Effect of gamma and electron beam irradiation on the physico-chemical and nutritional properties of mushrooms: A review

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Abstract

The short shelf-life of mushrooms is an obstacle to the distribution and marketing of the fresh product. Thus, prolonging postharvest storage, while preserving their quality, would benefit the mushroom industry as well as consumers. There has been extensive research on finding the most appropriate technology for mushrooms preservation. Gamma, electron-beam and UV irradiation have been shown to be potential tools in extending the postharvest shelf-life of fresh mushrooms. Studies evaluating the effects of ionizing radiation are available mainly in cultivated species such as *Agaricus bisporus*, *Lentinus edodes* and *Pleurotus ostreatus*. This review comprises a comprehensive study of the effects of irradiation on physico-chemical parameters (weight, colour, texture and pH), chemical compounds including nutrients (proteins, sugars and vitamins) and non-nutrients (phenolics, flavonoids and flavor compounds), and on biochemical parameters such as enzymatic activity of mushrooms for different species and from different regions of the world.

Keywords: Mushrooms; γ-radiation; electron-beam; physico-chemical parameters; chemical/biochemical properties

1. Introduction

1.1. The unique properties of mushrooms

The special place held by mushrooms in human food is well illustrated by the statistical data regarding world production of mushrooms and truffles which in 2007 reached a volume of 3 414 392 metric tons (USDA, 2009). Their global economic value is now staggering, and the reason for the rise in consumption is a combination of their value as food (Kalač, 2009) and their medicinal or nutraceutical properties (Ferreira, Barros, & Abreu, 2009; Ferreira, Vaz, Vasconcelos, & Martins, 2010).

In Europe, wild mushrooms are collected for consumption being a good source of digestible proteins, carbohydrates, fibres and vitamins (Kalač, 2009; Grangeia, Heleno, Barros, Martins, & Ferreira, 2011; Heleno et al., 2011; Ouzouni, Petridis, Koller, & Riganakos, 2009). Dry matter content is usually about 100 g/kg. Structural polysaccharides and proteins comprise the main components of dry matter, while the lipid content is low. Chitin, glycogen, mannitol and trehalose are typical carbohydrate constituents. The proportion of essential amino acids is nutritionally favourable, while the content of n-3 fatty acid is negligible (Kalač, 2009). Furthermore, macrofungi have a history of traditional use in oriental therapies and modern clinical practices continue to rely on mushroom-derived preparations. They accumulate a variety of bioactive metabolites (e.g. phenolic compounds, polyketides, terpenes, steroids and polysaccharides) with immunomodulatory, cardiovascular, liver protective, anti-fibrotic, anti-inflammatory, anti-diabetic, anti-viral, antimicrobial activities, and antitumor properties (Poucheret, Fons, & Rapior, 2006; Ferreira et al., 2010).

More than 3000 mushrooms are said to be ‘prime edible species’, of which only 100 are cultivated commercially, and only ten of those on an industrial scale (Chang & Miles, 2004). Nevertheless, those species have commercial importance and their cultivation

has emerged as a promising agro-based land independent enterprise. Only about 45% of mushrooms produced are consumed in the fresh form. The other 55% are processed (5% in dehydrated form and 50% in canned form) because their shelf-life in the fresh form is very short (Singh, Langowski, Wanib, & Saengerlaub, 2010).

1.2. Shelf-life of mushrooms

Mushrooms are one of the most perishable products and tend to lose quality immediately after harvest. The short shelf-life of mushrooms (1-3 days at ambient temperature) is a draw back to the distribution and marketing of the fresh product. Their shelf-life is short due to postharvest changes, such as browning, cap opening, stipe elongation, cap diameter increase, weight loss and texture changes, to their high respiration rate and lack of physical protection to avoid water loss or microbial attack (Akram & Kwon, 2010; Singh et al., 2010; Sommer, Schwartz, Solar, & Sontag, 2010) (**Figure 1**).

Bacteria, moulds, enzymatic activity (mainly, polyphenol oxidase, PPO) and biochemical changes can cause spoilage during storage (**Figure 1**). Furthermore, the browning of mushroom cells occurs when they are subjected to forces that can disrupt cellular integrity such as vibrations, rough handling, and ageing (Beaulieu, D'Aprano, & Lacroix, 2002; Jiang, Luo, Chen, Shen, & Ying, 2010). The most important factors determining the rate of enzymatic browning are the tissue concentrations of active PPO and phenolic compounds present, pH, temperature, water activity and oxygen availability. Browning is a result of two distinct mechanisms of phenol oxidation: (a) activation of tyrosinase, an enzyme belonging to the PPO family; and/or (b) spontaneous oxidation (Martinez & Whitaker, 1995; Jolivet, Arpin, Wichers, & Pellon, 1998; Singh et al., 2010). The PPO, present in the cap and stipe of mushrooms, is a

copper containing enzyme which catalyses two different reactions: (i) the hydroxylation of monophenols to the corresponding *o*-dihydroxy compounds and (ii) the oxidation of *o*-dihydroxy phenols to *o*-quinones, which condense to form the brown melanin pigments (Beaulieu et al., 2002). For example, in the presence of oxygen and tyrosinase, γ-L-glutaminyl-4-hydroxybenzene (GHB, the principal phenolic compound in mushrooms) is easily hydroxylated to γ-L-glutaminyl-3,4-dihydroxybenzene (GDHB) and oxidized to γ-L-glutaminyl-3,4-benzoquinone (GBQ), which further leads to the formation of polymerized melanin-like compounds (Beaulieu, D'Aprano, & Lacroix, 1999; Sommer et al., 2009) (**Figure 2**). Besides PPO, the activity of other enzymes like phenylalanine ammonia-lyase (PAL) and peroxidase (POD) has also been related to the development of browning pigments. PAL is the key enzyme for the metabolism of phenols, catalyzing the deamination of L-phenylalanine to yield ammonia and *trans*-cinnamic acid, from which phenolic compounds will be produced (Benoit, D'Aprano, & Lacroix, 2000). Otherwise, superoxide dismutase (SOD) and catalase (CAT) protect cells from the destructive effects of reactive oxygen species and constitute key components of the cellular antioxidant defense systems. SOD first converts superoxide anions into hydrogen peroxide, which is then removed by CAT. These combined activities are thought to extend food freshness by protecting the integrity of membranes (Xiong, Xing, Feng, Tan, & Bian, 2009).

Water loss or transpiration is another important physiological process that affects the main quality characteristics of fresh mushrooms, such as saleable weight, appearance and texture, and these processes are dependent on surrounding temperatures and relative humidity. Particularly, storage temperature is one of the main factors that affect post-ripening and quality such as respiration, transpiration, senescence and other physiological actions. Temperature fluctuation during storage is another key factor. It

can activate many kinds of oxidases and enhance physiological activities, increasing post-ripening of stored mushrooms (Pai, 2000; Singh et al., 2010).

Morphological changes, which involve exposure of the gills and sporulation, are supported by respiration substrates which are present in the sporophore at harvest, rather than substrates of mycelial origin, as is the case in the growing sporophore. Thus the substrate expended in postharvest sporophore development, and hence respiration, is also an important factor in determining the onset of senescence; the overall decline in respiratory activity seen after harvest is due to the exhaustion of substrates and senescence of the tissues (Singh et al., 2010).

Finally, the presence of high bacterial populations in fresh mushrooms is a major factor that significantly diminishes quality by causing a brown, blotchy appearance. The rate of postharvest deterioration of fresh mushrooms has been directly related to the initial microbial load (Doores, Kramer, & Beelman, 1987; Singh et al., 2010). *Pseudomonas tolaasii* is regarded as a normal constituent of the microflora of the mushroom bed that could produce a toxic metabolite to mushrooms under certain conditions; the infection appears as a brown injury on mushrooms (Bealieu et al., 1999; Bealieu et al., 2002). Other Gram-negative microorganisms, such as *Pseudomonas fluorescens* and yeasts, such as *Candida sake*, have been associated with mushroom spoilage (Masson, Ainsworth, Fuller, Bozkurt, & Ibanoglu, 2002; Jiang et al., 2010b). Molds can also affect the quality of the mushrooms. Contamination of *Verticillium maltousei* shows brown spots (Bealieu et al., 1999; Bealieu et al., 2002).

2. Irradiation in mushrooms

2.1. Extending the shelf-life of mushrooms

Prolonging postharvest storage, while preserving their quality, would benefit the mushroom industry as well as consumers. Extended shelf-life is a key factor for making any food commodity more profitable and commercially available for long periods of time at the best possible quality. The producer will benefit from the longer shelf-life to develop the market over greater distances (Akram & Kwon, 2010).

A general trend in food preservation research is towards the development of preservation techniques that are less severe and therefore less damaging to food products (Gould, 1989; Minnaar, Taylor, & McGill, 1995). There has been extensive research on finding the most appropriate technology for mushrooms preservation. Chemical treatments (Sapers, Miller, Pilizota, & Kamp, 2001), refrigeration (Murr & Morris, 1975), washing (Cliffe-Byrnes & O'Beirne, 2008), coating (Nussinovitch & Kampf, 1993), modified/controlled atmosphere packaging (Lopez-Briones et al., 1992; Roy, Anantheswaran, & Beelman, 1995), use of humectants, use of tyrosine inhibitors (Singh et al., 2010) and ozone treatment (Yuk, Yoo, Yoon, Marshall, & Oh, 2007) are frequently applied methods. However, all of them have associated drawbacks including safety considerations, discoloration, production of off-flavors, and contamination with pathogenic microorganisms, and are unsuitable for use on an industrial scale (Duan, Xing, Shao, & Zhao, 2010). Moreover, the majority of food preservation techniques operate by slowing down or inhibiting the growth of microorganisms. In contrast, heat and ionizing irradiation processing can inhibit or inactivate microbial growth completely, resulting in commercially sterile and shelf-stable food products (Gould, 1989; Minnaar et al., 1995).

2.2. Irradiation techniques

Food irradiation may be considered as a second big breakthrough after pasteurization. It is the process of exposing food to ionizing radiation (such as gamma and electron-beam) in order to enhance its shelf-life as well as its safety. The aim is to destroy microorganisms or insects that could be present in the food, and some time to improve the functional properties of food or to eliminate toxins, with the least compromise on sensory and nutritive quality (Akram & Kwon, 2010). Different forms of irradiation as food processing are well established as a physical, non-thermal mode of food preservation (cold-pasteurization) that processes foods at/or nearly at ambient temperature (Duan et al., 2010). The irradiated food amounts in the world, in 2005, was 405 000 ton comprising 186 000 ton (46%) for decontamination of spices and dry vegetables, 82 000 ton (20%) for disinfestations of grains and fruits, 32 000 ton (8%) for decontamination of meat and fish, 88 000 ton (22%) for sprout inhibition of garlic and potato, and 17 000 ton (4%) of other food items that included mushrooms (Kume, Furuta, Todoriki, Uenoyama, & Kobayashi, 2009).

Gamma-irradiation (Beaulieu et al., 2002) and electron-beam irradiation (Koorapati, Foley, Pilling, & Prakash, 2004) have been shown to be potential tools in extending the postharvest shelf-life of fresh mushrooms. Doses of γ-irradiation inhibited cap opening and browning, stalk elongation, reduced the level of microbial contamination, and generally extended the shelf-life of mushrooms without noticeable effects on taste qualities (Lescano, 1994). Gamma-irradiation alone or in combination with refrigeration has been shown to prolong shelf-life through reducing moisture loss and improving color and appearance (Ajlouni, Beelman, & Thompson, 1993). Electron-beam irradiation is also known to be highly effective in reducing harmful bacteria in fruits, vegetables, and other foods while preserving the fresh taste, aroma, texture,

wholesomeness, and nutritional content (Schmidt, Palekar, Maxim, & Castillo, 2006; Duan et al., 2010).

Food irradiation with ultraviolet radiation has been tested with UV-A (400-315 nm), UV-B (315-280 nm) and mainly with UV-C (280-100 nm), since it has more energy. Ultraviolet (UV-C) irradiation is widely used as an alternative to chemical sterilization and microbial reduction in food products and has been approved for use as a disinfectant for surface treatment of food (US-FDA, 2002). As a postharvest treatment on fresh products, UV-C irradiation has been proven beneficial to reduce respiration rates, control rot development, and delay senescence and ripening in different fruits and vegetables, as also in mushrooms (Guan, Fan, & Yan, 2012). Moreover, UV-C, UV-B and UV-A revealed the capacity to convert mushroom ergosterol in vitamin D2 (Teichmann, Dutta, Staffas, & Jägerstad, 2007), being the UV-B the most effective (Jasinghe & Perera, 2006; Ko, Lee, Lee, & Park, 2008).

The irradiation of mushrooms can be a safe and cost effective method to enhance shelf-life as well as to ensure hygienic and sensory quality (Akram & Kwon, 2010). The softening and browning process associated with the ripening of certain fruits and vegetables, as also in mushrooms, can be delayed by irradiation. Therefore, to preserve nutritional characteristics as well as to enhance shelf-life of mushrooms in conjunction with advanced food processing methods, irradiation can serve the purpose (Akram & Kwon, 2010). The irradiation of many food products has been approved by many reliable regulatory bodies, including European Union Commission (Directive 1999/3/EC), United States Food and Drug Administration (US-FDA, 1991), World Health Organization (WHO, 1981, 1994), the CODEX Alimentarius Commission (CAC/RCP 19-1979, Rev. 2-2003). These regulatory agencies assure that food

irradiation is a safe process with respect to food processing for humans (US-FDA, 1991; WHO, 1994).

The recommended dose for extending the shelf-life of fresh mushroom in different countries (such as Argentina, China, Croatia, Hungary, Israel, Korea, Mexico, Poland and United Kingdom) is 1-3 kGy, while the recommended dose regarding the decontamination of dried mushrooms (come under food additives with spices), used as seasonings, is 10-50 kGy (ICGFI, 1999).

2.3. Irradiated species

Studies evaluating the effects of ionizing radiation are mostly available in cultivated species with high production value such as *Agaricus bisporus*, *Lentinus edodes* and *Pleurotus ostreatus*. Studies on other species such as *Agaricus campestris*, *Cantharellus tubaeformis*, *Hypsizygus marmoreus*, *Inonotus obliquus*, *Pleurotus cystidus*, *Pleurotus nebrodensis*, *Tuber aestivum* and *Volvariella volvacea* are also available. Those mushroom species come from all over the world, North and South America (Argentina, Canada, Japan and USA), Asia (China, India, Korea, Philippines and Singapore) and Europe (Denmark, Netherlands, Spain and Sweden) (**Table 1** and cited references).

Gamma (^{60}Co), electron-beam (e-beam) and UV irradiation techniques were applied mostly to fresh (**Table 1** and cited references**)**, but also to freeze-dried (Teichmann et al., 2007) and air-dried (Rivera, Blanco, Marco, Oria, & Venturini, 2011) samples, and even to a dried aqueous extract (Kim et al., 2009). The applied doses for gamma and e-beam were up to 5 kGy and in the most cases around 1 and 2 kGy. Otherwise, UV doses were much more variable (**Table 1**).

Several analyses of physico-chemical and microbiological parameters were performed after different storage periods, most of them around 15 days but some up to 25 days for

fresh samples, or 42 days for air-dried samples. In general, the analyses of irradiated fresh samples were carried out daily or every 2-4 days (**Table 2**).

In the present review we will focus on physico-chemical (**Table 2**), chemical and biochemical (**Table 3**) parameters.

3. Influence of irradiation on mushrooms composition

3.1. Influence on physico-chemical parameters

The effects of irradiation on physico-chemical parameters such as weight, colour, texture and pH, were described by different authors in several mushroom species and were summarized in **Table 2**.

Skou (1974), Nayga-Mercado & Alabastro (1989), Narvaiz (1994) and Xing et al. (2007) reported weight losses in γ-irradiated samples similar to non-irradiated controls. Other authors reported a marginally (Gautam, Sharma, & Thomas, 1998) or even significantly reduction of the weight loss in γ- (Wani, Hussain, Meena, Dar, & Mir, 2009) or electron-beam (Duan et al., 2010; Jiang et al., 2010b) irradiated samples. Weight loss of *A. bisporus* was only indirectly affected since it was directly related to the retarding effect of irradiation on growth and ripening (Skou, 1974).

Regarding the effects of γ- or e-beam irradiation on colour, all the authors reported a delaying in browning and therefore an extension on the mushrooms shelf-life (Gill, Markakis, & Markakis, 1969; Skou, 1974; Gautam et al., 1998; Beaulieu et al., 1999; Benoit et al., 2000; Beaulieu et al., 2002; Koorapati et al., 2004; Wani et al., 2009; Xiong et al., 2009; Jian et al., 2010a). Bennoit et al. (2000) also reported a reduced rate of respiration of *A. bisporus* together with the delay of the browning confirmed by the coloration experiments, mainly after day 4. Besides the browning delaying effect, an irradiation dose of 1.2 kGy significantly delayed (by 6–9 days) the onset of *P.*

nebrodensis fruit body softening and splitting compared with non-irradiated controls (Xiong et al., 2009). With good packing conditions, irradiation improved the skin colour although it produced discoloration of the *A. bisporus* mushrooms flesh (Skou, 1974). Irradiated samples of *A. bisporus* (Lescano, 1994) exhibited a longer retention of whiteness and a marked delay in growth, cap opening, and desiccation, being suitable for marketing up to day 11 and still acceptable for eating on day 16. Longer retention of whiteness and/or colour improvement was also confirmed in irradiated *A. bisporus* (Gill et al., 1969), *I. obliquus* (Kim et al., 2009) and *V. volvacea* (Nayga-Mercado & Alabastro, 1989) samples. Nevertheless, a more severe browning with increasing dosage was observed in *A. bisporus* samples after UV-C irradiation (Guan et al., 2011).

Texture/tissue firmness remained unaffected in γ-irradiated samples of *A. bisporus* (Gill et al., 1969; Lescano, 1994), *A. campestris* (Nairvaiz, 1994) and *H. marmoreus* (Xing et al., 2007). Nonetheless, the same was not observed when higher γ- (Jiang et al., 2010b) or β- (Koorapati et al., 2004) doses were used. Several workers have reported a better retention of texture/higher firmness or delay in postharvest mushrooms softening in electron-beam (Duan et al., 2010), UV-C (Jiang, Jahangir, Jiang, Lu, & Ying, 2010) or γ-radiation (Nayga-Mercado & Alabastro, 1989; Guatam et al., 1998; Xiong et al., 2009) irradiated samples. Only Rivera et al. (2011) had reported a slight texture softening in *T. aestivum* samples after the electron-beam treatment and after one week.

The acidity observed in γ-irradiated *A. campestris* was similar to the one obtained in non-irradiated samples (Narvaiz, 1994).

3.2. Influence in chemical compounds and biochemical parameters

The effects of irradiation on chemical compounds including nutrients (proteins, sugars and vitamins) and non-nutrients (phenolics, flavonoids and flavor compounds), and on

biochemical parameters such as enzymatic activity of PPO (polyphenol oxidase), PAL (phenylalanine ammonia-lyase), CAT (catalase), SOD (superoxide dismutase), APX (ascorbate peroxidase) and GR (glutathione reductase), were described by different authors in several mushroom species and were summarized in **Tables 3**.

Samples of *H. marmoreus* treated with 0.8 kGy (Xing et al., 2007), *L. edodes* treated with 1.0 kGy (Jiang et al., 2010b) and *P. nebrodensis* treated with 1.2 and 1.6 kGy (Xiong et al., 2009) exhibited smaller initial declines in soluble protein content than non-irradiated controls; higher doses showed negative effects (Xing et al., 2007; Jiang et al., 2010b).

Gamma irradiated *H. marmoreus* (Xing et al., 2007) or electron-beam irradiated *A. bisporus* (Duan at al., 2010) with low doses exhibited smaller rates of decrease of reducing sugars during the storage period. Nevertheless, *L. edodes* treated with 1.0 kGy exhibited higher increases in total sugar content (Jiang et al., 2010b), while irradiation of *V. volvacea* at 0.5 and 1.0 kGy did not affect the reducing sugar content (Nayga-Mercado & Alabastro, 1989).

According to Ko et al. (2008), exposure to UV light in the B region offers an effective way of increasing the concentration of vitamin D2 in mushrooms; as the irradiation doses increased, the vitamin D2 concentration also increased in *A. bisporus* and *L. edodes*. Irradiation with UV light in the A region only slightly affected vitamin D2 content. In contrast, irradiation with UV light conducted in the C region increased vitamin D2 up to 9-fold (freeze-dried *C. tubaeformis*) and 14-fold (fresh *A. bisporus*), respectively (Teichemann et al., 2007). The same was concluded by Mau, Chen, & Yang, 1998) for *A. bisporus*, *L. edodes* and *V. volvacea* irradiated with UV-B and UV-C radiation. In fact, remarkably high amounts of vitamin D2 could be obtained by mushrooms UV irradiation; intensity or dose rate (W m^{-2}) of the UV radiation and the

dose of irradiation applied (J m^{-2}), also contributed to the conversion of ergosterol in mushrooms to vitamin D2. Even under normal conditions, 5 g of fresh shiitake mushrooms (*Lentinus edodes*) irradiated for 15 min with UV-A, or UV-B is more than enough to obtain the recommended allowances of vitamin D for adults (10 μg/day) (Jasinghe & Perera, 2006).

Regarding other vitamin, ascorbic acid, the reported results are contradictory. *A. bisporus* treated with UV-C had lower ascorbic acid content compared to non-radiated samples (Guan et al., 2012), while cold-stored *L. edodes* with the same treatment revealed an increase in ascorbic acid contents (Jiang et al., 2010a); gamma irradiated *L. edodes* samples gave similar contents to non-irradiated controls (Jiang et al., 2010b).

Sommer et al. (2009, 2010) evaluated the impact of gamma-irradiation on 5'-nucleotides and free amino acids tyrosine and phenylalanine in fresh *A. bisporus*, reporting that GMP, tyrosine and phenylalanine were not significantly influenced, and a decrease in GDP and AMP levels, the latter only at 5 kGy. Concerning total phenolic content, the same authors reported a non-significant influence, as also described for UV-C treated shiitake mushrooms. Nevertheless, an increase of flavonoids and enhancement of enzymatic activity acting as antioxidants was reported in the latter case (Jiang et al., 2010a). The same species (*Lentinus edodes*) treated with γ-radiation (1.0 kGy) exhibited higher accumulation of phenolics and flavonoids (Jiang et al., 2010b). Lower and similar phenolic levels were registered in *A. bisporus* also submitted to UV-C radiation, after 7 and 14 days of storage, respectively (Guan et al., 2012). Kim et al. (2009) reported that γ-irradiation could be considered a means for improving the antioxidant properties of *Ionotus obliquus* extract, though increase in total phenolic content.

Considering enzymatic activity, most of the studies reported a decrease in polyphenol oxidase (PPO) activity in irradiated samples of different mushroom species, in contrast to an increasing activity in the control along the storage period (Nayga-Mercado & Alabastro, 1989; Gautam et al., 1998; Beaulieu et al., 1999, 2002; Xing et al., 2007; Xiong et al., 2009; Duan et al., 2010). Beaulieu et al. (1999, 2002) reported that *A. bisporus* shelf-life was extended by 4 days with the lower dose rate irradiation, 4.5 kGy/h, and only by 2 days with the higher dose rate, 32 kGy/h. The authors explained the enhancement of the shelf-life at 4.5 kGy/h by the lower PPO activity that led to an increase of phenol concentration and, hence, to a lower rate of melanin formation. The more important browning observed at 32 kGy/h was explained by changes in the membrane permeability (entry of molecular oxygen into the cell cytoplasm) that favored both non-enzymatic and enzymatic oxidation of phenols. Using electron-beam irradiation, Duan et al. (2010) reported, after 10 days of storage, significantly lower PPO activity in samples irradiated with 1-4 kGy doses compared to that in control samples. No significant effects on PPO activity were found in *A. bisporus* samples also submitted to electron-beam irradiation (Koorapati et al., 2004). Superoxide dismutase (SOD) activity generally declined throughout the postharvest storage period in both irradiated and control samples, but no clear correlation between enzyme activity and electron-beam dosage was evident. Catalase (CAT) activity decreased more slowly and to a lesser extent in fruit bodies exposed to 1 kGy compared with that in the controls and the other irradiated samples (Duan et al., 2010). The same tendency for a decrease in SOD and CAT activities was observed in irradiated *P. nebrodensis* (Xiong et al., 2009). Otherwise, Xing et al. (2007) reported levels of SOD significantly higher in *H. marmoreus* samples exposed to 0.8 kGy compared with non-irradiated controls. Large initial increases in CAT activity were detected in samples irradiated with 0.8, 1.2, and

1.6 kGy and, although enzyme levels gradually decreased in all samples during further storage, residual levels after 25 days were still several fold higher in irradiated samples compared with controls. Nevertheless, there is a study reporting an increase in PPO activity until days 7, 9, and 12 for *A. bisporus* samples treated at 0.5, 1, and 2 kGy, respectively. Other workers have reported an increased phenylalanine ammonia-lyase (PAL) activity at the early stage of storage (days 1-4). As PAL is directly linked to the synthesis of phenols, γ-irradiation provoked also a significant increase of total phenols (days 1-3). From days 3-4, to the end of the storage period (day 12), both PAL activity and total phenols in the irradiated samples decreased to lower values (Benoit et al., 2000).

4. Conclusions

Research on fresh mushrooms is still needed to obtain microbiologically safe products, keep its nutritional value and sensory quality. Shelf-life has to be enhanced to allow distribution and marketing. Furthermore, a strong approach in the development of the technology required for processing and distribution of fresh mushrooms will solve some of the limitations that mushroom producers and processors find nowadays to maintain stable quality throughout the storage period. Food irradiation is one of the best and safest food preservation techniques designed to ensure the provision of better quality mushrooms with an extended shelf-life. It can also contribute significantly to community health, as the risk of food borne diseases can be minimized with the proper use of this advanced technology. Food irradiation is now being commonly used in many countries, as people are becoming more aware of the role of food irradiation in regards to food safety and product shelf-life extension. Particularly, the recommended dose for extending the shelf-life of fresh mushroom in different countries is 1-3 kGy.

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References

Ajlouni, S.O., Beelman, R.B., & Thompson, D.B. (1993). Influence of gamma irradiation on quality characteristics, sugar content, and respiration rate of mushrooms during postharvest storage. In Food Flavors, Ingredients and Composition; Charalambous, C., Ed.; Elsevier Publishing Co.: Amsterdam, The Netherlands, 103-121.

Akram, K., & Kwon, J.-H. (2010). Food Irradiation for Mushrooms: A Review. *Journal of Korean Society for Applied Biological Chemistry*, *53*, 257-265.

Beaulieu, M., D'Aprano, G., & Lacroix, M. (1999). Dose rate effect of γ irradiation on phenolic compounds, polyphenol oxidase, and browning of mushrooms (*Agaricus bisporus*). *Journal of Agricultural and Food Chemistry*, *47*, 2537-2543.

Beaulieu, M., D'Aprano, G., & Lacroix, M. (2002). Effect of dose rate of gamma irradiation on biochemical quality and browning of mushrooms *Agaricus bisporus*. *Radiation Physics and Chemistry*, *63*, 311–315.

Benoit, M.A., D'Aprano G., & Lacroix M. (2000). Effect of γ-irradiation on phenylalanine ammonia-lyase activity, total phenolic content, and respiration of

mushrooms (*Agaricus bisporus*). *Journal of Agricultural and Food Chemistry*, *48*, 6312-6316.

Chang, S.-T., & Miles, P.G. (2004). Mushrooms: Cultivation, nutritional value, medicinal effect, and environmental impact, 2nd ed.; CRC Press: Boca Raton.

Cliffe-Byrnes, V., & O'Beirne, D. (2008). Effects of washing treatment on microbial and sensory quality of modified atmosphere (MA) packaged fresh sliced mushroom (*Agaricus bisporus*). *Postharvest Biology and Technology*, *48*, 283–294.

Codex for Food Irradiation. Recommended International Code of Practice for Radiation Processing of Food (CAC/RCP 19-1979, Rev. 2-2003) http://www.codexalimentarius.net.

Directive 1999/3/EC of the European Parlement and of the Council of 22 February 1999 on the establishment of a Community list of foods and food ingredients treated with ionising radiation. http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:31999L0003:EN:NOT.

Doores, S., Kramer, M., & Beelman, R. (1987). Evaluation and bacterial populations associated with fresh mushrooms (*Agaricus bisporus*), in Cultivating Edible Fungi: Developments in Crop Science, ed. by Wuest PJ, Royce DL and Beelman RB. Elsevier, Amsterdam, 283–294.

Duan, Z., Xing, Z., Shao, Y., & Zhao, X. (2010). Effect of electron-beam irradiation on postharvest quality and selected enzyme activities of the white button mushroom, *Agaricus bisporus*. *Journal of Agricultural and Food Chemistry*, *58*, 9617–9621.

Ferreira, I.C.F.R., Barros, L., & Abreu, R.M.V. (2009). Antioxidants in wild mushrooms. *Current Medicinal Chemistry*, *16*, 1543-1560.

Ferreira, I.C.F.R., Vaz, J.A., Vasconcelos, M.H., & Martins, A. (2010). Compounds from wild mushrooms with antitumor potential. *Anti-cancer Agents in Medicinal Chemistry*, *10*, 424-436.

Gautam, S., Sharma, A., & Thomas, P. (1998). Gamma irradiation effects on shelf-life, texture, polyphenol oxidase ans microflora of mushroom *(Agaricus bisporus*). *International Journal of Food Science and Nutrition*, *49*, 5–10.

Gill, W.J., Markakis N., & Markakis, P. (1969). Irradiation of cultured mushrooms. *Food Technology*, *23*, 111–114.

Gould, G.W. (1989). Mechanisms of action of food preservation procedures. Elsevier Applied Science, London, 2, 4, 7, 9.

Grangeia, C., Heleno, S.A., Barros, L., Martins, A., & Ferreira, I.C.F.R. (2011). Effects of trophism on nutritional and nutraceutical potential of wild edible mushrooms. *Food Research International*, *44*, 1029-1035.

Guan, W., Fan, X., & Yan, R. (2012). Effects of UV-C treatment on inactivation of *Escherichia coli* O157:H7, microbial loads, and quality of button mushrooms. *Postharvest Biology and Technology*, *64*, 119-125.

Heleno, S.A., Barros, L., Sousa, M.J., Martins, A., Santos-Buelga, B., & Ferreira, I.C.F.R. (2011). Targeted metabolites analysis in wild Boletus species. *LWT*, *44*, 1343-1348.

International Consultative Group on Food Irradiation (ICGFI). (1999). In Facts about Food Irradiation. Buckinghamshire, United Kingdom.

Jasinghe, V.J., & Perera, C.O. (2006) . Ultraviolet irradiation: The generator of Vitamin D2 in edible mushrooms. *Food Chemistry*, *95*, 638–643.

Jiang, T., Jahangir, M.M., Jiang, Z., Lu, X., & Ying, T. (2010a). Influence of UV-C treatment on antioxidant capacity, antioxidant enzyme activity and texture of

postharvest shiitake (*Lentinus edodes*) mushrooms during storage. *Postharvest Biology and Technology*, *56*, 209-215.

Jiang, T., Luo, S., Chen, Q., Shen, L., & Ying, T. (2010b). Effect of integrated application of gamma irradiation and modified atmosphere packaging on physicochemical and microbiological properties of shiitake mushroom (*Lentinus edodes*). *Food Chemistry*, *122*, 761–767.

Jolivet, S., Arpin, N., Wichers, H.J., & Pellon, G. (1998). *Agaricus bisporus* browning: a review. *Mycological Research*, *102*, 1459–1483.

Kalač, P. (2009). Chemical composition and nutritional value of European species of wild growing mushrooms: A review. *Food Chemistry*, *113*, 9-16.

Kim, J.-H., Sung, N.-Y., Kwon, S.-K., Srinivasan, P., Song, B.-S., Choi, J., Yoon Y., Kim, J.K., Byun, M.-W., Kim M.-R., & Lee J.-W. (2009). γ-Irradiation improves the color and antioxidant properties of chaga mushroom (*Inonotus obliquus*) extract. *Journal of Medicinal Food*, *12*, 1343–1347.

Ko, J.A., Lee, B.H., Lee, J.S., & Park, H.J. (2008). Effect of UV-B exposure on the concentration of vitamin D2 in sliced shiitake mushroom (*Lentinus edodes*) and white button mushroom (*Agaricus bisporus*). *Journal of Agricultural and Food Chemistry*, *56*, 3671–3674.

Koorapati, A., Foley, D., Pilling, R., & Prakash, A. (2004). Electron-beam irradiation preserves the quality of white button mushrooms (*Agaricus bisporus*) slices. *Journal of Food Science*, *6*, 25–29.

Kume, T., Furuta, M., Todoriki, S., Uenoyama, N., & Kobayashi, Y. (2009). Status of food irradiation in the world. *Radiation Physics and Chemistry*, *78*, 222–226.

Lescano, G. (1994). Extension of mushroom (*Agaricus bisporus*) shelf life by gamma irradiation. *Postharvest Biology and Technology*, *4*, 255–60.

Lopez-Briones, G., Varoquaux, P., Chambroy, Y., Bouquant, J., Bureau, G., & Pascat, B. (1992). Storage of common mushroom under controlled atmospheres. *International Journal of Food Science and Technology*, *27*, 493–505.

Masson, Y., Ainsworth, P., Fuller, D., Bozkurt, H., & Ibanoglu, S. (2002). Growth of *Pseudomonas fluorescens* and *Candida sake* in homogenized mushrooms under modified atmosphere. *Journal of Food Engineer*, *54*, 125–131.

Martinez, M.V., & Whitaker, J.R. (1995). The biochemistry and control of enzymatic browning. *Trends in Food Science and Technology*, *6*, 195–200.

Mau, J.L., Chen, P.R., & Yang, J.H. (1998). Ultraviolet irradiation increased vitamin D_2 content in edible mushrooms. *Journal of Agricultural and Food Chemistry*, *46*, 5269–5272.

Minnaar, A., Taylor, J.R.N., & McGill, A.E.J. (1995). Heat-irradiation combination processing as an effective method of producing high quality shelf-stable, low-acid food products. *Food Control*, *6*, 165–170.

Murr, D. P., & Morris, L.L. (1975). Effect of storage temperature on postharvest changes in mushrooms. *Journal of American Society for Horticultural Science*, *100*, 16–19.

Narvaiz, P. (1994). Some Physicochemical measurements on Mushrooms (*Agaricus bisporus*) irradiated to extend shelf-life. *Lebensmittel-Wissenschaft & Technologie*, *27*, 7–10.

Nayga-Mercado, L., & Alabastrof, E.F. (1989). Effects of irradiation on the storage quality of fresh straw mushrooms *Volvariella volvacea. Food Quality and Preference*, *1*, 113–119.

Nussinovitch, A., & Kampf, N. (1993). Shelf life extension and conserved texture of alginate coated mushrooms (*Agaricus bisporus*). *Journal of Food Technology*, *26*, 469–475.

Ouzouni, P.K., Petridis, D., Koller, W.-D., & Riganakos, K.A. (2009). Nutritional value and metal content of wild edible mushrooms collected from West Macedonia and Epirus, Greece. *Food Chemistry*, *115*, 1575–1580.

Pai, T. (2000). Effects of storage environmental conditions on weight loss whiteness change and microbial activity of mushrooms (*Agaricus bisporus*). *Agricultural Chemistry and Biotechnology*, *43*, 161–164.

Poucheret, P., Fons, F., & Rapior, S. (2006). Biological and pharmacological activity of higher fungi: 20-Year retrospective analysis. *Mycologie*, *27*, 311-333.

Rivera, C.S., Blanco, D., Marco, P., Oria, R., & Venturini, M.E. (2011). Effects of electron-beam irradiation on the shelf life, microbial populations and sensory characteristics of summer truffles (*Tuber aestivum*) packaged under modified atmospheres. *Food Microbiology*, *28*, 141-148.

Roy, S., Anantheswaran, R.C., & Beelman, R.B. (1995). Fresh mushroom quality as affected by modified atmosphere packaging. *Journal of Food Science*, *60*, 334–340.

Sapers, G.M., Miller, R.L., Pilizota, V., & Kamp, F. (2001). Shelf-life extension of fresh mushrooms (*Agaricus bisporus*) by application of hydrogen peroxide and browning inhibitors. *Journal of Food Science*, *66*, 362–366.

Schmidt, H.M., Palekar, M.P., Maxim, J.E., & Castillo, A. (2006). Improving the microbiological quality and safety of fresh-cut tomatoes by low dose electron-beam irradiation. *Journal of Food Protection*, *69*, 575–581.

Singh, P., Langowski, H.-C., Wanib, A.A., & Saengerlaub, S. (2010). Recent advances in extending the shelf life of fresh *Agaricus* mushrooms: a review. *Journal of Science and Food Agriculture*, *90*, 1393–1402.

Skou, J.P. (1974). Effects of ionizing irradiation in mushrooms as influenced by physiological and environmental conditions. *Radiation Botany*, *14*, 287-299.

Sommer, I., Schwartz, H., Solar, S., & Sontag, G. (2009). Effect of γ-irradiation on agaritine, γ-glutaminyl-4-hydroxybenzene (GHB), antioxidant capacity, and total phenolic content of mushrooms (*Agaricus bisporus*). *Journal of Agricultural and Food Chemistry, 57*, 5790–5794.

Sommer, I., Schwartz, H., Solar, S., & Sontag, G. (2010). Effect of gamma-irradiation on flavour 50-nucleotides, tyrosine, and phenylalanine in mushrooms (*Agaricus bisporus*). *Food Chemistry*, *123*, 171–174.

Teichmann, A., Dutta, P.C., Staffas, A., & Jägerstad, M.J. (2007). Sterol and vitamin D2 concentrations in cultivated and wild grown mushrooms: Effects of UV irradiation. *LWT*, *40*, 815–822.

USDA—Economic research service. (2009). Mushroom Industry Report 94003. http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1395.

US-FDA. (1991). Irradiation in the production, processing and handling of food. Code Federal Register, Title 21, part 179.

US-FDA. (2002). United States Food and Drug Administration, Ultraviolet radiation for the processing and treatment of food, Code of Federal Regulations, 21 Part 179.39.

Wani, A.M., Hussain, P.H., Meena, R.S., Dar, M.A., & Mir, M.A. (2009). Effect of gamma irradiation and sulphitation treatments on keeping quality of white button mushrooms *Agaricus bisporus* (J. Lge). *International Journal of Food Science and Technology*, *44*, 967–973.

World Health Organization (WHO). (1981). Wholesomeness of irradiated food. Report of a Joint FAO/IAEA/WHO Expert Committee. WHO Technical Report Series 659. Geneva: WHO.

WHO (World Health Organisation). (1994). Safety and nutritional adequacy of irradiated food. WHO, Geneva.

Xing, Z., Wang, Y., Feng, Z., Zhao, Z., & Liu, X. (2007). Effect of ^{60}Co-irradiation on postharvest quality and selected enzyme activities of *Hypsizygus marmoreus* fruit bodies. *Journal of Agricultural and Food Chemistry*, *55*, 8126–8132.

Xiong, Q.-L., Xing, Z.-T., Feng, Z., Tan, Q., & Bian, Y.-B. (2009). Effect of ^{60}Co γ-irradiation on postharvest quality and selected enzyme activities of *Pleurotus nebrodensis*. *LWT*, *42*, 157-161.

Yuk, H.G., Yoo, M.Y., Yoon, J.W., Marshall, D.L., & Oh, D.H. (2007). Effect of combined ozone and organic acid treatment for control of *Escherichia coli* O157:H7 and *Listeria monocytogenes* on enoki mushroom. *Food Control*, *18*, 548–553.

Figure 1. Postharvest changes responsible for the short shelf-life of mushrooms (inner rectangle), and main factors contributing to those changes (ellipses). PPO- polyphenol oxidase, PAL- phenylalanine ammonia-lyase, POD- Peroxidase, SOD- superoxide dismutase, CAT- catalase, APX- ascorbate peroxidase, GR- glutathione reductase.

Figure 2. Reactions involved in mushrooms browning (adapted from Beaulieu et al., 1999). The PPO monophenolase-mediated hydroxylation of GHB (γ-glutaminyl-4-hydroxybenzene) produces γ-L-glutaminyl-3,4-dihydroxybenzene (GDHB); in this reaction, GHB is reported to act both as the substrate and as a cofactor. The PPO diphenolase-mediated oxidation of GDHB produces the corresponding benzoquinone (γ-L-glutaminyl-3,4-benzoquinone, GBQ), and the latter yields melanin by polymerization.

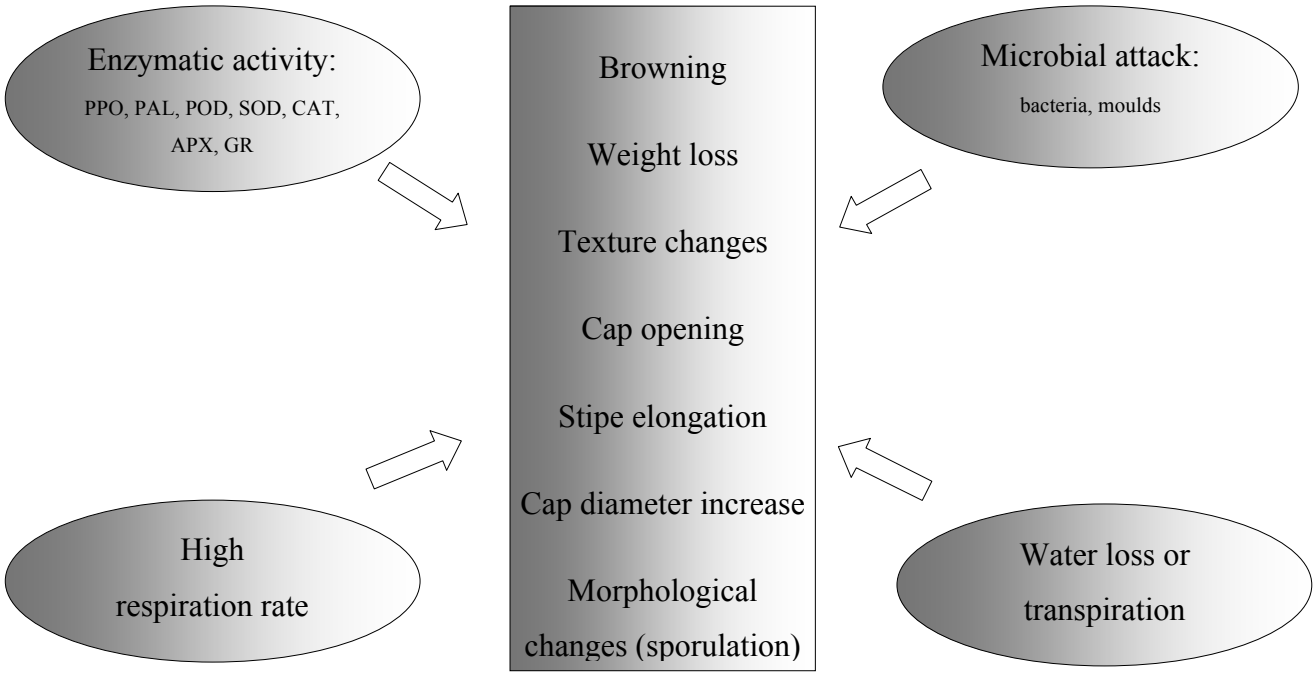
Enzymatic activity:
PPO, PAL, POD, SOD, CAT, APX, GR
Microbial attack:
bacteria, moulds
Browning
Weight loss
Texture changes
Cap opening
Stipe elongation
Cap diameter increase
Morphological changes (sporulation)
High respiration rate
Water loss or transpiration

Figure 1.

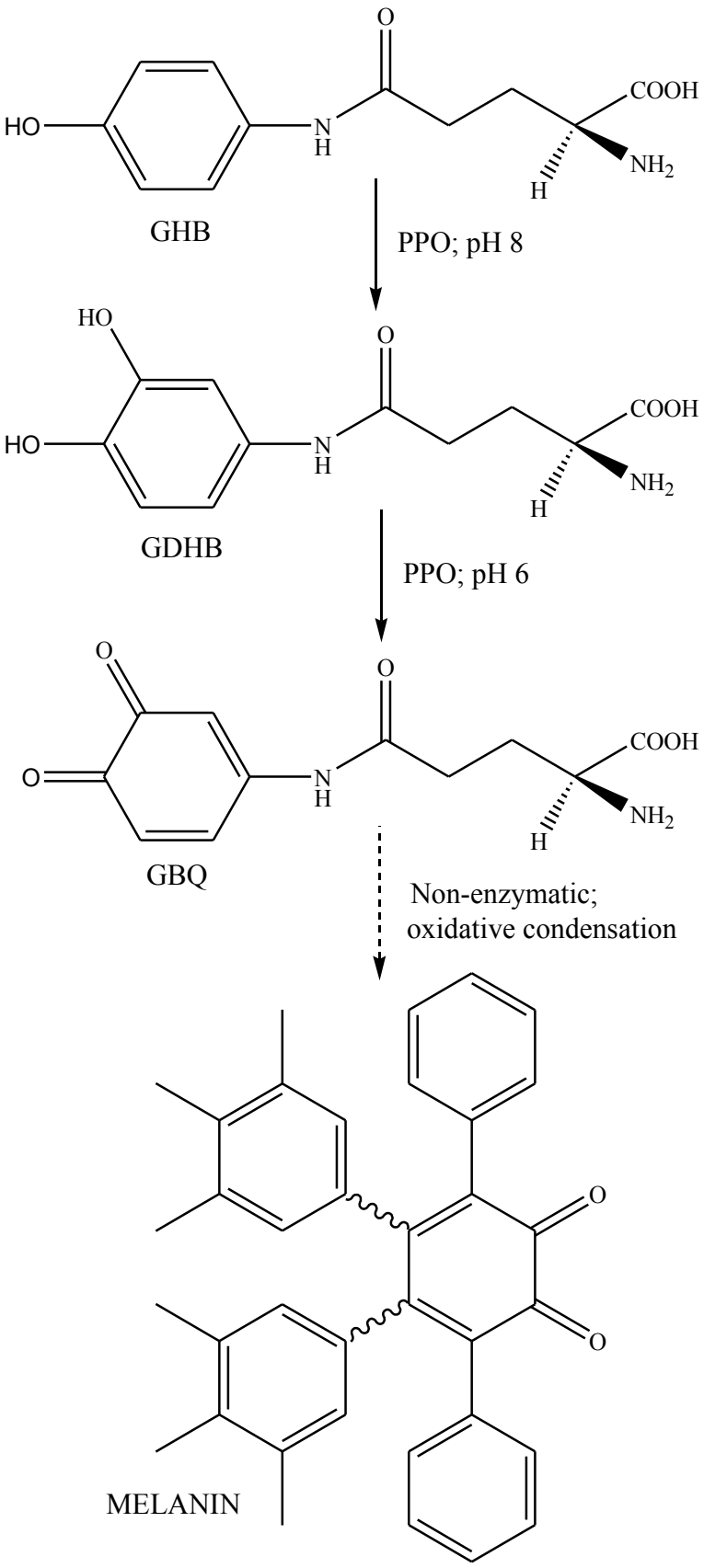
HO
O
N
H
COOH
NH2
H
GHB
PPO; pH 8
HO
HO
GDHB
PPO; pH 6
O
GBQ
Non-enzymatic;
oxidative condensation
MELANIN

Figure 2.

Table 1. Irradiated mushroom species and irradiation conditions.

Species	Origin	Sample	Radiation source	Doses	References
Agaricus bisporus	Argentina	Fresh	γ-radiation	3 kGy	Lescano (1994)
	Canada	Fresh	γ-radiation	2 kGy at 4.5 and 32 kGy/h	Beaulieu et al. (1999, 2002)
	Canada	Fresh	γ-radiation	0.5, 1.5 and 2.5 kGy	Benoit et al. (2000)
	Hungary	Fresh	γ-radiation	1, 3 and 5 kGy; 34 or 35 Gy/min	Sommer et al. (2009, 2010)
	India	Fresh	γ-radiation	0.5, 1, 1.5, 2 and 2.5 kGy at 0.028 kGy/min	Gautan et al. (1998)
	India	Fresh	γ-radiation	0.5 and 2 kGy at 200 Gy/h	Wani et al. (2009)
	USA	Fresh	γ-radiation	0.1 to 2 kGy at 0.05 to 2 kGy/h	Gill et al. (1969)
	Denmark	Fresh	γ and e-beam	10 MeV fast electrons	Skou (1974)
	China	Fresh	e-beam	1, 2, 3 and 4 kGy	Duan et al. (2010)
	USA	Fresh	e-beam	0.5, 1, 3.1 and 5.2 kGy	Koorapati et al. (2004)
	Korea	Fresh	UV-B radiation	10, 20 and 30 kJ/m^2	Ko et al. (2008)
	China	Fresh	UV-C, UV-B radiation	0.5, 1 and 2h	Mau et al. (1998)
	Singapore	Fresh	UV-C, UV-B, UV-A-Radiation	23.0, 35.3 and 25.2 kJ/m^2	Jasinghe and Perera (2006)
	Netherlands	Fresh	UV-C, UV-A radiation	94.7, 189.5 and 379.0 J/cm^2	Teichmann et al. (2007)
	USA	Fresh	UV-C radiation	0.225, 0.45 and 0.90 kJ/m^2	Guan et al. (2012)
Agaricus campestris	Argentina	Fresh	γ radiation	3 kGy	Narvaiz (1994)
Cantharellus tubaeformis	Sweden	Freeze-dried	UV-C, UV-A radiation	94.7, 189.5 and 379.0 J/cm^2	Teichmann et al. (2007)
Hypsizygus marmoreus	China	Fresh	γ-radiation	0.8 kGy at 0.2 kGy/h, 1.2 kGy at 0.3 kGy/h, 1.6 kGy at 0.4 kGy/h, 2.0 kGy at 0.5 kGy/h	Xing et al. (2007)
Inonotus obliquus	Korea	Dried aqueous extract	γ-radiation	3, 5, 7 and 10 kGy at 10 kGy/h	Kim et al. (2009)
Lentinus edodes	China	Fresh/ MAP	γ-radiation	1.0, 1.5 and 2.0 kGy at 2.1 kGy/h	Jiang et al. (2010b)
	China	Fresh	UV-C, UV-B radiation	0.5, 1 and 2h	Mau et al. (1998)
	Singapore	Fresh	UV-C, UV-B, UV-A radiation	23.0, 35.3 and 25.2 kJ/m^2	Jasinghe and Perera (2006)
	Japan	Fresh	UV-B radiation	25, 50 and 75 kJ/m^2	Ko et al. (2008)
	China	Fresh/MAP	UV-C radiation	4 kJ/m^2	Jiang et al. (2010a)
Pleurotus cystidus	Singapore	Fresh	UV-C, UV-B, UV-A radiation	23.0, 35.3 and 25.2 kJ/m^2	Jasinghe and Perera (2006)
Pleurotus nebrodensis	China	Fresh	γ-radiation	0.8 kGy at 0.2 kGy/h, 1.2 kGy at 0.3 kGy/h, 1.6 kGy at 0.4 kGy/h, 2.0 kGy at 0.5 kGy/h	Xiong et al. (2009)
Pleurotus ostreatus	Singapore	Fresh	UV-C, UV-B, UV-A	23.0, 35.3 and 25.2 kJ/m^2	Jasinghe and Perera (2006)

			radiation		
Tuber aestivum	Spain	Air-dried (laminar cabinet)/MAP	e-beam	1.5 and 2.5 kGy at 98 kGy/min	Rivera et al. (2011)
	China	Fresh	UV-C, UV-B radiation	0.5, 1 and 2 h	Mau et al. (1998)
Volvariella volvacea	Philippines	Fresh	γ-radiation	0.5 and 1.0 kGy at 2.57 and 2.60 kGy/h	Nayga-Mercado and Alabastro (1989)

γ-Radiation source is ^{60}Co; e-beam: electron beam; UV: ultra-violet radiation.

Table 2. Irradiation effects on physico-chemical parameters of mushrooms.

Species	Days for analysis	Weight	Colour	Texture	References
Agaricus bisporus	Daily until 18 days[a]	n.a.	Longer retention of whiteness	Firmness similar to non-irradiated samples	Lescano (1994)
	0, 2, 4, 7, 9 and 11[a]	n.a.	Delaying of browning	n.a.	Beaulieu et al. (1999, 2002)
	Daily until 12 days[a]	n.a.	Delaying of browning	n.a.	Benoit et al. (2000)
	Every 2/3 days until 15 days[a]	Marginally decrease in weight losses	Delaying of browning	Better retention of texture, maintaining the firmness during storage	Gautam et al. (1998)
	Every 3 days until 18 days[a]	Decrease in weight losses	Delaying of browning	n.a.	Wani et al. (2009)
	Every 3 days until 12 days[a,b]	Weight losses similar to non-irradiated samples	Changes towards the brownish, improved the skin colour although it produced discoloration	n.a.	Skou (1974)
	7 and 11 days[a]	n.a.	Delaying of browning, longer retention of whiteness	Firmness similar to non-irradiated samples	Gill et al. (1969)
	Every 3 days until 16 days[b]	Weight losses similar to non-irradiated samples	n.a.	Lower softening rate along storage; Higher firmness than non-irradiated samples	Duan et al. (2010)
	n.a.	n.a.	Colour preservation[b]	Firmness similar to non-irradiated samples except for the highest dose	Koorapati et al. (2004)
	1 , 7, 14 and 21 days[c]	n.a.	More severe browning with increasing dosage	n.a.	Guan et al. (2012)
Agaricus campestris	Every 4 days until 16 days[a]	Weight losses similar to non-irradiated samples	n.a.	Firmness similar to non-irradiated samples	Narvaiz (1994)[d]
Hypsizygus marmoreus	Every 3 days until 25 days[a]	Weight losses similar to non-irradiated samples	n.a.	Firmness similar to non-irradiated samples	Xing et al (2007)
Inonotus obliquus	Immediately[a]	n.a.	Increase of lightness	n.a.	Kim et al. (2009)

			and yellowness, decrease of redness with increasing dosage		
Lentinus edodes	Every 4 days until 20 days[a]	Decrease in weight losses	Delaying of browning	Firmness similar to non-irradiated samples; loss of firmness in higher doses	Jiang et al. (2010b)
	Every 3 days until 15 days[c]	n.a.	n.a.	Maintenance of a high level of firmness along storage	Jiang et al. (2010a)
Pleurotus nebrodensis	Every 3 days until 22 days[a]	n.a.	Delaying of browning	Firm texture	Xiong et al. (2009)
Tuber aestivum	Weekly until 42 days[b]	n.a.	n.a.	Slight texture softening after the treatment; similar effects after one week	Rivera et al. (2011)
Volvariella volvacea	Daily until 5 days[a]	Weight losses similar to non-irradiated samples	Improvement of the colour	Improvement of the texture	Nayga-Mercado and Alabastro (1989)

[a]γ-Radiation (^{60}Co); [b]Electron-beam; [c]Ultra-violet (UV) radiation; [d]These authors also evaluated the influence in pH and the results were similar to non-irradiated samples; n.a.- not available.

Table 3. Irradiation effects on chemical compounds, nutrients and non-nutrients, and on biochemical parameters of mushrooms.

Species	Proteins	Sugars	Vitamins	Flavour compounds	Phenolics or flavonoids	Enzymatic activity	References
Agaricus bisporus	n.a	n.a	n.a	n.a	Higher phenolic levels than non-irradiated samples	Decrease of PPO activity	Beaulieu et al. (1999, 2002)
	n.a	n.a	n.a	n.a.	Higher phenolic levels than non-irradiated samples; increasing in days 1-3 and decreasing in days 3-12[a]	Increase of PPO activity; increase of PAL activity in days 1-4 and decrease in days 4-12;	Benoit et al. (2000)
	n.a	n.a	n.a	Decrease in GDP and AMP levels; GMP, tyrosine and phenylalanine not affected	Similar phenolic levels to non-irradiated samples[a]	n.a.	Sommer et al. (2009, 2010)
	n.a.	n.a.	n.a.	n.a.	n.a.	Decrease of PPO activity[a]	Gautam et al. (1998)
	n.a	Smaller decrease along storage than non-irradiated samples[b]	n.a	n.a	n.a	Decrease of PPO activity in 10 days; decrease of SOD activity as in non-irradiated samples; decrease in CAT activity more slowly	Duan et al. (2010)
		n.a	n.a	n.a	n.a	Similar PPO activity[b]	Koorapati et al. (2004)
	n.a	n.a	Increase of vitamin D2[c]	n.a	n.a	n.a	Ko et al. (2008)
	n.a.	n.a.	Increase of	n.a.	n.a.	n.a.	Mau et al. (1998)

			vitamin D2[c]				
	n.a.	n.a.	Increase of vitamin D2[c]	n.a.	n.a.	n.a.	Jasinghe and Perera (2006)
	n.a	n.a	Increase of vitamin D2[c]	n.a	n.a	n.a	Teichmann et al. (2007)
	n.a	n.a	Decrease in ascorbic acid after 7 days; similar values after 14 days[c]	n.a.	Lower phenolic levels after 7 days than non-irradiated samples; similar values after 14 days	n.a.	Guan et al. (2011)
Cantharellus tubaeformis	n.a	n.a	Increase of vitamin D2[c]	n.a	n.a.	n.a	Teichmann et al. (2007)
Hypsizygus marmoreus	Smaller decrease (at the lowest dose) along 13 days storage than non-irradiated samples; similar levels after 25 days (at the lowest dose) and lower in other irradiated samples[a]	Smaller decrease along storage (at the lowest dose) than non-irradiated samples; similar decrease in other irradiated samples	n.a.	n.a.	n.a.	Decrease of PPO activity inversely proportional to dose; increase of SOD activity and CAT activity in irradiated samples	Xing et al. (2007)
Inonotus obliquus	n.a.	n.a.	n.a.	n.a.	Increase of total phenolics[a]	n.a.	Kim et al. (2009)
Lentinus edodes	Smaller decrease along storage than non-irradiated samples[a]	Higher increase along storage than non-irradiated samples	Similar contents of ascorbic acid to non-irradiated samples	n.a.	Increase of phenolic and flavonoid levels	n.a.	Jiang et al. (2010b)
	n.a.	n.a.	Increase of vitamin D2[c]	n.a.	n.a.	n.a.	Ko et al. (2008)
	n.a.	n.a.	Increase of vitamin D2[c]	n.a.	n.a.	n.a.	Jasinghe and Perera (2006)
	n.a.	n.a.	Higher ascorbic acid content[c]	n.a.	Higher flavonoid levels than non-irradiated	Increase of CAT, SOD, APX and GR activity along the storage	Jiang et al. (2010a)

					samples; no effects in phenolics	period	
	n.a.	n.a.	Increase of vitamin D2[c]	n.a.	n.a.	n.a.	Mau et al. (1998)
Pleurotus cystidus	n.a.	n.a.	Increase of vitamin D2[c]	n.a.	n.a.	n.a.	Jasinghe and Perera (2006)
Pleurotus nebrodensis	Smaller decrease along storage than non-irradiated samples[a]	n.a.	n.a.	n.a.	n.a.	Decrease in PPO, SOD and CAT activity	Xiong et al. (2009)
Pleurotus ostreatus	n.a.	n.a.	Increase of vitamin D2[c]	n.a.	n.a.	n.a.	Jasinghe and Perera (2006)
Volvariella volvacea	n.a.	n.a.	Increase of vitamin D2[c]	n.a.	n.a.	n.a.	Mau et al. (1998)
	n.a.	Similar content to non-irradiated samples [a]	n.a.	n.a.	n.a.	Decrease in PPO activity along the storage period	Nayga-Mercado and Alabastro (1989)

[a]γ-Radiation (^{60}Co); [b]Electron-beam; [c]Ultra-violet (UV) radiation; n.a.- not available; GDP- guanosine 5'-diphosphate; AMP- adenosine 5'-monophosphate; GMP- guanosine 5'-monophosphate; PPO- polyphenol oxidase; PAL- phenylalanine ammonia-lyase, SOD- superoxide dismutase, CAT- catalase, APX- ascorbate peroxidase, GR- glutathione reductase.