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# A review of chemical composition and nutritional value of wild-growing and cultivated mushrooms

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## Abstract

**Fruit bodies of about 200 mushroom species are consumed throughout the world, preferably as a delicacy. Knowledge of their chemical composition, nutritional value and health-promoting effects has expanded dynamically during the last few years. Dry matter (DM) is low: commonly about 100 g kg$^{-1}$. The usual contents of protein, lipids and ash are 200–250, 20–30 and 80–120 g kg$^{-1}$ DM, respectively. Various carbohydrates form the remaining DM. Nevertheless, great variations occur both among and within species. Energy is low, usually 350–400 kcal kg$^{-1}$ of fresh fruit bodies. The nutritional contribution of mushroom protein derived from earlier data seems to be overestimated. Fat content is low with markedly prevailing in linoleic acid and oleic acid, while the proportion of n-3 fatty acids is nutritionally marginal. The main carbohydrates are chitin, glycogen, trehalose and mannitol. Information on fibre content and composition is limited. Health-promoting $\beta$-glucans are an auspicious group of polysaccharides. High potassium content is characteristic of mushrooms. Several species can accumulate very high levels of both detrimental trace elements, particularly cadmium and mercury, and radiocaesium isotopes if growing on heavily polluted substrates. Mushrooms seem to be a considerable source of ergosterol, provitamin $D_2$, and phenolids with antioxidative properties. Hundreds of flavour constituents have been identified, particularly with eight-carbon aliphatic chains. Data on changes of mushroom components under various preservation conditions and culinary treatments have been fragmentary. Even more limited is knowledge of nutrient bioavailability.**



**Keywords:** edible mushrooms; nutritional value; proximate composition; proteins; lipids; carbohydrates; minerals; vitamins; sensory constituents

## INTRODUCTION

Fresh and preserved mushrooms are consumed in many countries as a delicacy, particularly for their specific aroma and texture. According to FAOSTAT data, total world production of mushrooms including truffles was nearly 6 million metric tons in 2010. China was by far the leading producer. Among over 20 cultivated species, *Agaricus bisporus* (button mushroom, white mushroom, brown mushroom or portobello) dominates worldwide, followed by *Lentinula edodes* (often called by its Japanese name of shiitake), *Pleurotus* spp. (particularly *P. ostreatus*, oyster mushroom, hiratake) and *Flammulina velutipes* (golden needle mushroom, enokitake).

Wild-growing mushroom consumption has been preferred to cultivated species in many countries of central and Eastern Europe. Mushroom picking in forests and grasslands as a lasting part of cultural heritage has recently become a highly valued recreational activity in these countries. Most collected mushrooms are used for pickers' own consumption; however, collection has been an economic activity for a part of the rural population. About 200 edible species have been collected in various parts of the world.

Knowledge of the composition and nutritional value of culinary mushrooms, particularly of wild-growing ones, was limited until the last decade as compared with vegetables and medicinal mushroom species. This is understandable, because culinary mushrooms have been perceived only as a delicacy and their consumption in many developed countries has been marginal and thus of little interest to researchers. Nevertheless, the situation has started to change noticeably; the yearly number of original papers is now several times higher than 10–15 years ago.

A synoptic knowledge of the composition and nutritional value of the most important cultivated mushroom species[1] and European wild-growing edible species is available.[2,3] Thus overall information from these reviews, supplemented by the most recent data, will be given in the following sections. Only the weightiest articles up until 2009 will be cited. Numerous further papers from the previous period are referred in the above reviews.

Medicinal mushrooms, mostly originating and used in east Asia, have been studied very extensively. The topic is beyond the scope of this review. Nevertheless, some results on the composition of some of them, often called culinary–medicinal mushrooms, will be referred to.

## MYCOLOGICAL TERMS

The term *mushroom* will be used for a consumable fruit body, mostly above ground, of higher fungi. A fruit body is formed

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from spacious mycelium, mostly underground, as a result of the fructification process. The lifetime of the bulk of fruit bodies is only 10–14 days.

Mushroom species can be divided into three categories according to their nutritional strategy. Mycorrhizal or symbiotic species form a close, mutually favourable relationship with their host vascular plant, usually a tree. Saprotrophic species or saprophytes derive their nutrients from dead organic material. Some of these species are the basis for cultivated mushroom production, while mycorrhizal species have not yet been successfully cultivated. The third group of parasitic species lives on other species in a non-symbiotic relationship.

## CHEMICAL COMPOSITION AND NUTRITIONAL VALUE

### Dry matter, proximate composition, energy value and bioavailability of nutrients

Dry matter (DM) of both wild-growing and cultivated mushrooms is very low, commonly ranging between 80 and 140 g kg$^{-1}$. A value of 100 g kg$^{-1}$ is used for calculations if actual DM content is unknown. High water content and activity are important factors participating in the short shelf life of fruit bodies. Dried mushrooms are known for their hygroscopicity.

Normal medians of crude protein, lipid and ash content of numerous wild-growing species were 250, 30 and 80 g kg$^{-1}$ DM, respectively, using earlier data.[2,3] Various carbohydrates form the rest of the proximate composition. Their proportion in dry matter is calculated as [100 − (crude protein + lipids + ash)]. Nevertheless, considerable differences in composition are evident not only among species but also within a species among data of various laboratories. The differences can be partly the result of the different stages of fruit body development. Total energy is calculated in original papers using the equation: kcal = 4 × (g protein + g carbohydrates) + 9 × (g lipids). Energy was low: about 360 kcal kg$^{-1}$ fresh mushrooms.[2,3] Additional recent data are collated in Table 1. Median values are 202, 19, 129 and 638 g kg$^{-1}$ DM for crude protein, lipid, ash and saccharide content, respectively, and 397 kcal kg$^{-1}$ fresh matter (FM).

Recent data on proximate composition and energy value of cultivated species are given in Table 2. Median values are 208, 22, 70 and 682 mg kg$^{-1}$ DM for crude protein, lipid, ash and carbohydrate content, respectively, and 419 kcal kg$^{-1}$ FM. Ash content is the steadiest value. The differences within a species seem to be even higher than in wild-growing species. The factor of cultivation substrate used is of significance, as was proved for *Pleurotus eryngii*.[15] Available information on expanding cultivated *Agaricus brasiliensis* (syn. *A. blazei* or *A. subrufescens*, sun mushroom) was reviewed by Largeteau *et al*.[16] Its proximate composition is comparable with species given in Tables 1 and 2. General information on chemical composition is also available for truffles as a specific group of highly evaluated mushrooms.[17]

Like results from the comparison of data for wild and cultivated mushrooms, the differences both among and within species seem to be more important than the effect of provenance. Low DM and lipid contents result in a low energy value of around 350 kcal kg$^{-1}$ FM. Mushrooms are thus a low-energy delicacy. Moreover, some carbohydrates are only partially digestible or indigestible (e.g. mannitol and chitin) and calculated energy value is thus somewhat overestimated.

Nevertheless, information on digestibility and bioavailability of nutrients from mushrooms has been very scarce. A high proportion of indigestible polysaccharide chitin apparently limits availability of other components. Moreover, most data are given for fresh mushrooms, while information on the changes of nutrients under various storage and cooking conditions remains very limited.

In spite of rapidly growing quantitative compositional data, it is not yet possible to draw generalized conclusions on the relations between chemical composition of mushrooms and their nutritional value and health effects.

### Proteins and amino acids

The informative data on crude protein in the previous section are comparable with mean contents of 228 and 249 g kg$^{-1}$ DM reported by Bauer Petrovska[18] and Uzun *et al*.[19] for 47 and 30 species, respectively.

Some papers reported crude protein contents determined by the Kjeldahl method using the usual conversion factor of 6.25. However, such values were overestimated due to a high proportion on non-protein nitrogen, particularly in chitin. A factor of 4.38 has been mostly used in recent publications. The data presented in this review were recalculated where necessary using the latter factor.

A unique paper[18] reported mean proportions of 248, 115, 74, 115, 57, 53 and 338 g kg$^{-1}$ total protein for albumins, globulins, glutelin-like material, glutelins, prolamine-like material and residues, respectively, in 24 mushroom species.

Limited data on amino acid composition of mushroom protein[2] suggest a higher nutritional value than in most plant proteins. Findings were bolstered by the results of Ayaz *et al*.[20] in 11 wild species. Ranges of 93.6–230 and 39.7–86.8 g kg$^{-1}$ DM were reported for total amino acid and essential amino acid contents, respectively. Methionine was the very limiting amino acid. Glutamic acid was widely present, with a maximum of 37.6 g kg$^{-1}$ DM in *Leucopaxillus giganteus* and a minimum of 10.9 g kg$^{-1}$ DM in *Cantharellus tubaeformis*.

Data on changes of protein and amino acid composition during mushroom preservation and cooking have been scarce. Protein content remained almost stable during air-drying of mushrooms at 40 °C, while boiling of fresh mushrooms caused a significant decrease.[21] The contents of arginine, glycine, serine, methionine and threonine decreased in canned *P. ostreatus*, while 12-month freeze-storage resulted in significant decreases of alanine, glutamine, cysteine and tyrosine.[14] Values of chemical score index were generally lower in frozen than in canned *P. ostreatus*, *A. bisporus* and *Boletus edulis*. The only observed limiting amino acids were leucine in frozen, and leucine and lysine in canned *B. edulis*.[22]

The reported contents of total free amino acids in wild species vary widely between 1.5 and 72 g kg$^{-1}$ DM.[3] The respective content for five common cultivated species is 121 g kg$^{-1}$ DM with prevailing glutamic acid, ornithine and alanine.[23] Nutritional contribution seems to be limited, but some of free amino acids participate in the taste of mushrooms.

Relatively high protein content and low dry matter are predispositions for short shelf life of mushrooms. Biogenic amines rank among products of protein decomposition. Putrescine was the amine occurring at the highest level, sometimes exceeding 150 mg kg$^{-1}$ FM, followed by phenylethylamine, in 17 freshly harvested wild species. The contents of histamine and tyramine, toxicologically the most detrimental amines, were negligible.[24]

Wild mushrooms were formerly called 'meat of poverty' in central Europe. Nevertheless, the usually low protein content of about 2.0–2.5 g 100 g$^{-1}$ FM, limited knowledge of essential amino acid proportion and lack of information on digestibility and

**Table 1.** Recent data on dry matter (g kg$^{-1}$), proximate composition (g kg$^{-1}$ DM) and energy (kcal kg$^{-1}$ FM) in some wild-growing mushrooms

| Species | Dry matter | Crude protein | Lipids | Ash | Carbohydrates | Energy | Ref. |
|---|---|---|---|---|---|---|---|
| *Agaricus campestris* | 118.3 | 185.7 | 1.1 | 231.6 | 581.6 | 364 | 4 |
| *Armillaria mellea* | 117.3 | 163.8 | 55.6 | 67.8 | 712.8 | 470 | 5 |
| | — | 172.5 | 65.6 | 123.4 | 638.5 | — | 6 |
| *Boletus aereus* | 83.5 | 178.6 | 4.4 | 88.7 | 728.3 | 306 | 7 |
| *B. armeniacus* | 285.0 | 182.5 | 15.6 | 120.9 | 681.0 | 1053 | 4 |
| *B. edulis* | 108.5 | 210.7 | 24.5 | 55.3 | 709.5 | 423 | 7 |
| *B. erythropus* | 116.4 | 209.2 | 7.5 | 259.0 | 524.3 | 349 | 8 |
| *B. reticulatus* | 89.0 | 225.7 | 25.5 | 197.2 | 551.6 | 297 | 7 |
| | — | 279.0 | 31.4 | 166.2 | 523.4 | — | 6 |
| *Calocybe gambosa* | 90.8 | 154.6 | 8.3 | 138.9 | 698.2 | 317 | 5 |
| *Calvatia utriformis* | 220.0 | 203.7 | 19.0 | 178.1 | 599.2 | 744 | 8 |
| *Cantharellus cibarius* | — | 357.9 | 14.7 | 64.2 | 563.2 | — | 6 |
| *Clitocybe odora* | 115.1 | 173.3 | 24.6 | 95.5 | 706.6 | 431 | 5 |
| *Coprinus comatus* | 148.1 | 156.7 | 11.3 | 128.5 | 703.5 | 525 | 5 |
| | — | 294.7 | 54.2 | 158.8 | 492.3 | — | 6 |
| *Fistulina hepatica* | 83.3 | 500.9 | 18.9 | 164.0 | 316.2 | 286 | 9 |
| *Flammulina velutipes* | 93.2 | 178.9 | 18.4 | 94.2 | 708.5 | 346 | 4 |
| *Laccaria laccata* | 117.5 | 627.8 | 37.6 | 206.9 | 127.7 | 345 | 9 |
| *Lactarius deliciosus* | — | 202.0 | 80.2 | 71.5 | 646.3 | — | 6 |
| *L. salmonicolor* | 122.8 | 372.8 | 20.3 | 232.8 | 374.1 | 389 | 9 |
| | — | 135.3 | 10.9 | 61.6 | 792.2 | — | 6 |
| *Lycoperdon echinatum* | 147.6 | 235.2 | 12.2 | 94.3 | 658.3 | 544 | 8 |
| *Pleurotus ostreatus* | — | 132.3 | 35.8 | 80.8 | 751.1 | — | 6 |
| *Russula cyanoxantha* | 155.6 | 168.0 | 15.2 | 70.3 | 746.5 | 590 | 8 |
| *R. delica* | 133.1 | 505.9 | 9.1 | 229.3 | 255.7 | 416 | 9 |
| *R. olivacea* | 154.2 | 168.4 | 19.9 | 377.8 | 433.9 | 399 | 8 |
| *Suillus mediterraneensis* | 88.0 | 243.2 | 26.1 | 276.4 | 454.3 | 266 | 9 |
| *S. variegatus* | 92.3 | 175.7 | 33.1 | 153.6 | 637.6 | 328 | 4 |
| *Tricholoma imbricatum* | 175.8 | 504.5 | 18.8 | 64.5 | 412.2 | 674 | 9 |

availability are factors challenging the widely used characteristic of mushrooms as a source of valuable protein.

Moreover, mushrooms contain various proteins with interesting biological and particularly medicinal activities, e.g. lectins. The topic was recently reviewed.[25]

## Lipids

Contents of total lipids (crude fat) are low, ranging mostly between 20 and 30 g kg$^{-1}$ DM. Levels above 60 g kg$^{-1}$ DM are scarce (Tables 1 and 2 and previously reviewed data[2,3]).

Tens of fatty acids have been identified in mushroom lipids. However, only linoleic acid (C18:2c,n-6) and oleic acid (C18:1c,n-9) markedly prevail, forming a proportion of two-thirds and more of the weight of all identified fatty acids. Saturated palmitic acid (C16:0) is third in order, but at a great distance. Previously collated data[2,3] were proved by further recent data for numerous wild species.[4,5,7–9,20,26] Surprisingly, a low proportion of oleic acid was determined in wild *A. bisporus, A. bitorquis* and *A. essettei*.[27] A similar situation occurred in cultivated *A. bisporus*, *L. edodes* and *F. velutipes*, while comparable levels within wild species have been found in *P. ostreatus* and *P. eryngii*.[1]

Nutritionally undesirable elaidic acid, being a *trans* isomer of oleic acid, was reported at very low levels. The contents of odd-, branched-chain and hydroxy fatty acids are negligible.

Testing *A. bisporus*, fatty acids were found to be the most important group of metabolites for predicting mechanical damage of mushrooms. The ratio between linolenic acid and pentadecanoic acid seems to be a useful chemometric tool.[28]

Lipids of *Macrolepiota procera* and *Collybia platyphylla* provoked an increase in erythrocyte membrane fluidity, a property beneficial for hypertension treatment.[29]

The nutritional contribution of mushroom lipids is limited due to low total lipid content and a low proportion of desirable n-3 fatty acids. Nevertheless, linoleic acid is a precursor of the attractive smell of dried mushrooms.

## Carbohydrates and fibre

Carbohydrates constitute about one-half of mushroom DM. The group comprises various compounds: sugars (monosaccharides, their derivatives and oligosaccharides) and both reserve and construction polysaccharides (glycans).

Mannitol and trehalose (Tables 3 and 4) are the main representatives of alcoholic sugars and oligosaccharides, respectively. Median values are 28.9 and 39.2 g kg$^{-1}$ DM for mannitol and trehalose, respectively, in Table 3. The contents vary widely both among species and probably within individual species. The data are comparable with previously collated reports.[2,3] Nevertheless, the data of Reis *et al*.[1] for mannitol and trehalose in some cultivated species (Table 4) are extraordinarily high. Mannitol participates in volume growth and firmness of fruiting bodies. Its digestibility for humans is low. Drying and freezing decreased the contents of mannitol and trehalose to a lower extent than boiling of four mushroom species.[21] Other sugars occur at a low level in



  

**Table 2.** Recent data on dry matter (g kg$^{-1}$), proximate composition (g kg$^{-1}$ DM) and energy (kcal kg$^{-1}$ FM) in some cultivated mushrooms

| Species | Dry matter | Crude protein | Lipids | Ash | Carbohydrates | Energy | Ref. |
|---|---|---|---|---|---|---|---|
| *Agaricus bisporus* | | | | | | | |
| White | 87.3 | 140.8 | 21.8 | 97.4 | 740.0 | 325 | 1 |
| Brown | 83.6 | 154.3 | 16.7 | 113.6 | 715.4 | 303 | 1 |
| Unspecified | — | 264.9 | 25.3 | 87.8 | 622.0 | — | 10 |
| Unspecified | 97.0 | 363.0 | 8.0 | 120.0 | 509.0 | — | 11 |
| *Agaricus brasiliensis* | — | 267.4 | 26.2 | 68.1 | 638.3 | — | 12 |
| *Flammulina velutipes* | 121.3 | 38.7 | 28.9 | 72.5 | 859.9 | 467 | 1 |
| | — | 266.5 | 92.3 | 75.1 | 566.1 | — | 10 |
| *Hypsizigus marmoreus* | | | | | | | |
| Normal strain | — | 196.0 | 40.9 | 77.5 | 685.6 | — | 13 |
| White strain | — | 210.6 | 56.2 | 82.6 | 650.6 | — | 13 |
| *Lentinula edodes* | 202.2 | 44.0 | 17.3 | 67.3 | 871.4 | 772 | 1 |
| | — | 204.6 | 63.4 | 52.7 | 679.3 | — | 10 |
| *Pleurotus ostreatus* | 108.3 | 70.2 | 14.0 | 57.2 | 858.6 | 416 | 1 |
| | — | 238.5 | 21.6 | 75.9 | 664.0 | — | 10 |
| | 100.0 | 416.0 | 5.0 | 60.0 | 519.0 | — | 11 |
| | 88.0 | 166.9 | 54.5 | 67.0 | 711.6 | — | 14 |
| *P. eryngii* | 110.0 | 110.0 | 14.5 | 61.8 | 813.7 | 421 | 1 |
| | — | 221.5 | 15.7 | 57.6 | 705.2 | — | 10 |
| *P. sajor-caju* | 100.0 | 374.0 | 10.0 | 63.0 | 553.0 | — | 11 |

most of the studied species. Mycorrhizal species revealed higher total sugar contents (160–420 g kg$^{-1}$ DM) than saprotrophic mushrooms (4–150 g kg$^{-1}$ DM).[8]

Glycogen is a reserve polysaccharide of mushrooms. Limited literature data report the contents of 50–100 g kg$^{-1}$ DM. The nutritional importance for humans is limited due to its content in meat and particularly in liver.

Chitin is a water-insoluble, structural N-containing polysaccharide. The polymer is characterized by $\beta$-(1→4)-branched *N*-acetylglucosamine units. Partial deacetylation of chitin yields chitosan. Chitin accounts for up to 80–90% DM in mushroom cell walls. Nitschke *et al.*[32] recently reported a mean chitin content of 7.6, 18.7, 31.6, 46.9 and 98.6 g kg$^{-1}$ DM in *P. ostreatus*, *L. edodes*, *P. eryngii*, *A. bisporus* and *F. velutipes*, respectively. Nevertheless, chitosan was detected only in a part of the samples. This indicates that most of the amino groups of the glucosamine units are acetylated. Chitin is indigestible for humans, and apparently decreases the digestibility of other mushroom components.

It is interesting that mushrooms contain glycogen and chitin, the polysaccharides occurring in animals – not starch and cellulose, typical for plants.

Extensive research has been focused on $\beta$-glucans possessing numerous positive health effects. These constituents (lentinan, pleuran etc.) of mushroom cell walls have been investigated particularly in cultivated species and have been used in east Asian medicine. The topic would require a self-reliant review. Thus, only several articles[33–36] providing general information can be mentioned.

Limited data on dietary fibre have been reviewed.[2] Contents are about 40–90 and 220–300 g kg$^{-1}$ DM for soluble and insoluble fibre, respectively. It is apparent from these values that mushrooms contain other structural polysaccharides alongside chitin. The relatively high content of particularly insoluble fibre seems to be a nutritional advantage; however, further research is needed. Information on changes in fibre during different preservation and cooking treatments is lacking.

## Mineral composition

The normal ash content of mushrooms ranges between 60 and 120 g kg$^{-1}$ DM (Tables 1 and 2). Greater variations occur in wild-growing species than in cultivated ones, probably due to the more variable substrates in the former group. Nevertheless, the variability of ash contents seems to be lower than that of crude protein, lipids and carbohydrates.

Among the rare data on inorganic anions, Isildak[37] reported medians of 22.6, 20.4 and 3.6 g kg$^{-1}$ DM for sulfates, nitrates and chlorates, respectively, in eight wild-growing species. The contents of phosphates, chlorides and nitrites were considerably lower, while fluorides and bromides were undetectable.

### *Major elements*

The usual contents of seven major elements are given in Table 5. Potassium is the prevailing element, while calcium and sodium are at the opposite side. However, exceptions do exist. For instance, calcium contents of 0.7–5.2 g kg$^{-1}$ DM were reported in species of the genus *Morchella*.

Potassium is distributed unevenly within fruit bodies. Its content decreases in the order cap > stipe > spore-forming part > spores. Potassium is highly accumulated; its levels in fruit bodies are usually 20- to 40-fold higher than in underlying substrate. However, considerably higher bioaccumulation factors of 120–500 between caps of *Macrolepiota procera* and substrate were recently reported.[39] Comparable accumulating abilities were observed for phosphorus.

Overall, the contents of ash and particularly of phosphorus and potassium are somewhat higher than or comparable to those of most vegetables.

### *Trace elements*

Several hundreds of original papers have been published on trace element contents in mushrooms, particularly in wild-growing



  

**Table 3.** Free sugar content (g kg$^{-1}$ DM) in selected species of wild-growing mushrooms

| Species | Arabinose | Mannitol | Trehalose | Ref. |
|---|---|---|---|---|
| *Agaricus campestris* | — | 169.4 | 36.2 | 4 |
| *Amanita caesarea* | n.d. | 21.0 | 31.5 | 26 |
| *Armillaria mellea* | 7.8 | 54.5 | 93.3 | 5 |
| *Boletus aereus* | n.d. | 13.4 | 46.5 | 7 |
| *B. edulis* | n.d. | 24.5 | 124 | 7 |
| | — | 58.8 | 32.7 | 12 |
| *B. erythropus* | — | 279 | 48.4 | 8 |
| *B. reticulatus* | n.d. | 29.3 | 39.2 | 7 |
| *Calocybe gambosa* | n.d. | 2.9 | 79.6 | 5 |
| *Calvatia utriformis* | — | n.d. | 4.0 | 8 |
| *Clitocybe odora* | n.d. | 5.9 | 77.7 | 5 |
| *Coprinus comatus* | n.d. | 4.0 | 428 | 5 |
| *Fistulina hepatica* | 77.6 | 21.2 | 29.5 | 9 |
| *Flammulina velutipes* | — | 59.8 | 150.8 | 4 |
| *Hygrophoropsis aurantiaca* | 15.3 | 43.1 | 75.6 | 9 |
| *Laccaria laccata* | n.d. | 6.4 | 58.1 | |
| *Lactarius salmonicolor* | n.d. | 135 | 3.5 | 9 |
| *L. volemus* | n.d. | 273 | 9.3 | 26 |
| *Lepista inversa* | n.d. | 18.6 | 43.2 | 9 |
| *Lycoperdon echinatum* | — | 8.5 | 13.8 | 8 |
| *Russula cyanoxantha* | — | 161.8 | 16.4 | 8 |
| *R. delica* | n.d. | 184 | 2.1 | 9 |
| *R. olivacea* | — | 152.5 | 7.1 | 8 |
| *Suillus luteus* | n.d. | 12.9 | 13.5 | 26 |
| *S. mediterraneensis* | 40.3 | 28.9 | 11.8 | 9 |
| *S. variegatus* | — | n.d. | 48.5 | 4 |
| *Tricholoma imbricatum* | n.d. | 105 | 65.6 | 9 |
| *Xerocomus chrysenteron* | n.d. | 58.1 | 41.6 | 30 |

n.d., content below detection limit.

species, since the 1970s. Overall information is available in reviews,[38,40] with numerous references therein. The research maintains its dynamics; over 40 original papers on the topic were recorded in the Web of Science during 2010 and 2011. The widespread use of laboratory instruments for trace element determination has been one of the reasons.

It is impossible to cite all relevant papers here and only general information can therefore be given. The background contents of 20 trace elements in wild-growing mushrooms from unpolluted rural areas and accumulating species or genera are given in Table 6. The results of recently published papers are comparable with data of Table 6.

The contents of many trace elements vary widely among species, sometimes by two orders of magnitude. There exist accumulating and even hyperaccumulating species. Great variations have been repeatedly reported within a species if a mushroom was grown on an unpolluted site or on a contaminated site such as in the vicinity of metal smelters, in mining areas (including historical ones), along roads with heavy traffic or within cities. The latter contents are considerably higher than levels found in contaminated plants. Cadmium and mercury are elements with high bioaccumulation from substrates in numerous mushroom species. Nevertheless, the relationship between soil contamination with a detrimental trace element and its level in the fruit body is not tight enough to enable usage of a mushroom species as a reliable marker of local pollution.

Most of the elements are distributed unevenly within a fruit body. The highest content is usually observed in the spore-forming part of the cap (but not in spores), a lower level in the rest of the cap and the lowest in the stipe.

A part of the risk elements, namely cadmium, mercury and lead, can be leached away. Short-term boiling is more efficient than soaking at ambient temperature. A higher proportion of the elements is leached from destroyed tissues of frozen mushroom slices than from fresh or dried slices or particularly from intact fruit bodies. Unfortunately, such culinary treatments decrease the content of valued volatile taste constituents.

A consensus exists that most wild-growing mushroom species from unpolluted areas do not pose a health risk. This cannot be applied to mushrooms from sites contaminated with the detrimental elements. Very limited information is so far available on chemical forms (species) of these elements in mushrooms. A recent report[42] that the proportion of methylmercury is below 5% of total mercury confirms several older studies. Only pilot data are available for arsenic and chromium species. Information on the availability of the detrimental elements is very limited. It seems from several earlier reports that the availability of cadmium from mushrooms is high.

The contents of the detrimental elements in cultivated mushrooms have been low, particularly due to the use of unpolluted substrates.

The reported relatively high selenium contents in popular mushrooms of the *Boletus* genera, particularly in *B. edulis*, seemed to be promising as a source of this essential element, deficient throughout Europe. However, a low bioavailability was determined in the 1980s. A comprehensive review on the topic is available.[43]

Research is in progress to increase the level and availability of several essential elements in cultivated mushrooms via the fortification of substrates.

### *Radioactivity*

The topic has been repeatedly reviewed[44–47] and therefore only general information will be given.

Natural radioactivity of mushrooms is commonly higher than that of plants due to high content of potassium, including radioisotope $^{40}$K. Activity concentrations are usually 0.8–1.5 kBq kg$^{-1}$ DM. Other natural radionuclides with leading $^{210}$Pb and $^{210}$Po are of lower importance.

Activities of $^{137}$Cs below 1 kBq kg$^{-1}$ DM from nuclear weapon testing were reported until 1986.

The situation changed dramatically after the disaster of the Chernobyl nuclear power station in Ukraine in April 1986. Activities of over 100 kBq kg$^{-1}$ DM of $^{137}$Cs and to a lesser extent of $^{134}$Cs were determined in some mushroom species, particularly mycorrhizal, during the following years in several parts of Europe. Among the widely consumed species, *Xerocomus badius*, *X. chrysenteron*, *Suillus variegatus*, *Rozites caperata*, *Laccaria amethystina* and *Hydnum repandum* are accumulators of radiocaesium. Most of the $^{137}$Cs (half-life 30.17 years) in forest soils has been available for mushrooms. Thus considerable consumption of accumulating species harvested from sites heavily polluted in 1986 can still be a health concern. A statutory limit in the European Union (EU) of 1.25 kBq kg$^{-1}$ FM (i.e. 12.5 kBq kg$^{-1}$ DM) has been established for wild-growing mushrooms.

The EU statutory limit of 0.6 kBq kg$^{-1}$ FM has sometimes been surpassed in meat of wild boars feeding on some mushroom species, particularly underground *Elaphomyces granulatus* (deer truffles) in highly contaminated areas.

**Table 4.** Free sugar content (g kg$^{-1}$ DM) in cultivated mushrooms

| Species | Ribose | Xylose | Mannose | Mannitol | Glucose | Fructose | Sucrose | Trehalose | Ref. |
|---|---|---|---|---|---|---|---|---|---|
| *Agaricus bisporus* | | | | | | | | | |
| Brown | n.d. | 1.45 | 84.6 | — | 4.68 | n.d. | n.d. | n.d. | 23 |
| | — | — | — | 480 | — | 4.78 | n.d. | 26.3 | 1 |
| White | — | — | — | 641 | — | 3.44 | n.d. | 18.3 | 1 |
| *A. brasiliensis* | — | — | — | 79.4 | 27.6 | — | — | 29.8 | 12 |
| *Flammulina velutipes* | 11.5 | 51.6 | 7.51 | — | 11.3 | n.d. | n.d. | 2.33 | 23 |
| | — | — | — | 80.0 | — | 379 | 7.42 | 217 | 1 |
| *Hypsizigus marmoreus* | n.d. | — | n.d. | 22.6 | — | 2.71 | — | 9.84 | 13 |
| Normal strain | | | | | | | | | |
| White strain | n.d. | — | 11.3 | 18.2 | — | 2.73 | — | 44.8 | 13 |
| *Lentinula edodes* | 2.40 | 7.98 | 23.1 | — | 36.3 | n.d. | 2.33 | 2.55 | 23 |
| | — | — | — | 495 | — | 34.1 | n.d. | 167 | 1 |
| *Pleurotus ostreatus* | 0.85 | n.d. | 10.6 | — | 14.3 | n.d. | n.d. | 3.03 | 23 |
| | n.d. | — | — | 31.6 | 11.5 | n.d. | n.d. | 32.8 | 31 |
| | — | — | — | 50.3 | — | 0.93 | n.d. | 412 | 1 |
| *P. eryngii* | 5.02 | 1.55 | 13.6 | — | 27.8 | n.d. | n.d. | 7.15 | 23 |
| | — | — | — | 54.5 | — | 2.73 | 2.73 | 728 | 1 |

n.d., content below detection limit.

**Table 5.** Usual content (g kg$^{-1}$ DM) of major mineral elements in wild-growing and cultivated mushrooms in descending order (adapted from the review[38] and original papers on cultivated species)

| Element | Content |
|---|---|
| Potassium | 20–40 |
| Phosphorus | 5–10 |
| Chlorine | 1–6 |
| Sulfur | 1–6 |
| Magnesium | 0.8–1.8 |
| Calcium | 0.1–0.5 |
| Sodium | 0.1–0.4 |

Artificial radioactivity of cultivated species has been negligible. Unfortunately, new data on mushroom radioactivity is awaited as a consequence of the accident of Fukushima nuclear power station, Japan, in March 2011.

## Vitamins and provitamins

Earlier limited data[3] on vitamins in cultivated mushrooms were recently enlarged by extensive information on ascorbic acid and tocopherol content in numerous wild species by a Portuguese laboratory.[4,5,7,8,26,30]

The normal content of ascorbic acid is 150–300 mg kg$^{-1}$ FM. The content in *Agaricus* spp. seems to be low, while above-average levels were reported for the popular *B. edulis* and *Cantharellus cibarius*.

For B-group vitamins, contents of 1.7–6.3, 2.6–9.0, 1.4–5.6 and 63.8–83.7 mg kg$^{-1}$ of thiamine, riboflavin, pyridoxine and niacin, respectively, were determined in four dried common cultivated species.[48] Considerably higher contents of 29.2 and 33.2 mg kg$^{-1}$ DM for niacin and riboflavin, respectively, were reported for fresh *B. edulis*. The levels of both vitamins decreased during mushroom soaking or blanching.[49] Phillips *et al.*[50] quantified total folates at between 124 and 442 μg kg$^{-1}$ FM in seven species of cultivated mushrooms, with border contents in *L. edodes* and *P. ostreatus*, respectively. Thus the information on B-group vitamins is only fragmentary.

The normal content of total tocopherols is 0.5–3 mg kg$^{-1}$ DM. This is a considerably lower level than in vegetables. Several species have significantly higher contents, particularly *Boletus reticulatus* (syn. *B. aestivalis*) and *Suillus variegatus*.[4,5,7,8,26,30] Cultivated species seem to be lower in tocopherols than wild mushrooms.[1] Generally, $\gamma$-tocopherol is the prevailing form.

$\beta$-Carotene, the most potent provitamin A, is less common in mushrooms than in plants. Moreover, its contents are low, from an undetectable level up to 6 mg kg$^{-1}$ DM.[4]

Increased attention has been focused on ergosterol, the provitamin of ergocalciferol (vitamin $D_2$). Both earlier and recent data reported 3000–7000 mg kg$^{-1}$ DM.[2,51,52] Ergosterol contents between 640 and 1770 mg kg$^{-1}$ DM were determined in fruit bodies of several *Tuber* species. Moreover, comparable contents between 480 and 1830 mg kg$^{-1}$ DM of several phytosterols, particularly brassicasterol, were reported.[53] A relatively high ergosterol content could be of significance for individuals with a limited intake of cholecalciferol from foods of animal origin, e.g. for vegans and vegetarians.

Several reports[54–57] deal with the effects of various ultraviolet irradiation of mushrooms on vitamin $D_2$ formation from ergosterol. There exists a consensus that the exposure to UV light considerably elevates content of bioavailable vitamin $D_2$. The treatment is more effective if mushrooms are placed in a single layer and evenly distributed than in those packaged together in layers. Vitamin $D_2$ content can surpass a level of 100 mg kg$^{-1}$ DM under optimum conditions.

## Flavour and taste compounds

Many consumers highly appreciate the characteristic flavour of many mushroom species, particularly dried. Hundreds of odorous compounds have been identified, being classified as derivatives of octane and octenes, lower isoprenoids, aldehydes and ketones, sulfurous (e.g. lenthionine) or heterocyclic compounds and others. Also, various products of the Maillard reaction participate in



  

**Table 6.** Usual content of 20 trace elements (mg kg$^{-1}$ DM) in fruit bodies of wild-growing mushrooms from unpolluted areas, and accumulating genera and species (adapted from Kalač[3] and Nitschke *et al.*,[36] with data for iodine from Gucia *et al.*,[39] and from Vetter.[41])

| Element | Content | Accumulators |
|---|---|---|
| Aluminium | 20–150 | *Amanita rubescens*, *Leccinum scabrum*, *Xerocomus chrysenteron* |
| Antimony | <0.1 | *Suillus* spp. |
| Arsenic | 0.5–5 | *Laccaria amethystea*, saprotrophic genera |
| Barium | 2–4 | |
| Cadmium | 1–5 | *Agaricus* spp. (group *flavescentes*) |
| Caesium | 0.5–10 | *Suillus luteus* |
| Cobalt | <0.5 | *Ramaria largentii*, *Hygroporus eburneus*, *Cantharellus cibarius* |
| Copper | 20–100 | *Agaricus macrosporus*, *A. silvicola*, *Macrolepiota procera*, *M. rhacodes* |
| Chromium | 0.5–5 | *Morchella elata*, *Armillaria mellea*, *Macrolepiota procera*, *Marasmius oreades* |
| Iodine | 0.07–0.5 | *Calvatia excipuliformis*, *Macrolepiota procera*, *Lepista nuda*, *Amanita rubescens* |
| Iron | 50–300 | *Suillus variegatus*, *S. luteus*, *Armillaria mellea* |
| Lead | <1–5 | Some saprotrophic species |
| Manganese | 10–60 | *Boletus edulis*, *Macrolepiota procera* |
| Mercury | <0.5–5 | *Boletus edulis*, *B. pinophilus*, *Calocybe gambosa* |
| Nickel | <1–15 | *Laccaria amethystina*, *Coprinus comatus* |
| Rubidium | Tens–hundreds | Boletaceae family |
| Selenium | <2–20 | *Albatrellus pes-caprae*, *Boletus edulis*, *B. pinophilus*, *B. reticulatus (syn. B. aestivalis)* |
| Silver | <10 | *Amanita strobiliformis*, *Agaricus* spp., *Macrolepiota procera* |
| Vanadium | <0.5 | *Coprinus comatus* |
| Zinc | 25–200 | *Calvatia utriformis*, *Lycoperdon perlatum* |

savorous properties of dried mushrooms.[58] Tissue disruption has an important effect on the profile of volatiles, both qualitatively and quantitatively.

The very typical character of mushroom aroma is ascribed to derivatives of octane, 1-octene and 2-octene, e.g. alcohols and their esters with volatile fatty acids, or ketones (often 3-octanone). 'Mushroom alcohol', 1-octen-3-ol, has a particular role. It occurs at low levels in fresh mushrooms, particularly in boletes. Its content increases considerably up to tens of milligrams per kilogram during drying and to a lower extent also during boiling and canning. Eight-carbon volatiles are produced by the oxidation of free linoleic acid under catalysis with lipoxygenase and hydroperoxide lyase. Such a process is specific for mushrooms and its intensity increases under drying conditions. Detailed information is available from a review by Combet *et al*.[59] Moreover, the aroma profile of truffles was recently reviewed.[17]

Among non-volatile taste compounds, values of 1–9 and 2–20 g kg$^{-1}$ DM for monosodium glutamate-like components and free 5′-nucleotides, respectively, were reported for nearly 20 wild-growing and cultivated species[12,13,31,60] and for several *Tuber* spp.[61] Calculated values of equivalent umami concentration varied widely. Losses of total 5′-nucleotides were 32%, 67% and 69% of the initial content during the preparation of soup from *A. bisporus* by microwave cooking, boiling and autoclaving, respectively.[62]

## Pigments

Pigments of various chemical groups occur in mushrooms. Two recent comprehensive reviews[63,64] are available.

As compared with plants, chlorophylls and anthocyans do not occur and carotenoids are not widespread in mushrooms. Noticeable colour changes, commonly darkening, appear in some species after mechanical damage of fruit body tissues. The changes are usually caused by enzymically catalysed oxidation of various polyphenols to quinones. Such types of reactions are undesirable particularly in commercial white *A. bisporus*. Tyrosine under catalysis with tyrosinase is oxidized to *o*-dihydroxyphenylalanine (DOPA), then to brown quinonic pigments and eventually to melanins.[65]

## Phenolics

There exists a consensus that phenolics, particularly phenolic acids, are the main mushroom antioxidants.

Phenolic acids can be divided into two major groups: hydroxy derivatives of benzoic acid and *trans*-cinnamic acid. Within the former group, *p*-hydroxybenzoic, protocatechuic, gallic, gentisic, vanillic and syringic acids have usually been detected in mushrooms, while *p*-coumaric, caffeic and ferulic acids represent the latter group. The acids are mostly bound in various complex structures. The reported total phenolic acid contents vary widely between 4 and 80 mg kg$^{-1}$ DM within wild-growing species, with *p*-hydroxybenzoic acid being the significantly prevailing compound. *Coprinus comatus*, *Calocybe gambosa* and *Clitocybe odora* are the species with the highest levels.[5,7,26,30]

Total phenolic compounds content is commonly expressed as gallic acid equivalent (GAE). Values of 2.74, 3.32 and 7.07 g kg$^{-1}$ DM have reported Kolayli *et al*.[66] for *P. ostreatus*, *Pleurotus cornucopiae* and *Clitocybe geotropa*, respectively, while considerably higher levels of 36.4 and 41.8 g kg$^{-1}$ of dried extract were determined in *Boletus* (*Leccinum*) *aurantiacus* and *B. edulis*, respectively. Contents for one order of magnitude lower, 0.18–0.67 g kg$^{-1}$ DM, were reported by Zeng *et al*.[67] in five wild species collected in Australia. Variegatic acid containing four phenolic groups in a couple of *o*-positions was named as the main antioxidant compound in the latter two species.[68] Great differences occurred in total phenolic contents of cultivated *A. bisporus* and seven strains of *A. brasiliensis* between years of harvest. These differences were higher than those between the species within a year.[69]

Earlier sporadic information on the occurrence of nutritionally desirable flavonoids in mushrooms was recently supported by several fragmentary results.[4,68,70]

### Antioxidants

Similar to the case in foods of plant origin, extensive research has recently focused on antioxidant potential (scavenging effects and reducing power) of both cultivated and wild-growing mushrooms. A thorough review of the topic with numerous references up until mid 2008 has been published.[71] Many original articles were published during the last years and their evaluation would require a further self-reliant review.

Thus only several comments are made here. The antioxidative value of mushrooms is comparable with vegetables. Phenolics are the main compounds with antioxidant potential, but additive and synergistic effects with further present antioxidants are presumed. Boiling probably decreases antioxidant potential to a greater extent than drying or freezing. Mycelium of numerous cultivated species seems to be a promising source for the isolation of antioxidants and their use as nutraceuticals.

### Various constituents

Numerous further mushroom constituents with either health-promoting or detrimental effects have been identified in various edible species.

Hundreds of milligrams per kilogram DM of total carboxylic acids, mostly in caps, were determined in four widely consumed wild European species. The contents of prevailing acids decreased in the order malic $>$ fumaric $\approx$ citric $>$ oxalic acid.[72]

Within 29 species of edible and medicinal mushrooms, *P. ostreatus* and *A. bisporus* were richest in lovastatin, *F. velutipes* and *B. edulis* in $\gamma$-aminobutyric acid (GABA) and *Pleurotus* spp. in ergothioneine (betaine of 2-mercapto-L-histidine), compounds with auspicious health effects.[73]

Mushrooms can be included among food items with a high level of biologically active polyamine spermidine, while spermine contents are considerably lower.[24]

The potentially procarcinogenic hydrazines agaritine and gyromitrin occur in *Agaricus* spp. and *Gyromitra esculenta*, respectively. While cultivated *A. bisporus* commonly contains 200–500 mg kg$^{-1}$ FM agaritine, nearly one half of 53 analysed wild *Agaricus* species contained above 1000 mg kg$^{-1}$ FM. An extremely high level was found in *A. elvensis*.[74] However, current evidence suggests that the consumption of cultivated *A. bisporus* poses no risk to healthy humans.[75]

Several outbreaks of rhabdomyolysis and cardio- and hepatotoxic effects were reported after the consumption of *Tricholoma equestre* (formerly *T. flavovirens*).

Coprine, a free amino acid, is present in several species of the genus *Coprinus*. Coprine is converted within the human body to cyclopropanone hydrate, which blocks oxidation of acetaldehyde, produced from consumed ethanol, to acetic acid. Thus ethanol intolerance occurs.

Individuals afflicted with gout need to restrict dietary intake of purine compounds. Kaneko *et al*.[76] reported total content of purine compounds in seven cultivated mushroom species between 95 and 1420 mg kg$^{-1}$ FM, with the highest levels in *P. ostreatus* and *Grifola frondosa*. These two species can be classified as purine-rich foods.

Widely variable contents of nine non-hallucinogenic indole compounds were detected in cultivated *A. bisporus* and in three wild species. Serotonin was the compound with the highest level, varying between 52 and 317 mg kg$^{-1}$ DM.[77] In a further study with five other species, serotonin content ranged between 5 and 296 mg kg$^{-1}$ DM with border levels in *Xerocomus badius* and *C. cibarius*, respectively. Serotonin and 5-hydroxytryptophan were not detected after thermal treatment simulating culinary processing; however, remaining levels of indole, L-tryptophan, 5-methyltryptophan and melatonin were high enough from a pharmacological point of view.[78]

During the last few years, up to 9.9 mg kg$^{-1}$ nicotine was detected in dried commercial mushrooms of *Boletus and Cantharellus* genera. The latest studies[79,80] report lower levels of tens of micrograms per kilogram of dried both cultivated and wild-growing mushrooms. It has not been convincingly explained why nicotine can be found in mushrooms.

Relatively high formaldehyde contents, hundreds milligrams per kilogram FM, have been observed in *L. edodes*. Formaldehyde is formed from lentinic acid, a dipeptide, by enzymic activity following mechanical damage of tissues. However, dietary exposure from mushrooms is not thought to be a cause for concern.

## CONCLUSION

Information on the chemical composition of culinary mushrooms, particularly wild growing, has dynamically expanded during the last decade. The data, however, can hardly be generalized owing to the very high number of consumed species and great variability in chemical composition within individual species. Overall, proximate composition is comparable with most vegetables. Apart from valued compounds affecting taste, mushrooms are nutritionally desirable because of their low energy value, fibre content and high antioxidant capacity. The ability of some species to accumulate detrimental elements including radioisotopes has to be taken into consideration, however.

The existing data have been mostly quantitative and have dealt mainly with fresh mushrooms. Information on the bioavailability of nutrients and other compounds has been lacking. Thus the evaluation of nutritional value and also health risk of detrimental compounds from their contents is doubtful.

Future research should elucidate polysaccharide composition, particularly its components forming dietary fibre and those with positive health effects. Information on the effects of various storage, preservation and culinary treatments on mushroom constituents is desirable, as are data on bioavailability. Moreover, some mushroom species probably contain components with various, as yet unrecognized, biological effects.

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