nitrogen compounds (Bhatti et al., 2007; Ulzizjargal et al., 2013; Cogorni et al., 2014). Mushrooms need to strike a balance in the substrate as the carbon and nitrogen ratio. The total carbon value in the C/N ratio represents the carbon contents, including recalcitrant cellulose and hemicelluloses (Ryu et al., 2015). Furthermore, the supplementation of the substrate with cereal brans or the use of new combinations may promote increased productivity and biological efficacy of the fungus (Donini et al., 2009 and Samuel and Eugene, 2012). Curvetto et al. (2002) observed that supplementation of sunflower seed skin with NH₄[±] for the production of *P. ostreatus* increased the productivity of this species in up to 50%, as it promotes mycelium development through the adjustment of the C/N ratio of the substrate used. One of the hypothesis discussed by Royse (2002) is the C/N ratio adequacy, which relates the supplementation of the substrates with different nutrients as a determining factor to the production of *P. cornucopiae*. In the fruit body development phase, the occurrence of a lower C/N ratio in the cultivation substrate is more favorable. Besides affecting the formation of fruit bodies, nitrogen excess may have affected the degradation of lignin, which may prevent the mycelium from developing. According to Urben (2004) Naraian et al. (2009) and Bellettini et al. (2015), the C/N ratio (28–30% carbon and 1% nitrogen) is an important condition for mushroom production (spawn running). However, recently, Schüttmann et al.

(2014) studied the effect of different natural substrates on versatile peroxidases activity in *P. sabidus*. They showed that the highest versatile peroxidases activity was measured when fungus was cultured on biogas plant material residues, in which the C/N ratio was 10:1. This finding supports previous findings, demonstrating that ligninolytic activity is induced in nitrogen-rich medium (Knop et al., 2015). If more nitrogen than carbon is used, a super mycelial growth inhibition occurs in the mushroom (Zanetti and Ranal, 1997). The slower rate of spawn running on the cottonseed hulls substrate may be due to its high C/N ratio, because nitrogen deficiency is known to inhibit mycelial growth, whereas slow growth on perilla stalks substrate may be caused by an excess of nitrogen, which is known to delay the formation of the fruiting body (Yang et al., 2013a). Li et al. (2015) related that higher C/N value was beneficial to high levels of crude protein, amino acids, 5'-nucleotides and equivalent umami concentration, while lower C/N value was beneficial to carbohydrate, polysaccharides and trehalose production. In their studies, Chang and Miles (2004) address the growth stimulus *Pleurotus* spp. in the presence of glucose, galactose, mannose and fructose and reduced growth in the presence of arabinose and xylose. During mycelium development, there was an increase in reducing monosaccharides and a decrease after fruiting. Glucose supplementation with lignocellulosic promotes the growth and rapid establishment of the fungus in solid raw material and it offers the white rot fungus additional easily metabolizable carbon sources to degrade lignin from lignocellulosic substrates (Kaal et al. 1995). Bano and Rajarathnam (1988) explain that the decrease in reducing sugar values is associated with its use as an energy source in mushroom production. Eira (2003) cites three substrate groups whereupon mushrooms can be grown in natural non-aseptic conditions:

- Substrates in nature with C/N ratio greater than 100/1, such as wood logs without any prior preparation;
- Agro-industrial waste with C/N ratio between 50 and 100/1, such as pre-treated straw for short composting and severe pasteurization or only severe pasteurization;
- Straw and agricultural residues with C/N ratio between 25 and 50/1, prior to composting, pasteurization and packaging, and after packaging the C/N narrows to an amount between 16 and 17/1;
- Substrate having a C/N ratio between 15 and 25/1 may be used with some advantages to the culture medium, which has a narrow C/N ratio, leading to high productivity in view of the sterilization process costs, asepsis and market demand.

2.4. pH

Each mushroom has its optimal pH range for development, and it is variable; for example, pH between 4.0 and 7.0 for the mycelium and 3.5 to 5.0 for formation of basidiocarp (Urban, 2004). The optimum pH for mycelial growth and subsequent fruiting body development is obtained at between 6.5 and 7.0 (Kalmis et al., 2008). With fungal colonization, the substrate pH is reduced to values close to 4.0 for the reduction of organic acids, primarily oxalic acid in step preceding the cutting of the package fruiting crop of solid-state fermentation. Velioglu and Urek (2015) reported that the pH of the

medium was adjusted to 6.0 for *P. djamor* in solid-state fermentation.

2.5. Moisture

Water is one of the main factors that influence the success in mushroom growth. Nutrients are transported from the mycelium to the fruiting bodies by a steady moisture flow (Oei and Nieuwenhuijzen, 2005). High moisture content in the substrate will result in difficult breathing for the mycelium, inhibiting perspiration, rendering the development of fruiting body impossible, even with elevated inoculum amounts or number of holes in mushroom cultivation packages, resulting in the development of non-desired organisms such as bacteria and nematodes (Urban, 2004). Low moisture content will result in the death of the fruiting body. The optimum moisture content for growth and substrate utilization depends upon the organism and the substrate used for cultivation. Increasing moisture level is believed to reduce the porosity of the substrate, thus limiting oxygen transfer. For this reason, the use of high moisture content limited the growth within the whole substrate, resulting in surface growth (Patel et al., 2009). According to Chang and Miles (2004), the appropriate moisture in the substrate should encompass a range between 50% and 75% in the substrate, enabling the satisfactory growth of *Pleurotus* spp. Similarly, Moonmoon et al. (2010) and Ryu et al. (2015) also cultivated *P. eryngii* where the moisture was maintained at 65–68%. Moisture above 70% makes the development of diseases and competing molds possible. According to Mejía and Albertó (2013), tap water was added up to 70% of final moisture. Souza et al. (2006) obtained similar results for laccase production after five days of cultivation using *P. pulmonarius* CCB-19 cultures at 75% initial moisture content. According to Lechner and Albertó (2011), final humidity in the substrate was adjusted (w/w) to 74% accounting for the initial moisture content of substrate to the cultivation of *P. albidus*, *P. cystidiosus*, *P. djamor* and *P. ostreatus*. Water contaminated with heavy metals like mercury, lead and copper can cause undesirable flavor to the product and be a source of human contamination.

2.6. Minerals

The amount of minerals in mushrooms of the same species is directly related to factors such as species, growing area, growing time of fruiting body, genetic factors, substrates and distance from pollution sources (Sánchez, 2004; Genççelep et al., 2009; Gučia et al., 2012). Generally, lignocellulosic materials are low in mineral content, and they require additives to provide them with different minerals, and thus, enhance mushroom production (Mangat et al., 2008; Alananbeh et al., 2014). Minerals such as phosphorus, magnesium, sulfur, calcium, iron, potassium, copper, zinc, manganese and cobalt, as well as vitamins, are used in culture media. Some mushrooms, as for example, *Coprinus comatus*, do not grow in the absence of vitamins. The supplement ratio should not be high due to the possibility of yield reduction (Fanadzo et al., 2010), contamination possibility (Yildiz et al., 2002), and increase in the bed temperature, and possibility of killing of the mycelium (Upadhyay et al., 2002). This addition, when excessive, may result in an undesirable flavor to food (Lima et al., 1975).

The sulfur ions, phosphorus, potassium and magnesium stimulate the development of *Pleurotus* spp. The calcium, zinc, manganese, iron, copper and molybdenum cations are trace elements that may supplement the substrate for these mushrooms (Chang and Miles, 2004). Potassium was the highest in its concentration compared to other nutrients due to a high content of potassium in agro-waste used for mushroom cultivation. However, Oyetayo and Ariyo (2013) who measured proximate and mineral analysis for *P. ostreatus* cultivated on different agro-wastes found that phosphorus had the highest value among all the minerals analyzed. Copper as a micronutrient has a key role as a metal activator. It induces laccase transcription, and also plays an important role in laccase production (Palmieri et al. 2000; Ikehata et al., 2004). An increased concentration of copper sulfate from 0.06 to 0.28 mM (optimum) raised laccase production by *P. ostreatus* HP-1 in solid-state fermentation (Patel et al., 2009). According to Almeida et al. (2015), the mycelium of *P. ostreatus* bioaccumulated at least five times more iron than its basidiocarp. Thus, iron bioaccumulated mycelium could be an alternative food with iron concentration from a non-animal source. Altogether, the variation in mineral content probably reflects the mineral composition of the substrate used in different cultivations (Gucia et al., 2012). Similar results were found by Patil et al. (2010) and Alananbeh et al. (2014) in oyster mushroom cultivation *P. ostreatus* on different lignocellulosic agro-wastes.

Among all of the pollutants, heavy metals are one of the most important and hazardous types. Living organisms require trace amounts of some heavy metals, including iron, cobalt, copper, manganese, chromium and zinc. However, some other metal elements are considered to be harmful, such as arsenic, cadmium and lead (Liu et al., 2015). It is well documented that the fruiting bodies of mushrooms have the ability to bioaccumulate metal ions, and the accumulation of heavy metals in macrofungi has been proven to be affected by environmental and fungal factors (Garcia et al., 1998; Llorente-Mirandes et al., 2016). Heavy metal concentrations and those of several trace minerals in mushroom are considerably higher than those in agricultural crop plants, vegetables and fruit (Dursun et al., 2006). The presence of heavy metals in the white-rot fungi substrate is an important factor because it affects the biodegradation process and growth of the fungus through affecting the activities of cellulolytic and hemicellulolytic enzymes (Baldrian and Gabriel, 2003). Therefore, many studies have granted considerable attention to the accumulation of heavy metals in several mushroom species (Chen et al., 2009; Cocchi et al., 2006). Mercury can be an example of a metal that is much more enriched in fruiting bodies of mushrooms than in plants or animals (Melgar et al., 2009). Cadmium is known as a main toxic element, since it inhibits many life processes. Minerals such as cadmium and lead can be absorbed by bioaccumulative species of these minerals or when mushrooms grow in polluted areas (Kalač and Svoboda, 2000). Mushrooms, *Pleurotus* spp., in particular, can be very rich in cadmium (Demirbas, 2001). However, contamination of mushrooms by heavy metals represents a low risk to the public health, in general, but it could be a serious problem for those with a weakened and immune-suppressed health (Almeida et al., 2015).

Mushrooms are known for absorbing radionuclides (^{131}I , ^{134}Cs and ^{137}Cs) (Kalač and Svoboda, 2000). Fruiting body

radioesium activities may easily exceed 100 Bq kg^{-1} when contaminated substrates are used for cultivation. Heavy metal amounts in fruiting bodies might be cause for concern. It has been proposed that ^{137}Cs uptake of mushrooms could be prevented by providing additional rubidium or potassium at contaminated sites, given that fungi showed a greater preference for rubidium and potassium over cesium (Terada et al., 1998; Vinichuk et al., 2010). Hiraide et al. (2015) investigated methods for reducing radioesium transfer from sawdust media into *P. ostreatus* fruiting bodies and verified a satisfactory result when using the nanoparticle insoluble Prussian blue.

2.7. Particle size

A desirable property in solid-state fermentation, is that its small particles (substrates can be cut into 5–6 cm) provide a larger surface area used by the microorganism (average bulk density of 428 lb/yd^3) (Lohr et al., 1984; Yildiz et al., 2002). However, very small particles result in a compressed substrate, interfering with the aeration system and in oxygen used by microorganisms (Bellettini et al., 2015). Zhang et al. (2002) found that when straw was ground into too small particles, the mushroom yield decreased. On the other hand, particles with large size cause an increase in space between particles, thus improving the oxygen transfer related processes, however, limiting the surface area of the particles, which cause mass transfer processes (nutrients and moisture) required for the microorganism (Pandey et al., 2000). According to Owaid et al. (2015), in their studies with recycling with cardboard wastes to produce blue oyster mushroom *P. ostreatus*, the small size of gradients of the substrate wheat straw has large influence on oyster mushroom growth, compared with pieces of cardboard (big), which lead to an increase in decomposed wheat straw and big biomass of mycelia formed because of an increased substrate surface area for mycelia growth, thus clusters were grown on this substrate (Aswad, 2005).

2.8. Levels of spawning

Increasing spawning rate shortens mycelial colonization time, primordia formation, the time to the first mushroom crop (Yang et al., 2013a) and narrows the gap of opportunity for competitor invasion (Stamets, 2000). The increased nutrient level available in spawn at higher rates would provide more energy for mycelial growth and development (Royse et al., 2004). Alananbeh et al. (2014) studied three levels of spawning (5%, 7.5%, and 10%) and related that the yield, biological efficiency, and total fruiting bodies increased as the percentage of cultivating *P. ostreatus* increased. Zhang et al. (2002) evaluated three tested spawn levels (12%, 16% and 18%), and the 12% level resulted in a significantly lower mushroom yield than the other two levels of *P. sajor-caju* cultivation. According to Eira (2003) and Oei and Nieuwenhuijzen, 2005, the amount of inoculum should not exceed 10% of the weight of the substrate (commercial production 7–10%), because there is not a significant increase of biological efficiency, resulting in economic loss. Smita (2011) also showed that highest biological efficiency was obtained at 8% and there was no significant difference in yield from 6%, 8% and 10% spawn doses. A lower inoculum level may not be sufficient to initiate growth, whereas a higher

level may cause competitive inhibition (Sabu et al., 2005). An increase in inoculum size enhanced the utilization of solid substrate, thereby improving laccase activity. However, with further increase in inoculum above the limits, laccase production is decreased due to a fast depletion of nutrients, resulting in a decreased metabolic activity (Patel et al., 2009).

2.9. Surfactant

Surfactants, especially Tween®80, can increase the bioavailability of less soluble substrates for the fungi, stimulating of the fungal spore growth (Zheng and Obbard, 2001). El-Batal et al. (2015) confirmed that the addition of surfactant Tween®80 (0.02% (v/v)) has resulted in higher yields of lignolytic enzymes in *P. ostreatus* under solid-state fermentation because there is evidence that these surface acting agents result in higher permeability of oxygen and extracellular enzyme transport through the cell membranes of fungi. However, the specific mechanism by which surfactants enhance extracellular enzyme production in filamentous fungi has not been elucidated yet (Patel et al., 2009).

3. Effects of extrinsic factors

3.1. Temperature

3.1.1. Heat treatment

Mushroom production techniques may involve previously composted and/or steam pasteurized natural substrates (Owaid et al., 2015) or may use axenic cultivation, which consists of using a sterile substrate (Eira et al., 1997). According to Laborde and Delmas (1974) and Siqueira et al. (2012), a number of different methods for substrate pasteurization or sterilization have been proposed: autoclaving (axenic), axenic and inoculation with thermophilic microorganisms, rapid substrate steam treatment between 80 and 100 °C for several hours, pasteurization at 72 °C for four or five days, and pasteurization by substrate steam treatment for several days (60 °C) in a tunnel. The most common pasteurization process uses vapor injected into chambers or tunnels, where the substrate is packaged and pasteurization time varies as a function of the temperature (Zadrazil, 1980). In the non-axenic culture (steam pasteurization), the substrate is packaged and subjected to heat treatment at 75–100 °C for 4–10 h. In this technique, only a fraction of the microorganisms is eliminated. The objective is to destroy the microorganisms that are in the vegetative form, forcing the rest to stay in spore form. The rapid cooling causes the microorganisms remain static, disadvantaging the optimal conditions that stimulate spore germination. As these temperatures are easily reached, pasteurization can be done even in containers less resistant to high temperatures, such as those polyethylene bags (Bellettini et al., 2015).

Substrates also can be saturated in water for 24 h, pasteurized for 2 h, drained from excess of water, mixed as their combination and cooled for ready to inoculated (Owaid et al., 2015). Houdeau et al. (1991) considered that the immersion of substrate in water can have different consequences according to the type of raw material. They pointed out that there is a “nutrient washing” effect that can be negative when old

raw material is used, but useful in new raw material because there is a decrease in soluble sugars that can prevent the development of antagonistic microorganisms. Mejía and Albertó (2013) related that the hot water immersion treatment of substrate reduces yields in at least 20% when compared to other straw treatments, such as steam, chemical or untreated wheat straw. Compounds which are hydro-soluble are lost during wheat straw immersion in hot water. The loss of these nutrients would be the cause of yield decrease. Although this method is inexpensive and easy to implement, crop reduction is very important, causing significant loss, especially when the majority of *Pleurotus* farmers in Latin America, India or Africa use this methodology to treat the substrate. Additionally, another important factor to take into account is that this method uses a high amount of water, which could be a negative factor due to scarcity of this resource in some areas.

Although there are a lot of alternative procedures for substrate preparation, most of the papers published by the scientific community report a preference for axenic cultivation, cultivation in a substrate previously sterilized in an autoclave, with some variations (Dias et al., 2003; Silva et al., 2007; Gonçalves et al., 2010). According to Felinto (1999) the technique of axenic cultivation is unfeasible in a commercial scale due to the required investment in equipment. However, in developed countries this is the technique that presents best results. Sterilization is an important step for mushroom cultivation. Several studies have reported the use of heat treatment such as sterilization, as reported by Moonmoon et al. (2010), Kim et al. (2013), Mejía and Albertó (2013) and Ryu et al. (2015), wherein the cultivation packages were sterilized in an autoclave for 1, 1.40 and 2 h, respectively, at 121 °C 1.2 psi of pressure. Previous studies tested different sterilization techniques including hot water, autoclave, formalin and bavistin (Hussain et al., 2002). According to Alananbeh et al. (2014), sterilizing with formalin and bavistin and autoclave found to have better spawn running, pin head and fruiting body formation, and yield. In a similar study, Banik and Nandi (2004) related the disinfection of the substrate was conducted by 0.1% KMnO₄ plus 2% formalin solution in hot water which resulted in a 42.6% increase in yield of *P. sajor-caju* over control.

A mycovirus affecting the basidiocarp of *P. florida* and *P. ostreatus* was related by Reddy et al. (1993). The symptoms induced in *Pleurotus* spp. include: pileus curling upwards, swollen stalks and greatly distorted basidiocarps. Premature spore shedding and elongation of stalk are typical symptoms of the disease. According to Kim et al. (2015a) the bacterial pathogen *Pantoea* sp. causes severe soft rot disease in king oyster mushroom, *P. eryngii*, including water-soaked lesions and soft rot symptoms. To prevent the development of competing microorganisms and subsequent economic loss, it is also important to thoroughly clean the vessels (sanitation), often applying heat treatment.

3.1.2. Temperature of the culture house

The major ecological factors that affect stalk height, stalk diameter and cap size in mushroom are air temperature, humidity, fresh air, and compact material (AMGA, 2004). *P. ostreatus* can be widely cultivated, and it can adapt to different temperatures. It exists on every continent except Antarctica

Table 1 Temperature ranges for mycelial growth and fruiting of *Pleurotus* spp.

<i>Pleurotus</i> species	Incubation temperature*	Induction temperature*	Optimal frutification temperature*	Harvest temperature*	Reference(s)
<i>P. abalonus</i>	15–35	12–18	20–30	25–30	Oei and Nieuwenhuijzen (2005)
<i>P. citrinopileatus</i>	24–29	21–27	21–29	23–25	Stamets (2000), Wang et al. (2005)
<i>P. cystidiosus</i>	18–33	18–24	21–28	22–28	Stamets (2000); Hoa and Wang (2015)
<i>P. cornucopiae</i>	15–35	12–18	20–28	15–25	Stamets (2000), Oei and Nieuwenhuijzen (2005)
<i>P. djamor</i>	15–35	18–25	24–30	20–30	Oei and Nieuwenhuijzen (2005), Bellettini et al. (2015)
<i>P. eryngii</i>	10–35	10–15	20–25	15–22	Oei and Nieuwenhuijzen (2005), Dias (2010)
<i>P. ostreatus</i>	5–35	10–15,6	20–25	5–25	Oei (1991), Stamets (2000), Marino et al. (2003), Owaïd et al. (2015)
<i>P. pulmonarius</i>	5–35	5–27	20–25	13–20	Oei and Nieuwenhuijzen (2005), Donini et al. (2009), Lechner and Albertó (2011)

* (°C).

and grows throughout the year (Qu et al., 2016). Oyster mushroom can grow at moderate temperatures, ranging from 18 to 30 °C (Mejía and Albertó, 2013). Li et al. (2015) related that the substrate containing inoculum was subsequently kept in a darkened spawn-running room at 23 °C. According to Ahmed et al. (2013), for the cultivation of *P. high-king*, *P. ostreatus* and *P. geesteranus*, temperature of culture house was maintained at between 22 and 25 °C. Similarly, Kim et al. (2013) also cultivated *P. eryngii*, where incubation room temperature was maintained at 22–24 °C. According to Hoa and Wang (2015), the optimal temperature for both *P. ostreatus* and *P. cystidiosus* was found to be 28 °C. Neelam et al. (2013) indicated that the optimal temperature for mycelium growth in oyster mushroom *P. florida* was 25–30 °C. This optimal temperature result indicated that *Pleurotus* species were able to grow better during the summer and autumn in subtropical and tropical regions as a potential opportunity to develop oyster mushroom production in poor and developing countries (Oei, 1991; Kashangura, 2008). The optimal environmental situation for mycelial growth and the subsequent fruiting is usually very distinct (Table 1). Fruiting body development is often induced after drastically altering environmental circumstances (Pandey et al., 2008).

When substrates were fully colonized, the temperature can be changed to 10–16 °C (cold shock, a difference of 5–10 °C) to induce fructification (Oei, 2003; Ruiz-Rodriguez et al., 2010; Owaïd et al., 2015). Lechner and Albertó (2011), for fruiting bodies production, *P. albidus*, *P. cystidiosus* and *P. djamor* were kept at 18–20 °C. Dahmardeh (2013) related that temperature was controlled by electric heaters at 25 °C for spawn running and at 17–20 °C for fruiting body formation.

In the solid-state fermentation systems, during the fermentation process, the temperature of fermenting mass increases due its respiration process (Niladevi et al., 2007). According to Mahmud and Ohmasa (2008), mycelium of long culture age (70 days) showed significantly higher temperature tolerance when compared to mycelium of shorter culture ages of 14 and 30 days. Lower temperatures and dry condition reduced stalk height and cap size of mushroom (Sher et al., 2010). On the other hand, high temperatures in growing environment can reduce mushroom development in different ideal growth tracks, allowing the development of competitive microorganisms better adapted to high temperatures (Urban, 2004).

3.2. Humidity

For most fungi, the wide humidity range is 20–70% (Pandey et al., 2001). According to Chang and Miles (2004) and Li et al. (2015), the appropriate humidity during the darkened spawn-running and mycelia stimulation should encompass a range between 60–75% and 85–97%, respectively, in the environment, enabling a satisfactory growth of *Pleurotus* spp. High humidity is favorable for pinning and fruiting (Pandey et al., 2008). During the *P. high-king*, *P. ostreatus* and *P. geesteranus* growth on wheat bran-supplemented sawdust, the relative humidity of the culture room was maintained at 80–85% by spraying water three times per day (Ahmed et al., 2013). Similarly, Kim et al. (2013) and Ryu et al. (2015) also cultivated *P. eryngii* where the humidity of the incubation room was maintained at 85–95%.

3.3. Luminosity

Photoperiod is not necessary to induce the primordium formation but it is needed for fruiting body production. Recent advances in fungal photobiology using molecular tools and genomic analysis have shown specific phytochromes, photoreceptor proteins, transcription factors, light-regulated genes, and to a certain extent common regulatory pathways leading to mushrooms development and spore viability (Colavolpe and Albertó, 2014). There are species that develop in the dark and other ones in partial light. It seems likely that all mushrooms, which require light, use a common regulatory pathway for basidioma development (Kurtzman and Martinez-Carrera, 2013). Some mushrooms such as *Pleurotus* spp. or *L. edodes* require light for primordia formation (Nakano et al., 2010). A publication by Kaufert (1936) seems to be the first indication that *Pleurotus* species required light. In general, the photoperiod of mycelia stimulation to promote mushroom fruit bodies formation should be sufficient to read a sheet of paper (200–640 lux 8–12 h a day⁻¹) at a temperature compatible with the mushroom (Ahmed et al., 2013; Mejía and Albertó, 2013). Environments that have a lot of light can cause paleness, deformations, elongated stipe (Urban, 2004) and reduction of pileus coloration (Marino et al., 2003). Eira and Bueno (2005) report that bright white color of the cap (pileus) of

Pleurotus spp. can be changed to dark and opaque in the presence of light, due to phenoloxidase release that oxidize phenols, forming melanoidins. Both in solid-state fermentation as submerged fermentation, the presence of light induces the appearance of primordia, reducing the fruiting body formation and weight of fruiting body, consequently the yield is ultimately reduced (Sarker et al., 2007). According to Kues and Liu (2000), whenever tested, the active wavelengths that control fruiting body initiation and maturation were found to be in the blue light/UV range. In the complete absence of light, oyster mushrooms will form no cap but stipes (mushroom stalks) forming a coral-like structure (Oei and Nieuwenhuijzen, 2005).

Pulsed light is a rapid technology to convert ergosterol into vitamin D₂ in mushrooms that use a UV lamp with broad spectrum (100–800 nm) to deliver irradiation in the form of high-intensity pulses, which can significantly increase vitamin D₂ content in mushrooms for a short time (Koyyalamudi et al., 2009, 2011). According to Chen et al. (2015), the highest and lowest vitamin D₂ contents were generated in *P. citrinopileatus* and *P. eryngii* for 9 pulses, respectively (2.78 and 0.36 µg g⁻¹ FW). The UV irradiation acts only on the surface of mushrooms (Ko et al., 2008). Therefore, the fruiting body of *P. citrinopileatus* had more flat surface areas than other four *Pleurotus* mushrooms did. The author suggests that *P. citrinopileatus* might absorb more pulsed light, and thereby produce more vitamin D₂ than other *Pleurotus* mushrooms.

3.4. Air composition

Gaseous environment control in aerobic solid-state fermentation is an important factor in the development of microorganisms, dependent on oxygen flow speed through the substrate and the speed of O₂ consumption by microorganisms. Aeration has different functions, being O₂ provision for aerobic growth and metabolism; moisture regulation; temperature adjustment; water vapor, CO₂ and some volatile metabolite elimination. Aerobic mushrooms require oxygen for their survival and development. During the darkened spawn-running, it is important to keep CO₂ concentration at 2000–2500 mg L⁻¹. After the completion of spawn-running and mycelia stimulation, fruit bodies were allowed to develop at CO₂ concentration 1500–2000 mg L⁻¹ (Li et al., 2015). Since air contains high CO₂ levels, it will produce mushrooms with thick and short stipe pileus (Urban, 2004). Therefore, during the fruiting stage is a reduction in CO₂ concentration is required, as well as an increase in O₂. This is possible by opening packages of cultivation and ambient air change through ventilation (rational room cubic capacity / cultivation area in cubic meter ration should not be lower than 1.85:1). The maximum number and size of holes (air entrance) can be made, provided that there is no contamination by being careful not to damage the mycelium (Oei and Nieuwenhuijzen, 2005). An increased number of holes in the cultivation of packets results in smaller mushroom (Eira, 2003). It is expected that the level of O₂ required for solid-state fermentation is lower than the submerged fermentation mycelia. However, according Lonsane et al. (1991), the problem with O₂ diffusion, in solid-state fermentation, comes down to the transfer of gas among the particles. An ideal situation would be to increase the ability of a microorganism to achieve directly the atmospheric O₂ gas (Ramana-Murthy

et al., 1993). However, whatever the form of O₂ transport is, it is noted that transfer speed in solid-state fermentation is higher than in submerged fermentation mycelial.

3.5. Envase

Substrates are usually filled into pasteurized polyethylene (LDPE and HDPE) and autoclavable polypropylene (PP), polyvinyl chloride (PVC) bags (Moonmoon et al., 2010; Lechner and Albertó, 2011), and bottles (Bao et al., 2004). A recommended size for the cultivation bag is 30 × 50 cm with 1500 g in wet weight (Owaid et al., 2015). In the pasteurization process, a previous study revealed that polyethylene bags resulted in higher biological efficiency compared to pottery, plastic trays, and polyester net (Mandeel et al., 2005). Owaid et al. (2015), in their studies with recycling with cardboard wastes to produce blue oyster mushroom *P. ostreatus*, the lesser biological efficiency was observed on wheat straw alone that reached to 5.4% and 9.1% using large and small bags, respectively. The conclusion was that big bags best than small ones in yield and biological efficiency because more substrates allows more growing than smaller container (Royse, 2002). However, the number of flushes was increased in small bags compared with big ones. The decline in caps in small bags with all substrates may be return to close fruiting bodies from others because of small area with these packets, which lead to small size of fruiting body in small bags. Whereas in the big containers; fruiting bodies have the best chance of growing and extending; that due to big size of container that gave big size of fruiting body.

4. Conclusion

The survival and multiplication of mushrooms is related to a number of factors, which may act individually or have interactive effects among them. The combination of the best air temperature, moisture, nutrient conditions as well as other variables, provides a synergistic effect optimizing the production of mushrooms, with a consequent loss and cost reduction. This review points out that in order to comprehend the challenges in handling *Pleurotus* genus mushroom requires a fundamental understanding of their physical, chemical, biological and enzymatic properties. An in-depth understanding of the intrinsic and extrinsic factors is needed for a suitable and efficient production of *Pleurotus* spp.

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