Antioxidant Properties of Edible Mushrooms

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ABSTRACT

Antioxidants or molecules with radical scavenger capacity gained attention a few years ago because of their potential protective effect against free radical damage. Epidemiological studies have shown that a higher intake of these compounds is associated with lower risk of mortality from cancer and coronary heart disease. Recent scientific studies confirmed that many edible mushrooms, described before in the traditional folklore of Asian culture as medicinal remedies towards a variety of disorders and diseases, indeed contained specific bioactive compounds. These were shown to lower cholesterol levels, to protect against tumours and other disorders, microbes and viruses. Most of these properties were directly or indirectly related to the high antioxidant activity exhibited by specific compounds. The bioactive compounds are not yet well defined in all the species. Their antioxidant activity has been associated with minerals such as selenium and zinc. Also biomolecules such as ergothioneine, polysaccharide-protein complexes (β-1,2-glucans, etc.) phenolic compounds and, in lower quantities, peptides, vitamins A, C, and E (quantification depend on species) have been identified. However, flavonoids and related polyphenols are rare in mushrooms suggesting that these edible fungi might be an interesting source of new bioactive compounds different than plant antioxidants.

Keywords: Agaricus, fungi, Lentinula, Pleurotus

Abbreviations: ABTS, 2,2-azobis-3-ethylbenzthiazoline-6-sulfonic acid or ABTS⁺; DAA, 6-deoxyascorbic acid; t-Dopa, 3,4-dihydroxyphenilalanine; DPPH, 2,2-diphenyl-1-picrylhydrazyl or DPPH⁺; EAA, erythroascorbic acid; ERT, ergothioneine; FRAP, ferric reducing antioxidant power; GDHB, γ-l-glutaminyl-3,4-dihydroxybenzene; GHB, γ-L-glutaminyl-4-hydroxybenzene; GRD, glutathione reductase; GSH-PX, glutathione peroxidase; GST, glutathione S-transferase; HORAC, hydroxyl radical averting capacity; LDL, low-density lipoprotein; NORAC, peroxynitrite radical averting capacity; ORAC, oxygen radical absorbance capacity; SOD, superoxide dismutase; SORAC, superoxide radical averting capacity; TEAC, trolox equivalent antioxidant capacity

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INTRODUCTION

There are approximately 12,000-20,000 species of macrofungi which produce fruiting bodies, most of them belonging to the Basidiomycetes class but there are also a few others from the Ascomycetes class. The life cycle of these fungi is complex and may involve a number of different morphological forms including mycelium and fruiting body stages. These macroscopic fruiting bodies are the so-called ‘mushrooms’ and they showed different degrees of edibility, some are palatable, even delicious and others deadly poisonous (Oot 2000).

Actually, only a few of these mushrooms species can be cultivated since many of them need to form mycorrhizae with pines, oaks and other types of trees. The latter are usually harvested during autumn or spring depending on the
place and species from woods or shadowed locations. The common button mushroom (Agaricus bisporus) is the largest cultivated crop in the Western hemisphere covering more than 80% of the market followed by other species such as Oyster mushroom (Pleurotus spp.), and shiitake (Lentinus edodes). However, Asian countries have a millenarian tradition on mushroom cultivation producing wider range of mushroom crops such as wood ear (Auricularia spp.), enokitake or winter mushroom (Flammulina velutipes), reishi o manakeite (Ganoderma lucidum), maitake (Grifola frondosa), pholiota or nameko (Pholiota nameko), white jelly or silver ear (Tremella fuciformis), straw mushroom (Volvariella spp.), etc.

Mushrooms have been traditionally utilized by medicine men as domestic remedies to cure diseases, improve health, to stimulate sexual reactions, hallucinations even to provoke death and harmful reactions. Scholars believed that the ancient Greek word ‘agari-kon’ originates from a Scythian tribe called Agari who were well versed in the use of medicinal plants and employed a fungus called ‘agarikon’ (probably referring to Fomitopsis officinalis) as if it was the panacea, able to cure almost everything. It was so important to them that it took to them as a totem and named themselves after the fungus (Stamets and Chilton 1983). The name of a fungal class: Agaricales, to which the common button mushroom (Agaricus bisporus) belongs, derive from this word. At the present, numerous reports with a better scientific background have shown that mushrooms contain many bioactive compounds with significant medical properties such as immunomodulatory, anti-cancer, antioxidant, blood pressure-lowering, cholesterol lowering, liver protective, anti-inflammatory, anti-diabetic, antiviral and antimicrobial activities, etc. (Lindequist et al. 2005).

Many plant crops have shown similar bioactivities. They contain compounds such as flavonoids (anthocyanins, isoflavones, etc.) and other polyphenols, glucosinolates, stilbenes, tannins, phytosterols, etc. pointed as the major metabolites responsible for the activities. However, although mushrooms are placed at the same location as vegetables in supermarkets, they belong to the fungal kingdom which is phylogenetically far from plants and they share few biochemical and metabolic similarities. They contain only phenolic compounds but only a few of the potentially active molecules described for plants such as tocophers, carotenoids, ascorbic acid or specific polysaccharides and many others still unidentified. Therefore, mushrooms are a potential source of new bioactive compounds.

**ANTIOXIDANT PROPERTIES**

The most frequently consumed mushrooms (wild and cultivated) have been evaluated utilizing most of the standardized in vitro tests such as TEAC, β-carotene–linoleic acid method, conjugated diene method, scavenging ability on hydroxyl or DPPH radicals, chelating ability against ferrous ions, reducing power, inhibition of lipid oxidation, etc. and they showed intermediate values if compared to fruits and vegetables. For instance, cultivated mushrooms such as portabella and crimini (A. bisporus) contain many bioactive compounds with significant medical properties such as flavonoids (anthocyanins, isoflavones, etc.) and other polyphenols, glucosinolates, stilbenes, tannins, phytosterols, etc. pointed as the major metabolites responsible for the activities. However, although mushrooms are placed at the same location as vegetables in supermarkets, they belong to the fungal kingdom which is phylogenetically far from plants and they share few biochemical and metabolic similarities. They contain only phenolic compounds but only a few of the potentially active molecules described for plants such as tocophers, carotenoids, ascorbic acid or specific polysaccharides and many others still unidentified. Therefore, mushrooms are a potential source of new bioactive compounds.

### Table 1 Edible mushroom species organized according to the scavenging effect of their extracts on 1,1-diphenyl-2-picrylhydrazyl radical and approx. EC_{50} values

<table>
<thead>
<tr>
<th>Type of extract</th>
<th>EC_{50} or EC_{25} (mg/mL)</th>
<th>Order (from higher to lower DPPH scavenging capacity)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ethanol</td>
<td>EC_{50} (1.2 - 5.2)</td>
<td>Agaricus blazei &gt; Agaricus cylindracea &gt; Boletus edulis</td>
</tr>
<tr>
<td>Methanol</td>
<td>EC_{50} (0.01 - 0.02)</td>
<td>BHA &gt; a-tocopherol &gt; Lepista nuda &gt; Russula delica &gt; Polyergus squamosus &gt; Pleurotus ostreatus &gt; Agaricus bisporus &gt; Vitea conica &gt; Boletus badius</td>
</tr>
<tr>
<td>Methanol</td>
<td>EC_{50} (0.2 - 4.5)</td>
<td>Lactopus giganteus = Sarcodon imbricatus &gt; Agaricus arvensis</td>
</tr>
<tr>
<td>Methanol</td>
<td>EC_{50} (&lt;0.25 - &gt;1.5)</td>
<td>B. edulis &gt; Xerocomus chrysenteron &gt; Suillus collinus</td>
</tr>
<tr>
<td>Methanol 80%</td>
<td>EC_{50} (0.4 - &gt;0.8)</td>
<td>A. bisporus &gt; Hypsizigus marmores &gt; Volvariella volvacea &gt; Flammulina velutipes &gt; Pleurotus eryngii &gt; P. ostreatus &gt; Lentinus edodes &gt; H. erinaceus</td>
</tr>
<tr>
<td>Ethanol 75%</td>
<td>EC_{50} (0.31 - 2.42)</td>
<td>A. bisporus &gt; V. volvacea &gt; P. ostreatus &gt; L. edodes &gt; F. velutipes</td>
</tr>
<tr>
<td>Methanol</td>
<td>EC_{50} (2 - 6)</td>
<td>V. volvacea &gt; L. edodes</td>
</tr>
<tr>
<td>Methanol</td>
<td>EC_{50} (4 - 8)</td>
<td>P. ostreatus &gt; L. edodes (1) &gt; P. cystidiosus &gt; F. velutipes (1) &gt; L. edodes (2) &gt; F. velutipes (2)</td>
</tr>
<tr>
<td>Methanol</td>
<td>EC_{50} (0.1 - &gt;3.5)</td>
<td>Auricularia fuscosuccinea (white strain) &gt; Auricularia mesenterica &gt; Auricularia polystichica &gt; Auricularia fuscosuccinea (brown strain) &gt; Tremella fuciformis</td>
</tr>
<tr>
<td>Methanol</td>
<td>EC_{50} (8.52 - 22.9)</td>
<td>Lactarius delicissus &gt; Tricholoma portentosum</td>
</tr>
<tr>
<td>Methanol</td>
<td>EC_{50} (6.95 - 33.7)</td>
<td>Macrolepiota procera &gt; Macrolepiota mantleoida &gt; S. imbricatus &gt; L. delicissus</td>
</tr>
<tr>
<td>Methanol</td>
<td>EC_{50} (1.24 - 14.5)</td>
<td>Termitomyces tynerance &gt; B. edulis &gt; Morchella conica &gt; Russula brevisis &gt; Termitomyces microcarpux &gt; Termitomyces shimperii &gt; Cantharellus clavatus &gt; Lentinus sajor-caju &gt; Pleurotus djamor &gt; Morchella angusticeps &gt; Pleurotus volvaria &gt; Cantharellus cibarius &gt; Auricularia polystichica &gt; Hydnum repandum</td>
</tr>
<tr>
<td>Methanol</td>
<td>EC_{50} (0.4 - 2.5)</td>
<td>P. ostreatus &gt; A. bisporus &gt; M. esculenta &gt; B. edulis &gt; L. edodes &gt; A. cesarea &gt; C. cibarius &gt; L. delicissus</td>
</tr>
<tr>
<td>Water (100°C)</td>
<td>EC_{50} (1.10 - 10.9)</td>
<td>Tricholomopsis rutillan &gt; Suillus bellii &gt; B. edulis &gt; Suillus granulatus &gt; Amanita rubescens &gt; Suillus luteus &gt; Hygrocybus agathosmus &gt; Tricholoma eucrstet &gt; Russula cyanoxanthat</td>
</tr>
<tr>
<td>Water (100°C)</td>
<td>EC_{50} (0.81 - 10.0)</td>
<td>A. blazei &gt; Agrocybe cylindracea &gt; B. edulis</td>
</tr>
<tr>
<td>Water (100°C)</td>
<td>EC_{50} (0.18 - 0.83)</td>
<td>B. edulis &gt; Suillus granulatus &gt; Amanita rubescens &gt; Russula cyanoxanthat</td>
</tr>
<tr>
<td>Water (80°C)</td>
<td>EC_{50} (0.88 - 3.5)</td>
<td>A. bisporus &gt; B. edulis &gt; V. volvacea &gt; P. ostreatus &gt; F. velutipes</td>
</tr>
<tr>
<td>Water (100°C)</td>
<td>EC_{50} (14.8 - 22.9)</td>
<td>P. ostreatus &gt; P. ferulae &gt; C. maxima</td>
</tr>
<tr>
<td>Water (100°C)</td>
<td>EC_{50} (2 - 1.2)</td>
<td>L. edodes &gt; V. volvacea</td>
</tr>
</tbody>
</table>

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different mushroom species. most of the publications were aimed to compare between paring plants, animals or food products with mushrooms, species depending on their evaluated antioxidant properties. It is hard to organize or classify all the analyzed mushroom active percentages for a fixed concentration, etc. Therefore, it is still not completely identified. Many publications correlate the compounds responsible for the described activities are usually calculated by comparison of a few mushroom spe-

<table>
<thead>
<tr>
<th>Common name</th>
<th>Strain</th>
<th>ERT (mg/g dw)</th>
<th>Reference</th>
<th>ERT (mg/kg fw)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>White button</td>
<td>A. bisporus</td>
<td>0.21 - 0.47</td>
<td>Dubost et al. 2006, 2007</td>
<td>0.46</td>
<td>Ey et al. 2007</td>
</tr>
<tr>
<td>Crimini</td>
<td>A. bisporus (brown variety)</td>
<td>0.40 - 0.83</td>
<td>Dubost et al. 2006, 2007</td>
<td>0.93</td>
<td>Ey et al. 2007</td>
</tr>
<tr>
<td>Portabella</td>
<td>A. bisporus (mature brown variety)</td>
<td>0.45 - 0.72</td>
<td>Dubost et al. 2006, 2007</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maitake</td>
<td>G. frondosa</td>
<td>1.13 - 1.84</td>
<td>Dubost et al. 2006, 2007</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oyster</td>
<td>P. ostreatus</td>
<td>2.59 - 2.01</td>
<td>Dubost et al. 2006, 2007</td>
<td>118.91</td>
<td>Ey et al. 2007</td>
</tr>
<tr>
<td>King bolete</td>
<td>B. edulis</td>
<td>-</td>
<td>Dubost et al. 2006, 2007</td>
<td>528.14</td>
<td>Ey et al. 2007</td>
</tr>
<tr>
<td>Chaterelle</td>
<td>C. cibarius</td>
<td>-</td>
<td>Dubost et al. 2006, 2007</td>
<td>0.06</td>
<td>Ey et al. 2007</td>
</tr>
<tr>
<td>P. eryngii</td>
<td>-</td>
<td>1.72</td>
<td>Dubost et al. 2006</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Winter (water extracts)</td>
<td>F. velutipes</td>
<td>3.03 (mg/mL)</td>
<td></td>
<td></td>
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b.d.l.: below detection level ; ERT: ergothioneine

The DPPH (2,2-diphenyl-1-picrylhydrazyl or DPPH) scavenging activity was one of the in vitro tests more frequently utilized to evaluate the antioxidant activity of many mushroom species (Table 1). Results varied from author to author probably because of different environmental conditions, cultivation methodologies, development stage when they were harvested and genetic variation within strains. However, both methanol and water (or hot water) extracts showed antioxidant activities with EC50 values ranging from 0.01 to 34 mg/mL (similar to plants) and most of the commonly consumed mushrooms such as Agaricus bisporus, Pleurotus ostreatus, Boletus edulis and Lentinus edodes were generally highlighted as mushrooms with high antioxidant activities compared to other less common species.

ABTS (2,2-azobis-3-ethylbenzthiazoline-6-sulfonic acid or ABTS+) is another radical often utilized to study the scavenging capacities of water-soluble compounds extracted from mushrooms. But as occurred with DPPH, results differed within the reports and it is hard to point to only one specific mushroom species as the best strain. For instance, A. bisporus showed the best ABTS scavenging capacity in a comparison carried out by Lee et al. (2004) with 5 other species, Pleurotus eryngii was highlighted by Choi et al. (2005) out of 8 other species and B. edulis and Amanita cesaria were the best of other different 8 species (Ramirez-Anguiano et al. 2007). Similarly when the reducing powder was analyzed Termitomyces heimii was identified as the best strain out of 23 species by Puttaraju et al. (2006), but according to the results of Elmastas et al. (2007) the methanoic extracts of Russula delicata and Verpa conica were better than 5 other strains that were not included in the previous comparison. In addition, standard controls were not often included and results were differently expressed. Some authors calculated the antioxidant activities as their EC90 or EC25 values but others preferred to indicate them as effective percentages for a fixed concentration, etc. Therefore, it is hard to organize or classify all the analyzed mushroom species depending on their evaluated antioxidant properties.

**Ergothioneine**

One of the most powerful antioxidants found in some mushroom species is ergothioneine (ERT) and it is present in high amounts (Table 2) compared to other important sources such as liver (10.78–8.71), bean (13.49–4.52), garlic (3.11), egg yolk (0.68), trout (0.07 mg/kg fw), etc. B. edulis showed by far the highest ERT level among many food items, 528.14 mg/kg (Ey et al. 2007).

**Fig. 1** Chemical structure of L-Ergothioneine.

**Table 2** Ergothioneine content in several mushroom species.

<table>
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<tr>
<th>Common name</th>
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**Fig. 1** Chemical structure of L-Ergothioneine.

**ANTIOXIDANT COMPOUNDS IN MUSHROOMS**

The compounds responsible for the described activities are still not completely identified. Many publications correlate the antioxidant activity with the total phenolic content (Mau et al. 2002; Cheung and Cheung 2005) but this does not apply to all species for instance for Auricularia sp. and Tremella fuciformis (Mau et al. 2001). No correlations were found with other compounds such as ascorbic acid, tocopherols, β-carotene, etc. However, these correlations were usually calculated by comparison of a few mushroom spe-

![Fig. 1 Chemical structure of L-Ergothioneine.](image-url)
but lower than quercetin, ellagic acid, etc. Its FRAP values (0.89 mmol Fe (II)/L) were lower than many flavonoids and phenols except for rhamnetin and isorhamnetin (Soobrattee et al. 2005).

This compound can also be easily extracted and concentrated, i.e. extractions from *Flammulina velutipes* fruiting bodies yielded a specific fraction containing 3.03 mg/mL ERT. However, the obtained extract showed higher DPPH scavenging activity and higher capacity to suppress lipid oxidation than authentic ergothioneine added at the same concentration suggesting that other water-soluble compounds might also be involved in the mushroom antioxidant properties (Bao et al. 2008).

**Phenols and organic acids**

Oxalic, citric, malic, quinic and fumaric acids are organic acids almost omnipresent in many mushroom species such as *Suillus bellini*, *Tricholomopsis rutilans*, *Hygrophorus agathosmus*, *Amanita rubescens*, *Russula cyanoxantha*, *Boletus edulis*, *Thricholoma equestre*, *Suillus luteus* and *Suillus granulatus*. Some of them also contained aconitic, ketoglutaric, succinic and shikimic acids. Quantification of the identified compounds indicated that malic and quinic acids were the main compounds in all analyzed species (35-84% of non-aromatic acids), usually followed by citric acid (9-10% of non-aromatic acids). However, no correlation was found between the total amount of organic acids and the antioxidant potential (as DPPH scavenging activities) (Ribeiro et al. 2006).

When the phenolic compounds were studied only *p*-hydroxybenzoic acid was identified in *A. rubescens*, *R. cyanoxantha* and *T. equestre* species. Tannic, gallic, protocatechuic, gentisic, vanillic, syringic, caffeic, coumaric, ferulic and cinnamic acids were detected in the water and methanolic extracts obtained from many species including common mushrooms such as *Boletus edulis*, *Lactarius deliciosus*, *Pleurotus sajor-caju*, *Cantharellus cibarius*, etc. The water extracts from *Termitomyces heimii* showed the highest amount of tannic acid (15.54 mg/g) while *Morchella conica* showed the highest levels of gallic acid (12.85 mg/g), *Helvella crispa* water extracts showed high values of protocatechuic (18.48 mg/g) and gentisic (4.89 mg/g) acids (Puttaraju et al. 2006; Ribeiro et al. 2006). *S. granulatus* and *S. bellini* also showed high levels of phenolic compounds but they could not be identified. They were present in lower concentrations than organic acids and, according to Ribeiro et al. (2006), their total values did not correlate with their antioxidant activity.

*Agaricus bisporus* contained significant amounts of phenolic amino acids (tyrosine, γ-3,4-dihydroxyphenylalanine and γ-L(+)glutaminyl-3,4-dihydroxybenzene (GDHB)) (Soler-Rivas et al. 1998). Cinnamic, *p*-hydroxybenzoic, protocatechuic and caffeic acids were also detected (2.69, 0.51, 0.3, and 0.82 μg/g, respectively) (Mattila et al. 2001) (Fig. 2). They might be involved, perhaps together with ergothioneine, in the relatively high antioxidant activity observed for this strain. However, agaritine (γ-L(+)glutaminyl-4-hydroxymethylphenylhydrazine) was the phenolic compound present in higher concentration (on average 15.1 μmol/g in the skin of *A. bisporus* (Fig. 3) being higher in
9.05 mg/g. Later, Yang et al. (2002) and Elmastas et al. (2003) showed a remarkable reduction in their antioxidant activities if their oxidative enzymes were active while antioxidant levels remained similar if the enzymes were inhibited or separated from the phenolic substrates. Other species such as *Morchella esculenta* did not show any reduction suggesting that the high antioxidant activity found in the latter was due to other compounds which were not substrates of the oxidative enzymes (Ramirez-Anguiano et al. 2007).

### Polysaccharides

At present, fungal polysaccharides are the subject of several studies because their specific carbohydrate composition and structure appears to confer important biological activities as anti-inflammatory and immunomodulator agents. These polysaccharide fractions, usually bound to proteins forming specific complexes, showed antioxidant properties too. However, it is still not clear whether these important biological activities are or not related (Liu et al. 1997).

Polysaccharide extracts from *Ganoderma lucidum*, *Grifola umbellata*, followed by *Tricholoma lobayense*, *Tremella fuciformis* and *Volvariella volvacea* were reported to have scavenging effects on superoxide and hydroxyl radicals while lentinan (from *L. edodes*) and schizophyllan (polysaccharide extracts from *Schizophyllum commune*) had only negligible activity. Superoxide radicals could be quenched rapidly in the presence of PSK, a protein-bound polysaccharide from *Coriolus versicolor*, in a cell-free system consisting of hypoxanthine-xanthine oxidase. The superoxide radical scavenging activity of polysaccharide extracts appeared to depend on the amount of protein (peptide) present as polysaccharide-protein complexes. For example, lentinan and schizophyllan, which contained only a trace amount of protein in the polysaccharide samples, demonstrated almost no scavenging activities. The previously mentioned mushroom polysaccharides were not able to inhibit microsomal lipid peroxidation and on the contrary, lentinan and PSK significantly increased microsomal lipid peroxidation (Liu et al. 1997).

Chitosan, another polysaccharide extract obtained from *L. edodes* stipes showed interesting abilities such as scavenging of hydroxyl radicals and chelating of ferrous ions (Yen et al. 2007).

Besides their in vitro properties, mushroom polysaccharides were able to enhance the in vivo defense systems against oxidative damage. A polysaccharide-peptide complex (F22) extracted from *Pleurotus abalonus* fruiting bodies was able to increase activity and gene expression of antioxidant enzymes and reduced lipid peroxidation in senescence-accelerated mice (Li et al. 2007). Pleuran, another β-1,3-β-glucan extracted from *Pleurotus ostreatus* improved the rats’ antioxidant status (increased superoxide dismutase (SOD), glutathione peroxidase (GSH-PX) activity and glutathione reductase (GRD) activity in liver) and diminished the effect of dimethylhydrazine-induced precancerous lesions in rat colon (Bobek and Galbavy 2001) and a *Lentinus edodes* polysaccharide extract significantly raised activities of serum antioxidant enzymes and decreased levels of serum, mucosal interleukin-2 and tumor necrosis factor alpha in rats with oral ulceration (Yu et al. 2009).

### Ergosterol and derivatives

The major fungal sterol, ergosterol, is abundant in all mushroom species since it is a constitutive compound of the hyphae membranes and it is known as a vitamin D2 (ergocalciferol) precursor. Ergosterol was shown to inhibit phorbol-12-myristate 1-acetate (TPA)-induced inflammatory ear edema in mice and vitamin D2 has been shown to contribute to prevention of prostate and colon cancer. They both showed DPPH scavenging activities; in fact, part of the activity detected in methanol extracts was due to ergosterol-derivatives structures (Soler-Rivas et al. 2010). The peroxide of ergosterol, 5a,8epidioxy-22E-ergosta-6,22-dien-3b-ol (ergosterol peroxide), is also common in mushrooms and it was not only able to inhibit the growth of some cancer cells by inducing apoptosis, or inhibit inflammations and tumour in mice but was also able to decrease...
lipid peroxidation of rat liver microsomes (Kobori et al. 2007).

Ergosterol in *B. edulis* was estimated between 9.61-4.89 mg/g depending on authors, *Chantharellus cibarius* 2.78-3.04, *A. bisporus*, *P. ostreatus* and *L. edodes* 7.8-4.4, *Suillus granulatus* showed 7.02 mg/g ergosterol and 0.8 mg/g fungissterol, other species such as *Russula cyanoxantha* and *Clitocybe nebularis* contained 1.28 and 1.04 mg/g fungissterol, too (Mattila et al. 2002; Teichmann et al. 2007; Kalac 2009).

Ergocalciferol levels from *C. cibarius* and *C. tubaiformis* ranged from 0.84 to 1.94 μg/g dw and these concentrations were rather stable to frying or freezing since, after processing, concentrations of 0.77-0.72 and 1.94 μg/g dw were still detectable (Mattila et al. 1999).

**Vitamin C**

According to a few publications, mushroom genera such as *Auricularia*, *Agaricus* and *Cantharellus* spp. showed moderate-high to low vitamin C contents. *Auricularia fuscospiculnea, A. polytricha* and *A. mesenterica* were the species with a higher level of vitamin C from all the analyzed samples ranging from 1.63 to 11.24 mg/g. Other more common species such as *Volvariella* species, *C. cibarius* and *Craterellus cornucopioides* contained 0.8-1.2 mg/g dw, *Flammulina velutipes*, *L. edodes* and *Calocybe gambosa* contained 0.4-0.6 mg/g followed by some *Pleurotus* (0.36-0.58 mg/g). No ascorbic acid was found in *B. edulis* and in the common button mushroom *Agaricus bisporus* although traces (0.03-0.04 mg/g) were described for other *Agaricales* spp (Mau et al. 2001; Fu and Shihe 2002; Barros et al. 2008a). However, in these works the ascorbic acid was quantified using a colorimetric method with 2,6-dichloroindophenol as reactive agent. This determination might be highly inaccurate depending on the analyzed matrix because many compounds such as tannins, sulphydryl compounds and metals are able to interfere oxidising the dye and leaving the ascorbic acid values overrated (Arya and metals are able to interfere oxidising the dye and leaving the ascorbic acid values overrated (Arya et al. 1998; Raghut et al. 2007).

HPLC determinations showed no ascorbic acid in mushrooms such as *Suillus sp.*, *B. edulis*, *Hygrophorus agathomu*, *Tricholoma equestre*, *Russula cyanoxantha*, etc. (Ribeiro et al. 2006).

However, Okamura (1994, 1998) in more detailed studies using an HPLC system specific for hydrazine-treated derivatives (osazones) detected ascorbic acid but in various forms, i.e. 6-deoxyascorbic acid (DAA), erythroascorbic acid (EAA) and their glycosides. Ascorbic acid compounds were analyzed in several mushroom species and *Pleurotus ostreatus* was found to contain all the previously mentioned forms as well as an unexpected analogue. The absorption spectrum of the analogue indicated it to be a glycoside, suspected from further investigation to be 5-O-(α-D-xylopyranosyl)-EAA. In *Lentinus edodes*, glycosides comprised 97% of total ascorbic acid, although small amounts of EAA and DAA were detected. In *Hypsipilis marmoreus*, *Flammulina velutipes* and *Agaricus bisporus*, single glycosides comprised >80% of total. In *Agrocybe cylindracea* and *Pholiota nameko*, DAA and EAA predominated. *Grifola frondosa* contained 78% DAA glycoside and 20% DAA.

**Tocopherols**

Many mushroom strains showed α-, γ- and δ-tocopherols, α-tocopherol usually being in higher concentrations. Concentrations ranged between 29.54 mg/g α-tocopherol in *Auricularia fuscospiculae* and 2 mg/g in *A. blazei* and *A. cylindracea*. The latter showed high levels of γ- and δ-tocopherols, ranging from 1.6 to 0.7 mg/g (Mau et al. 2001; Tsai et al. 2007). β-Tocopherol were also described by Barros et al. (2008a) in mushroom strains such as *Agaricus* spp., *B. edulis*, *Calocybe gambosa*, *Cantharellus cibarius*, *Craterellus cornucopioides* and *Marasmius oreades* (0.03–8.9 μg/g).

Other authors found total tocopherol concentrations ranging from 0.7 to 0.11 mg/g dw in *Clitocybe maxima*, *Pleurotus ferulaceus* and *P. ostreatus* (addition of α-, γ- and δ-tocopherols and in *L. edodes*, *Pleurotus cystidiosus* and *P. ostreatus* but not in *Flammulina velutipes* (Yang et al. 2002). The tocopherol distribution within the sporophore tissues (Fig. 3) differed since higher γ-tocopherol concentration was found in *C. maxima* caps while δ-tocopherol was the dominant form detected in the stipe (Tsai et al. 2009).

**Carotenoids**

Mushrooms such as *L. giganteus*, *S. imbricatus* and *A. arenris* showed very low β-carotene and lycopene concentrations: 1.88, 2.53 and 2.97 μg/g β-carotene and 0.69, 1.3 and 1 μg/g lycopene, respectively (Barros et al. 2007c) while other strains such as *Agaricus silvicola* (0.32 and 2.63 μg/g, respectively) and *Agaricus silvaticus* (5.42 and 2.63 μg/g, respectively) showed higher β-carotene and lycopene concentrations but the highest values were found in orange-colored mushrooms such as *Chantharellus cibarius* (13.56 and 5.06 μg/g) and *Clitocybe maxima*. The latter showed a higher β-carotene level in the cap (50 μg/g) than in the sporophore stipe (40 μg/g) (Barros et al. 2008a; Tsai et al. 2009).

**Selenium**

Mushrooms are also considered as an excellent source of selenium besides other minerals and vitamins such as copper, potassium, phosphorus, riboflavin (vitamin B2), pantothentic acid (vitamin B5) and nacin (vitamin B3). Selenium plays an important role in antioxidant systems throughout the human body by acting as cofactor of GSH-PX, enhancing α-tocopherol activities and helping the DNA repairing mechanisms. Relatively high selenium content was detected in *Boletus* mushrooms 1.5 mg/kg dw (*B. edulis*, *B. pinicola* and *B. aestivalis*) (Kalac 2009). However, mushrooms with lower Se levels such as *A. bisporus* might be fortified by adding sodium selenite to their cultivation substrate. Selenium might be fortified by adding sodium selenite to their cultivation substrate. Selenium might be fortified by adding sodium selenite to their cultivation substrate. Selenium plays an important role in antioxidant systems throughout the human body by acting as cofactor of GSH-PX, enhancing α-tocopherol activities and helping the DNA repairing mechanisms. Relatively high selenium content was detected in *Boletus* mushrooms 1.5 mg/kg dw (*B. edulis*, *B. pinicola* and *B. aestivalis*) (Kalac 2009). However, mushrooms with lower Se levels such as *A. bisporus* might be fortified by adding sodium selenite to their cultivation substrate. Selenium plays an important role in antioxidant systems throughout the human body by acting as cofactor of GSH-PX, enhancing α-tocopherol activities and helping the DNA repairing mechanisms. Relatively high selenium content was detected in *Boletus* mushrooms 1.5 mg/kg dw (*B. edulis*, *B. pinicola* and *B. aestivalis*) (Kalac 2009). However, mushrooms with lower Se levels such as *A. bisporus* might be fortified by adding sodium selenite to their cultivation substrate.

**Flavonoids?**

According to various authors mushroom species such as *B. edulis*, *Lactarius deterrimus*, *Suillus collimitus*, *Xerocomus chrysenteron*, *Laetiporus sulphurus*, *L. edodes*, *Agaricus spp.*, *L. deliciosus*, *M. mastoidea*, *M. procera*, *Tricholoma matsutake* and *S. imbricatus* showed high levels of flavonoids (Choi et al. 2006; Barros et al. 2007c; Lim et al. 2007; Turkoglu et al. 2007; Barros et al. 2008a; Sarikurkcu et al. 2008). However, flavonoids were quantified in these publications as total flavonoid content using a colorimetric method which utilizes aluminium chloride (AlCl₃) as an agent apparently able to react with flavonoids showing a pink colour measured at 510 nm. This referred assay was used by Jia et al. (1999) to measure the flavonoid content in mulberry and it was, indeed, correlated with the flavonoid content evaluated by HPLC in these berries. However, in forms complexed with hydroxyls and neighbouring ketones and with ortho-dihydroxy groups (Nikolovskaya-Coleska et al. 1995). Therefore, besides flavonoids, AlCl₃ might react with many of the endogenous phenolic compounds from mushrooms with structural similarities. Only one work detected by HPLC the presence of quercetin in a single sample of *S. luteus* (Ribeiro et al. 2006). However, this flavonoid might have been absorbed from closely located plants (perhaps forming mycorrhizae) because the fungal kingdom lacks the key enzymes to undergo the meta-
bolic pathways to synthesize flavonoids from the phenolic compounds generated by the shikimate pathway. According to the USDA, mushrooms are regarded as non-sources of flavonoids (Iwalokun et al. 2007).

**FACTORS INFLUENCING THE MUSHROOM ANTIOXIDANT ACTIVITIES**

As previously mentioned, many factors might influence the antioxidant capacities of edible mushrooms since they are cultivated or harvested from the woods until they are served as elaborated dishes ready to eat. Later on, mushroom antioxidants have to survive human digestion and pass through the intestinal barrier in order to exert their beneficial activities.

**Influence of fruiting bodies development and culture conditions**

A few reports indirectly described the influence of cultivation substrates or environmental conditions on mushroom antioxidants. For instance, mushrooms cultivated in the dark or wild mushrooms receiving day/night light cycles showed different Vitamin D2 contents (Teichmann et al. 2007) being higher in the illuminated fruiting bodies. *A. bisporus*, a mushroom cultivated in the dark, showed Vitamin D2 levels ranging from 0.3-0.6 μg/100g fw while wild mushrooms such as *B. edulis* and *Cantharellus* sp. showed 10.7-58.7 μg/100g fw. Vitamin D2 is synthesized from ergosterol in the presence of light and the latter compound showed 19 fold higher activity as inhibitor of liposomal lipid peroxidation than vitamin D2 (Wiseman 1993) therefore, higher vitamin D2 content resulted in lower antioxidant properties.

Moreover, ethanol extracts from *A. bisporus* fruiting bodies harvested at different maturity stages (Fig. 4) showed effective antioxidant activities determined by the conjugated diene method but, fruiting bodies harvested at stages 1, 4 and 5 were more effective than those at stages 2 and 3. However, their reducing power and scavenging activities were not significantly different between the developmental stages (Tsai et al. 2008). *A. blazei* young and mature fruiting bodies showed similar antioxidant activities except for their chelating ability for ferrous ions, being higher in mature than young fruiting bodies. These differences were not due to their phenolic compounds but probably due to their variation on dicarboxylic acids levels (Soares et al. 2009). In *Lactarius piperatus* mushrooms, the highest antioxidant contents were obtained in the mature stage with immature spores (Barros et al. 2007a).

As previously indicated, some mushroom antioxidants seemed to be differently distributed within the sporophore constitutive tissues (Fig. 3). Methanol extracts obtained from gills showed higher DPPH and ABTS scavenging activities than the caps and stipes of *A. bisporus* fruiting bodies (Savoie et al. 2008) while caps appeared to contain higher reducing power and free radical scavenging capacity than their stipes in mushroom species such as *Lactarius deliciosus*, *Tricholoma portentosum*, *Russula cyanoxantha*, *B. edulis* and *Suillus granulatus* except for *Amanita rubescens*, which showed higher activity in the stipes. Differences seemed to correlate with variations in several constituents; for instance, phenolic compounds, organic acids and alkaloids, which were preferably fixed in the cap except for *B. edulis*, which showed equal alkaloid distribution, and *A. bisporus* stipes, which showed higher phenolic content (Ferreira et al. 2007; Ribeiro et al. 2008; Savoie et al. 2008).

**Influence of industrial and domestic processing**

The high antioxidant activities were usually measured in raw freshly harvested fruiting bodies, but an important part of the mushroom crops (approx. 35% for *A. bisporus*) are often submitted to industrial processes such as freezing, canning or drying to preserve the fruiting bodies during long transportation and storage. These treatments modified their chemical composition which means that their antioxidant properties might also change. However, not many reports describe their precise effect on antioxidant compounds or activities.

Freezing of *B. edulis* fruiting bodies reduced the ascorbic acid content (measured by the 2,6-dichloroindophenol method) from 0.18 to 0.16 mg/g due to the blanching pre-treatment before cold storage. Afterwards, a 47% reduction was observed after 12 months storage at -25°C (Jaworska and Bernas 2009).

Canning of *A. bisporus* fruiting bodies in water, salt and citric acid or drying and re-hydrating Boletus mushrooms did not modify significantly their nutritional value only heating treatments seemed to decrease their level of dietary fibres (β-glucans) and phenolic compounds (Manzi et al. 2001, 2004). Heating was also the most detrimental process for DPPH scavenging activity, reducing power, β-carotene bleaching inhibition and lipid peroxidation inhibition of *L. deliciosus*, *M. mastoidea*, *M. procera* and *S. imbricatus* fruiting bodies when compared with freezing or drying as preservative processes (Barros et al. 2007b).

Both fresh and processed mushrooms are usually submitted to culinary treatments before intake. Raw *A. bisporus* extracts showed higher DPPH and ABTS scavenging activities and higher total phenolic content than pickled mushrooms (prepared using a standardized traditional recipe). Both total phenolic content and antioxidants decreased in mushrooms fried in mustard oil prior to pickling, the decrease followed a strong negative correlation with increasing frying time but no further decrease in either total
phenolic or antioxidants was observed thereafter following pickling and storage of the mushrooms (Ganguli et al. 2006). Results demonstrated frying time to be a critical factor in the current traditional recipe for preparation of mushroom pickles. Other cooking treatments such as boiling or microwaving have been found more detrimental than frying (Soler-Rivas et al. 2009). The effect of different cooking methods was species dependent since A. bisporus water and methanol extractions more resistant to heat treatments than L. edodes and B. edulis indicating the presence of different antioxidant compounds within the selected strains. Microwaving of L. edodes fruiting bodies increased their scavenging capacities during the first cooking minutes but later their EC50 increased. Results suggested that the thermal treatments at the beginning might improve antioxidants’ extractability but later reduce their levels depending on the cooking time. Other reports (Manzi et al. 2004; Barros et al. 2007b) also proved that cooked mushroom showed lower nutrient concentration (including phenols) and lower antioxidiant activity. Only the study by Choi et al. (2006) reported an increase in both phenol concentrations and antioxidant properties of L. edodes mushrooms. However, differences with respect to the first mentioned results could be due to unaccounted losses of moisture and soluble solids that concentrates the sample per unit weight and/or greater extractability depending on heating time or temperature.

**Influence of human digestion and absorption**

Culinary treatments seem to be more detrimental for mushrooms antioxidants than human digestion (Soler-Rivas et al. 2009). Grilled mushrooms were submitted to mastication, gastric and intestinal digestion following an in vitro digestion model and, depending on the mushroom species, mastication and gastric digestion reduced the ABTS and DPPH scavenging activities but later, the intestinal digestion step appeared to increase them to levels similar to grilled mushrooms, probably by liberating or generating new antioxidant compounds. Moreover, 47.6 and 33.4% of A. bisporus and B. edulis antioxidants, respectively were absorbed by Caco-2 monolayers suggesting that the observed antioxidant activity might be partially bioavailable. The scavenging capacity of the L. edodes bioavailable fraction was higher than that initially applied indicating that Caco-2 cells might transform original antioxidants from the digestates into other derivatives with higher antioxidant activity. Phenolic compounds and not proteins or digestion products from polysaccharides seemed to be related with the bioavailable antioxidant activity.

**AGARICUS BISPORUS AND RELATIVES**

The common button mushroom, Agaricus bisporus (J. Lange) Imbach, is the most widely cultivated species of edible mushrooms in the world. However, it has been considered less tasty and nutritive that other wild species and with less bioactive properties than Asian species. However, recent studies indicated that this mushroom is an interesting strain because of the wide amount of biological properties that have been ascribed (Grube et al. 2001; Shi et al. 2002; Savoie et al. 2008).

Concerning the A. bisporus antioxidant activity, the ethanol extracts obtained from this species showed higher scavenging activity of DPPH, ABTS and \( \text{H}_2\text{O}_2 \) radicals than other less bioactive mushrooms from Asia (Spaëlove et al. 2004b). However, A. brasiliensis (Barros et al. 2008b).

Agaricus blazei (also called Agaricus brasiliensis) was also pointed out as an excellent source of ethanol-soluble (Oliveira et al. 2007) and thermotable antioxidants according to the results obtained in a particular system to screen for antioxidant activities. Cytosolic thioredoxin is a negative regulator for the oxidative stress response transcription factor, Yap1p (yeast AP-1-like transcription factor), i.e., this transcription factor is constitutively concentrated in the nucleus in the thioredoxin-deficient mutant (trx1Δ/trx2Δ) due to an impairment of the reactive \( \text{O}_2 \) species-scavenging activity of this mutant. Based on these findings, antioxidant activity was evaluated by monitoring the subcellular localization of Yap1p. As Yap1p is oxidized and accumulates in the nucleus in trx1Δ/trx2Δ cells, antioxidant activity is easily identified by observing the localization of green fluo-
resistant protein (GFP)-tagged Yap1p. If exogenous substan-
ces taken in by trx1A/trx2A cells were able to function as 
antioxidants to reduce the oxidized form of Yap1p, GFP1-
Yap1p would diffuse into the cytoplasm. A. blazei showed 
the highest activity of all the investigated mushroom strains 
(Izawa and Inoue 2004).

**PLEUROTUS GENUS**

Pleurotus spp. or oyster mushrooms are the second com-
mercialized mushroom in the world after A. bisporus, but 
they are more commonly found in Western European super-
markets than in those in North America. Their cultivation 
conditions are less standardized than for the button mush-
room but nowadays mushroom growers manage to obtain 
high yields with more or less controlled environments.

The methanol extracts obtained from Pleurotus ostre-
atus (3 different oyster varieties) showed the highest 
scavenging activities compared to others such as the white 
and yellow varieties of Flammulina velutipes, two Lentimus edo-
des strains and Pleurotus cystidiosus. These three oyster 
mushrooms showed a 54.3% scavenging of hydroxyl-free 
radicals while the other samples ranged from 29.2 to 36.6% 
at 40 mg/mL. However, all mushroom extracts demon-
strated moderate to high antioxidant activity in the TBARS 
assay, with percentages of lipid peroxidation of 24.7-62.3 
(at extract concentration 1.2 mg/mL), in comparison with a 
value of 66.1% with 10 mg/mL BHA. HPLC analysis re-
vealed that the major antioxidant compounds in the mush-
rooms were phenols. According to the authors (Yang et al. 
2002), ascorbic acid and β-carotene were not detected and 
tocopherols were only present in small amounts. The three 
oyster mushrooms also contained higher phenol content 
than the other samples.

In *in vivo* experiments demonstrated that *P. ostreatus* ex-
tracts were effective agents to reduce the incidence and size 
of atherosclerotic plaques in rabbits (Lindequist et al. 2005) 
since the mushrooms extracts showed ability to inhibit lipid 
peroxidation and a pronounced hypocholesteremic effect 
because of the production of lovastatine, a powerful HMG-
Co A reductase inhibitor (Bobek and Galbavy 1999). Both 
reactive oxygen species and increased levels of blood lipids 
are key elements in the pathogenesis of atherosclerosis. 
Moreover, other authors showed that the administration of *P.
osteatus* extracts to aged rats improved their antioxidant 
status during ageing and alleviated the hepatotoxicity in-
duced by CCL4 (Jayakumar et al. 2006, 2007).

Pleurotus citrinopileatus, a popular edible mushroom 
from Taiwan, also showed important physiological activi-
ties in both humans and animals. An *in vivo* study using 
hyperlipidaemic hamster rats indicated that powdered dry 
fruitsing body, hot-water extract and 2 specific extracts sig-
nificantly reduced serum triglycerides and total cholesterol 
levels as compared with control groups that received no 
mushroom additive. High-density lipoprotein levels in these 
experimental groups were also significantly higher than 
those in the negative control group. The rats that were fed 
with the extra had higher serum GSH-PX, and SOD activi-
ties. The extracts showed *in vitro* DPPH free radical sca-
venging activities and ferric-reducing abilities and their 
major constituents were identified as ergosterol and nico-
tinic acid. Results suggested that *P. citrinopileatus* extracts 
might have *in vivo* antihyperlipidemic and antioxidant activi-
ties (Hu et al. 2006).

Pleurotus eryngii was another mushroom with antioxid-
ant activities similar to Ganoderma lucidum, a mushroom 
considered as medicinal because of its many biological 
activities tested *in vivo* (even with humans trials), including 
the antioxidant activities. Their ethanol extracts (compared 
with 8 edible mushrooms grown in Korea) showed the high-
est DPPH and ABTS scavenging activities. Authors found 
positive correlations between total phenols contents and 
these antioxidant activities (Choi et al. 2005).

The methanolic extract of *Pleurotus pulmonarius* fruit-

ing bodies reduced carrageenan-induced and formalin-

induced paw edema in mice. The activity was comparable 
to the reference diclofenac. The effect seemed to be related 
to the significant antioxidant activity of the extract since the 
EC50 value for hydroxyl-radical scavenging was 476 μg/mL 
and for lipid peroxidation inhibition 960 μg/mL (Lindequist 
et al. 2005).

**Pleurotus florida** extracts (water, methanol and ethyl 
acetate) showed hydroxyl radical scavenging activity and 
inhibition of lipid peroxidation and the methanol extracts 
also showed inhibition of tumor growth, still the mechanism 
of action is unknown but it seemed to be related to the pro-
tective effect of the extracts against DNA oxidation (Jose 
and Janardhanan 2000).

**OTHER CULTIVATED MUSHROOMS CROPS**

*L. edodes* is another cultivated mushroom which contains 
several therapeutic compounds with many biological activi-
ties including antioxidant properties (Ooi 2000). This mush-
room and *Volvariella volvacea* were tested using methods to 
study their potential effect against lipid peroxidation of rat 
brain homogenate and against the oxidation of human low-
density lipoprotein (LDL). Results indicated that both or-

ganic and aqueous extracts from those mushrooms showed 
high antioxidant activities with EC50 values of 0.11 and 1.05 
mg/mL against lipid peroxidation (Cheung and Cheung 
2005). Both mushrooms showed also the ability to inhibit 
haemolysis of rat erythrocyte induced by peroxyl radicals 
(Cheung et al. 2003). Because of these interesting proper-
ties Kitzberger et al. (2007) developed a method to pro-
duced food-grade *L. edodes* extracts using green technolo-
gies such as supercritical fluid extraction (SFE) to obtain 
antioxidant enriched fractions that could be used to prepare, 
for instance, functional foods with improved antioxidant 
properties.

As described for *L. edodes* and *V. volvacea*, the metha-

nol extracts of Agrocybe aegerita showed high radical sca-
venging activities and inhibition of lipid peroxidation of rat 
brain homogenate, too. A sub-fractionation of the extract 
revealed that ethyl acetate fraction showed the most potent 
antioxidant activity and was further fractionated by Sepha-
dex LH-20 column into 4 fractions. The third fraction 
showed very high radical scavenging activities and showed 
a similar extent of *in vitro* inhibition of human LDL oxi-
dation to caffeic acid. Significant correlation was found 
between the total phenolic content and the activities (Lo 
and Cheung 2005).

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