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History, Health Benefits, Market, and Production Status of Button Mushroom

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Abstract

Mushrooms represent a small branch in the evolution of the fungal kingdom Eumycota and are commonly known as the 'fleshy fungi.' They are non-photosynthetic organisms that evolved from algae (Stamets and Chilton, 1983). Out of 1.5 million existing fungi species, 160,000 species are considered as mushrooms (Hanksworth, 2012). Around 2% of global fungal biota and around 10% of global mushroom biodiversity have been discovered to date by mycologists. Thus, the bulk of fungal biodiversity remains hidden. For the last 10 years, modern sequencing methods enabled a discovery rate of 1200 new species per year (Chang and Wasser, 2017). Of the recognized mushroom species, about 7000 species are considered to possess varying degrees of edibility, and more than 3000 species from 231 genera are regarded as prime edible mushrooms. Of the prime edible mushrooms, 100 are economically cultivated, around 60 are commercially cultivated, and more than ten are produced on an industrial scale in many countries (Wasser, 2010).

Mushrooms are generally classified under the phylum Basidiomycota, division Eumycota, subdivision Basidiomycotina, and class Hymenomycetes. Under this class, mushrooms were separated into different orders (Barros *et al.*, 2007). Under the order Agaricales, the genus *Agaricus* comprises

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saprobic mushrooms and economically important species like *Agaricus bisporus* (Savoie *et al.*, 2013). Moving from an easy backyard crop in the early days of cultivation, to a significant money maker, the mushroom industry grew widely. Mushroom crops became one of the most widely cultivated in the world (McGee, 2017). In recent years, interest in mushrooms has become increasingly apparent all over the world due to their nutritional and medicinal properties. They may lack the deep green or brilliant red hues consumers have come to associate with nutrient-rich fruits and vegetables, but they are a 'powerhouse of nutrition.' The white button mushroom (*A. bisporus*), of high economic, nutritional and medicinal value, ranks among the world's most produced and consumed mushrooms.

1.1 Edible Fungi in History

Mushrooms fruited in the forests and grasslands occupied by our hominid ancestors and have been a familiar part of nature throughout human history. From very early times, humans have used mushrooms collected in the wild as food (Chang and Miles, 2004). Human use of edible mushrooms 13,000 years ago in the Andes has been confirmed through archaeological records. Mushrooms have been recognized as important food items because of their nutritional values and therapeutic properties. For instance, the mummified Iceman Ötzi carried material from *Piptoporus betulinus* mushrooms that were likely used for medicinal purposes and *Fomes fomentarius* mushrooms to start a fire (Peintner *et al.*, 1998).

Many cultures identified that certain mushrooms could have profound health-promoting benefits. Ancient Egyptians believed mushrooms could grant immortality and thus, only pharaohs were deemed worthy of eating or even touching them. Pre-colonial Indian cultures used *Psilocybe* species in shamanic rituals (Díaz, 1977) and Vikings may have ingested the *Amanita muscaria* mushroom to induce a trance before going to war (Fabing, 1956). The ancient Chinese believed that the mushroom strengthens the human body and preserves health and youth for as long as possible. The consumption of wild mushrooms in China was first reliably noted more than 2000 years ago (Aaronson, 2000). Edible mushrooms were gathered from the forest in ancient Greek and Roman times and were highly valued, though more by high-ranking people than by peasants (Buller, 1914). In ancient Rome, mushrooms were often referred to as 'food for the gods' and Romans had mushrooms on their list of foods which were served only on festive occasions (Rahi and Malik, 2016). They also used mushrooms as drugs and in decorating their buildings and places of worship. The Mayans used psychoactive mushrooms mainly for religious rites, and some regions of Latin America still retain these traditions (Matsushima *et al.*, 2009). The folklore of Russian, Chinese, Mexican and other cultures held that mushrooms conferred superhuman strength. In southern Africa, people have eaten mushrooms for centuries, although little information about the use of wild edible mushrooms has been known (Piearce, 1985; Morris, 1994).

Mushroom growing also has a long tradition in eastern Asian countries. It is estimated that the first intentional cultivation of mushrooms took place around AD 600, almost 1400 years ago, in China, which was the first country to cultivate many popular mushroom species (Chang and Miles, 2004). The modern mycologist Shu-Ting Chang noted that Chinese literature first recorded the cultivation of mushrooms, most likely the wood ear (*Auricularia auricula*) and then the velvet foot (*Flammulina velutipes*) mentioned in around AD 800 (Bertelsen, 2013). *Lentinula edodes* (AD 1000–1100), *Volvariella volvacea* (AD 1700) and *Tremella fuciformis* (AD 1800) were later cultivated in China (Chang and Miles, 1987, 2004). The method of cultivation of Jew's ear (*Auricularia* spp.) has been recorded in the ancient Chinese publication *Liki* about 300 BC and in *Shih* about 230 BC (Kabir, 1999). With time, people continued Greek and Roman practices and cultivated mushrooms at the household level. It was the French who seriously undertook the task of cultivating mushrooms on a larger scale.

From 1626 to 1723, a critical mass of scientific inquiry and publishing began and propelled France into mushroom growing such as *De la Nature, Vertu et Utilité des Plantes*, in which the author Guy de la Brosse (1626) termed the mushroom seeds 'suckus' and explained that mushrooms grow from these suckers and could be cultivated this way. Later, Nicolas de Bonnefons was the first to describe the mushroom cultivation in his book *Le Jardinier François* (de Bonnefons, 1651), and followed by *Les Délices de la Campagne* (de Bonnefons, 1654). Additional works were subsequently published, such as *Mémoires de l'Académie des Sciences* by Joseph Pitton de Tournefort (1707) and Botanicon Parisiense by Sebastien Vaillant (1723), where mushrooms or mushroom growing techniques were included.

John Abercrombie wrote the first book in English devoted completely to the cultivation of mushrooms, entitled *The Garden Mushroom* (Abercrombie, 1779). French cuisine predominated at the higher levels of English society with translations of French cookbooks. The Americans then got into the game, where French cuisine became the cuisine of diplomacy. The USA's interest in mushroom cultivation was reflected through the books published during the 19th century, such as *The Vegetable Cultivator* by John Rogers (1839) and *Mushrooms: how to grow them, a practical treatise on mushroom culture for pleasure and profit* compiled by William Falconer (1891). During this century, scientists who engaged with the new scientific and rationalist thought bursting all over Europe and the USA continued to write about mushroom cultivation.

The extensive use of mechanized cultivation techniques for producing mushrooms in great quantities for food is a phenomenon of the 20th century (Chang and Wasser, 2017). The first truffle plantations were established in Italy and France in the 1970s (Samils *et al.*, 2008).

The greatest increase in the number of mushroom species brought into cultivation was in the 1980s and 1990s (Bertelsen, 2013). While commercial harvesting of wild mushrooms continues today, most of the world's supply comes from commercial mushroom growers.

1.2 History of *Agaricus bisporus* Cultivation

A. bisporus was first cultivated in France in 1630 as reported by Atkins (1978). Some accounts say that it was cultivated during the time of Louis XIV, when gardeners first grew it on beds fertilized with dung and later on, in cellars and catacombs underneath the ground (Ainsworth, 1976). This species was mainly grown on open ground in fields; at some point it was realized that mycelium, or what is referred to as the spawn of the mushroom, was what gave rise to the fruiting bodies and could be utilized much like the seed of plants to grow mushrooms. It was observed later that this mushroom could grow without light. Therefore, its successful culture was undertaken inside caves (Delmas, 1978). A French gardener, Chambry, began to cultivate mushrooms in underground quarries in Paris, making possible year-round production. In 1810, France was the first country to commercialize the mushroom and established the first specialist syndicate (Status of French Mushroom Growers). Other farmers followed the example of Chambry setting up farms near Paris, and the first mention of production was near Lilles in 1848 in Bordeaux. Later in 1895, mushroom production was introduced into the Loire Valley, in caves. *A. bisporus* production grew rapidly in France and spread later to other European countries. In Holland, mushroom production started in 1825 in caves, according to Vedder (1978). With experimentation with spawn and publicity in journals and magazines, mainly those of Richard Bradley's and Philip Miller's publications: *New improvements of planting and gardening* in 1726 and *Methods of cultivating and improving the kitchen fruit and flower garden* in 1731 (Bertelsen, 2013). In 1831, Callow shared the design of a cropping house, and by 1870, guidelines on cultural practices of *A. bisporus* and inoculum (spawn) were available in England (Spencer, 1985). It was noted that the mushroom growing method in the standard house was developed and adopted by the English-speaking countries (Chang and Wasser, 2017). The earliest commercial production in the USA was in the vicinity of New York and Long Island, about 1880 (Thomas, 1965), where mushrooms were grown on the floor of cellars and caves.

In 1893, the Pasteur Institute discovered pure culture spawn in Paris to cultivate composted horse dung (Genders, 1969). Costantin and Matrichot carried out the first experimental culture of mycelium from spores in 1893 in Paris. Production of spawn by industrial producers began during the 19th century (Blanchon, 1906). In 1903, the USA started to produce its own spawn culture, 'brick spawn' by the American Spawn Company of St. Paul, Minnesota (Bertelsen, 2013).

France led the world as a mushroom producer until the outbreak of World War II. Not until 1914 did industrialized cultivation of button mushroom begin in the USA, whereas following World War II, there was a great surge in mushroom production. From that time on, the USA has assumed the dominant position (Chang and Wasser, 2017). In 1925, the term 'mushroom' was used in its widest sense to include all edible fungi, but later Atkins (1966) clarified that the cultivated mushroom of commerce should be referred to as *A. bisporus*. In 1933, mushroom cultivation was introduced to Latin America from Europe, where production became concentrated in Mexico, followed by Argentina, Colombia, Brazil, and Chile (Muhammad and Suleiman, 2015). In 1980, France, Holland, and Italy were ahead of Britain as mushroom producers.

The most significant progress in mushroom cultivation was when *A. bisporus* was grown on an agricultural media specially prepared for the purpose: composted substrate (Chang and Miles, 2004). First composts used for growing the button mushroom were issued from melon crops (Delmas, 1978). Until 1990, repeating experiments of researchers like San Antonio (1975), Chang and Hayes (1978), van Griensven (1988), and Quimio *et al.* (1990) have established the specifics of this mushroom. Until 1995, the natural history and resource status of the button mushroom has been poorly known. At that time, five and perhaps six genetically distinctive, reproductively isolated populations of this species from North America, Europe, and western Asia have been located, sampled, and partially characterized. According to Kerrigan (1995), the cultivation of European germplasm has invaded North American populations. The first strain isolation took place from cultures of mushroom tissue by Boyer (1918). One other move in *A. bisporus* cultivation was to use hybrid strains. Fritsche (1983) carried out the first commercial hybrid strain. This evolution enabled growers to produce the quality mushrooms necessary for expanding the domestic and export sales of fresh mushrooms (Chang and Wasser, 2017).

1.3 The Genus *Agaricus*

1.3.1 History of the name *Agaricus*

From the time of Linnaeus onward to about the middle of the 19th century most fungi having fruit bodies with gills were placed in the genus *Agaricus*. Some species were subsequently removed from this genus. Simultaneously, the group of species already recognized as *Agaricus tribus Psalliota* by Fries (1821) was raised to generic rank under the name *Psalliota* (Kummer, 1871). By this time, the name *Agaricus* had disappeared after the entire genus *Agaricus* had been subdivided into new genera. Although Karsten (1879) became conscious of the fact that *Psalliota* represented the very core of the old genus *Agaricus* and restored the name *Agaricus* for the genus *Psalliota*, the use of the name *Psalliota* persisted until around 1950 (Møller, 1950). Finally, sophisticated nomenclatural reasons made it necessary to conserve the name *Agaricus* L.: Fr. with *A. campestris* as type species, so that the generic name *Agaricus* would be forever fixed (Bas, 1991).

1.3.2 Taxonomy

Within the order Agaricales, the genus *Agaricus* belongs to the family Agaricaceae (Bas, 1991). Agaricaceae Fr. sensu Singer (1986) initially included several genera distributed in four tribes: Leucocoprinae Singer, Agariceae Pat., Lepiotae Fayod and Cystodermatae Singer. After Singer (1986), many changes occurred in this family as reported in a good number of works (Redhead *et al.*, 2001; Moncalvo *et al.*, 2002; Vellinga and Yang, 2003; Vellinga *et al.*, 2003; Vellinga, 2004a), where the exclusion of the tribe Cystodermatae on grounds of morphological analyses (Bas, 1988) and sequence analyses (Johnson and Vilgalys, 1998; Moncalvo *et al.*, 2002) was a major change. According to Kirk *et al.* (2001) Agaricaceae comprises 51 genera and 918 species, including several genera with gasteroid and secotioid basidiomata (Vellinga, 2004b). Specifically, the genus *Agaricus* is placed in tribe Agariceae, which is distinguished from the other tribes by the dark brown color of the spores (Bas, 1991).

The infrageneric classification of *Agaricus*, according to Singer (1986), was as follows:

Genus Agaricus L.: Fr.
Subgenus Agaricus
Section Agaricus cosmopolitan
'Sanguinolenti'
'Arvenses'
'Xanthodermi'
'Brunneopicti' (sub)tropical
Subgenus
'Lanagaricus'
'Conioagaricus'

It is noteworthy that the subgenus *Agaricus* is cosmopolitan, while the subgenus *Lanagaricus* Heinem. and *Conioagaricus* Heinem. are of tropical and subtropical distribution (Heinemann, 1978). Specifically, subgenus *Lanagaricus* covers the (sub)tropical species with a rather loose, wooly outer layer on cap and lower part of stem and subgenus *Conioagaricus* accommodates the (sub)tropical species with very short to round cells on the cap (Bas, 1991). Up to the year 2000, species were grouped in sections according to their discoloration (pink, red, yellow, or none). However, these criteria did not help much for classification of *Agaricus* species; for instance, about one-third of tropical species were classified in sections based on temperate species despite the efforts of mycologist Paul Heinemann to propose new subgenera and sections for tropical species. During that period of time, taxonomic classification did not reflect the phylogeny of the species (Callac and Chen, 2018). Still, it progressed constantly until the year 2010 when phylogenetic reconstruction of two sections *Bivelares* (including *A. bisporus*) and *Xanthodermatei* (including toxic species of *A. xanthodermus*), closely related to each other (Mitchell and Bresinsky, 1999; Geml *et al.*, 2004), was performed by DNA sequencing (r-DNA-ITS sequences; Challen *et al.*, 2003; Kerrigan *et al.*, 2005, 2008). Accordingly, eight sections are recognized in the subgenus *Agaricus: Agaricus, Arvenses, Bivelares, Chitonioides, Minores, Sanguinolenti, Spissicaules,* and *Xanthodermatei* (Parra, 2008; Zhao *et al.*, 2011).

With time, efficient tools for the identification and classification of fungi were developed based on DNA sequencing and databases of genetic and taxonomic information, allowing the exploitation of phylogenic analyses to deduce evolutionary relationships among agaric taxa (Challen *et al.*, 2003; Geml *et al.*, 2004; Kerrigan *et al.*, 2008; Zhao *et al.*, 2011). Major criteria of classification became the structure of annulus (superior vs inferior; simple vs double or two-layered), microscopic features, odor, and cross-reaction of Schäffer (alanine × nitrogen acid; Callac and Chen, 2018). Gradually, many studies (Zhao *et al.*, 2011; Parra, 2013; Kerrigan, 2016) have contributed more or less to the revision of the classification of *Agaricus* genus; specifically, a revised system was proposed by Zhao *et al.* (2016) and amended by Chen *et al.* (2017), Parra *et al.* (2018), and He *et al.* (2018). In this revised system of classification, the number of traditional sections of genus *Agaricus* (eight sections) increased to 13 after *Agaricus* sect. *Sanguinolenti* was split to three new sections (*Bohusia, Nigrobrunescentes,* and *Sanguinolenti;* Peterson *et al.*, 2000; Parra, 2008; Parra *et al.*, 2014, 2015; Zhao *et al.*, 2011, 2016); *Agaricus* sect. *Spissicaules* was split into three new sections (*Rarolentes, Spissicaules,* and *Subrutilescentes*; Zhao *et al.*, 2011, 2016; Kerrigan, 2016); and *Agaricus* sect. *Xanthodermatei* was split into two new sections (*Hondenses* and *Xanthodermatei*; Kerrigan *et al.*, 2005; Zhao *et al.*, 2011, 2016; Thongklang *et al.*, 2014; Kerrigan, 2016). In general, excellent and frequently consumed species belong to the sections *Agaricus, Arvenses, Bivelares, Nigrobrunnescentes,* and *Sanguinolenti* (Kalač and Svoboda, 2000).

Up to 2016, the concept of sections initially described from temperate species had evolved (Parra, 2008; 2013) but not sufficiently to incorporate tropical diversity (Karunarathna *et al.*, 2016). It was hard to classify *Agaricus* species in climatic groups. In fact, *Agaricus* belongs to clades that are not strictly tropical or temperate (Callac and Chen, 2018): the geographical range of some temperate species (*A. bisporus* and *A. bitorquis)* can extend into tropical areas (Kerrigan, 2005); reciprocally, the tropical species *A. endoxanthus* Berk. and Broome is sometimes found in greenhouses in Europe and is suspected to have been introduced with plants (Parra *et al.*, 2002). There are also some tropical species, such as *A. flocculosipes* that extends to neighboring subtropical climatic areas. *Agaricus* species are poorly known in a relatively arid/hot climate, including the hot Mediterranean or temperate areas, because the fruiting periods are short or unpredictable. In the revised system of classification, tropical species are placed more accurately; one subtropical genus and 11 tropical sections were retained. However, despite recent advances in taxonomy and phylogeny, enormous taxonomic work remains to map out the evolutionary history of this genus, in which climate and geography seem to have been the main factors of diversification (Callac and Chen, 2018).

1.3.3 Characterization and distribution

The genus *Agaricus* has a worldwide distribution. It occurs on the arctic tundra as well as in tropical rainforests. The saprophytic representatives of this genus are found on the turf of alpine meadows, grassy dunes, salty seaside grasslands, humus and litter of coniferous, deciduous woods, all kinds of accumulated vegetable matter, and nearly all types of soil. It seems, however, to avoid very acid and wet soils and is rarely found on dung in nature (Bas, 1991).

Distinctively, mushrooms of this genus are characterized by having white to dull-colored fleshy carpophores with scaly or arcuately warted cap, pinkish or brown to chocolate brown free gills, annulate stipe, hyphal pileus cuticle, and presence or absence of chelocystidia and pleurocystidia (Kaur *et al.*, 2017). The genus is also characterized by a stipe separable from the pileus provided with one or several annuli and free lamellae that produce brown basidiospores (Callac and Chen, 2018).

1.3.4 *Agaricus* species

From a mycological point of view, large areas of the world are underexplored; thus, estimations on the total number of *Agaricus* species in existence are always approximate. The number of recognized *Agaricus* species has been in constant increase, as reported in taxonomic monographs and other taxonomic studies (Murrill, 1912, 1918, 1941; Hotson and Stuntz, 1938; Smith, 1944; Møller, 1950, 1952; Pilát, 1951; Orton, 1960; Huijsman, 1960; Bohus, 1975, 1990, 1995; Heinemann, 1978, 1986; Freeman, 1979a, b; Pegler, 1983, Pegler, 1990; Cappelli, 1984; Kerrigan, 1985, 1989; Wasser, 1989; Callac *et al.*, 1993; Albertó and Wright, 1994; Flower *et al.*, 1997; Grgurinovic, 1997; Saini *et al.*, 1997; Valenzuela *et al.*, 1997; Albertó, 1998; Esteve-Raventós, 1998; Mitchell and Walter, 1999; Nauta, 1999, 2000; Peterson *et al.*, 2000; Lanconelli, 2002; Parra, 2003, 2008, 2013; Lacheva and Stoichev, 2004; Natarajan *et al.*, 2005; Geml *et al.*, 2007; Ludwig, 2007).

In 1991, Bas indicated the total number of recognized *Agaricus* species in the world as lying between 300–400, with 70–90 species in Europe. In 2011, Zhao and colleagues reported on 386 recognized species among which 203 were temperate, and 183 were tropical. From this date, more species were discovered with 170 new species described from 2011 to 2018. The number of species recognized today exceeds 500 (Karunarathna *et al.*, 2016; Kerrigan, 2016; Chen *et al.*, 2017). According to Callac and Chen (2018), many putative new species have not yet been named, and species diversity remains poorly known in many regions. Indeed, 185 new species that have been proposed and included in phylogenetic analyses since 2000 are heterogeneously distributed as follows: 102 species were described from Asia, mostly from China and Thailand, and some from India, Iran, and Pakistan; 47 species were from the Americas, mainly from North America and some from the Caribbean and South America; 26 species were from Europe; nine species were from Oceania; and one species was from Africa. Callac and Chen (2018) provided a list of the different studies depicting such a species diversity, and speculated that *Agaricus* species in the tropics were less documented.

Among *Agaricus* species, some are collected in the wild for consumption, but have never been successfully domesticated, such as *A. augustus* and *A. campestris* while some others are not encountered frequently in the wild but have been domesticated, such as *A. bisporus*. Moreover, some species are cultivated to a lesser extent, like *A. bitorquis* and *A. arvensis*, or cultivated only for medicinal use, such as *A. subrufescens* (the almond mushroom; Callac and Chen, 2018).

1.4 The Species *Agaricus bisporus*

1.4.1 Taxonomy and naming

In the genus *Agaricus*, *A. bisporus* is a species belonging to the section *Bivelares* (Kerrigan *et al.*, 2008; Parra, 2013). The Latin name of the cultivated mushroom changed several times. Peck (1900) described from North America a brown, two-spored *Agaricus* under the name *A. brunnescens*. According to Malloch (1976), this species is identical to *A. bisporus*, and its name is the oldest one for the cultivated species. In fact, during the early 1980s, the name *A. brunnescens* Peck was used especially in the USA. Singer (in Singer and Harris, 1987), however, proved that *A. brunnescens* and *A. bisporus* are different species. In Europe, the name *A. bisporus* was maintained based on arguments put forward by Elliott (1983).

One other confusion was made by early mushroom growers who called the *Agaricus* under cultivation *Agaricus* or *Psalliota campestris*. This was further debated by Bas (1991) who explained that the true *A. campestris* L.: Fr. is a rather widespread species from grasslands that is easily distinguished from *A. bisporus*. It was Jacob Lange (1926) who first clearly defined the cultivated, two-spored *Agaricus*. He named it *Psalliota hortensis* var. *bispora*. Twenty years later, Imbach (1946) raised this variety to specific rank, which made *A. bisporus* (J.Lange) Imbach the correct name. Despite all confusions on the species name, that proposed by these authors (*A. bisporus* (J.Lange) Imbach) is adopted today.

Table 1.1. Natural habitats and geographical distribution of *Agaricus bisporus* (Patyshakuliyeva, 2015).

Habitat type	Vegetation type	Location
Temperate forest	*Cupressus* (cypress)	California, USA; Mexico; continental Greece and Crete; Italy; France
	Picea (spruce)	Alberta, Canada; Washington, USA
Mixed montane forest	*Eucalyptus*	Israel; Morocco; Congo; New Mexico
Boreal forest	*Picea* (spruce) *Populus* (poplar) *Betula* (birch)	Alaska, USA
Arid places	*Prosopis* (mesquites) *Tamarix* (salt cedar)	Sonoran Desert, California, USA
Coastal dunes	*Cupressus* (cypress) *Poaceae* (true grasses)	France
Pastoral land use area (plant wastes and manure)		UK; France; Russia; Portugal; China; Tasmania, Australia; Argentina

Nowadays, the cultivated *A. bisporus* may be variously named based on its maturity stage and its color. When immature and white it is known as ‘common mushroom,’ ‘button mushroom,’ ‘cultivated mushroom,’ ‘table mushroom,’ ‘Crimini mushroom,’ and ‘champignon mushroom.’ When immature and brown, it may be known as ‘Swiss brown mushroom,’ ‘Roman brown mushroom,’ ‘Italian brown mushroom,’ ‘Cremini/Crimini mushroom,’ or ‘chestnut mushroom.’ When mature, the mushroom is known as ‘Portobello mushroom.’

In the wild, *A. bisporus* has a wide geographical distribution from the boreal region of Alaska (Geml *et al.*, 2008) to the equatorial climate of Congo (Heinemann, 1956), and from coastal dunes to mountains (Table 1.1; Kerrigan, 1995; Xu *et al.*, 1997; Callac *et al.*, 2002). It can be found at more than 3000 m elevation (Largeteau *et al.*, 2011).

A. bisporus is mainly cultivated in temperate regions since current cultivars of this species are unable to fruit at 25°C. However, fruiting tests revealed that the percentage of wild isolates able to fruit in cultivation at 25°C varied on average from 35% to 78% with a lower yield among different populations of *A. bisporus* var. *bisporus* from temperate regions of Europe and North America (Largeteau *et al.*, 2011). Callac and Chen (2018) have recently suggested that temperate populations of this species retain an evolutionary potential to adapt to a hot climate. In regions with hotter climates, including India (Heinemann, 1978; Cappelli, 1984; Kerrigan, 1986) and Spain, *A. bitorquis* (the pavement mushroom) is grown instead

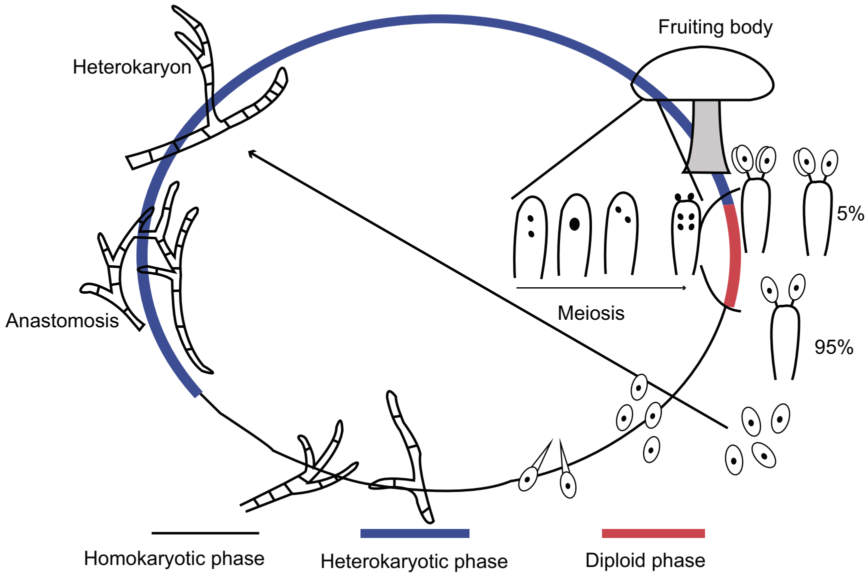

Fig. 1.1. Typical life cycle of *Agaricus bisporus* var. *bisporus*. Most basidia produce two spores, each receiving non-sister nuclei. Due to the low recombination frequency between homologous chromosomes, these spores retain (almost) all alleles of the parental nuclei. The homologous chromosomes have an altered distribution over the constituent nuclei. From Sonnenberg *et al*., 2011.

of *A. bisporus* in hot summers as it has a slightly higher growth temperature (Largeteau *et al*., 2011).

1.4.2 Life cycle

The most typical feature of Basidiomycetes is that they carry sexual spores externally on structures called 'basidia.' *A. bisporus* is an amphithallic species, secondarily with homothallism or heterothallism depending on the ploidy level of the spores, which can be homokaryotic (n) or heterokaryotic (n+n), respectively (Largeteau *et al*., 2011). Three varieties of *A. bisporus* can be distinguished by the average number of spores carried by their basidia and their life cycle: *A. bisporus* var. *bisporus* (Fig. 1.1; bisporic basidia, pseudohomothallic life cycle; Raper *et al*., 1972); *A. bisporus* var. *burnettii* (tetrasporic basidia, predominantly heterothallic life cycle; Kerrigan *et al*., 1994); and *A. bisporus* var. *eurotetrasporus* (tetrasporic basidia, homothallic life cycle; Callac *et al*., 2003). However, all the traditional cultivated and most of the wild strains belong to *A. bisporus* var. *bisporus*. In this variety, most of the basidia are bisporic and produce heterokaryotic spores which confer upon it a predominant pseudohomothallic life cycle (Raper *et al*., 1972).

In basidia, meiosis takes place where the fusion of two haploid nuclei, meiosis I and meiosis II, lead to the formation of four recombinant haploid nuclei (Kerrigan *et al.*, 1993). Non-sister nuclei are paired into one spore, causing an intratetrad mating which leads to the formation of spores that germinate into heterokaryons containing nuclei with different mating types, a prerequisite to producing fruiting bodies.

The majority of the basidia produce only two spores, and only a minority produce three or four spores which will generate homokaryons containing one type of haploid nucleus. These homokaryons need to be mated with compatible homokaryons to produce mushrooms, and are thus useful for outbreeding. Homokaryotic single spore isolates (SSI) show, in general, a lower growth rate than heterokaryotic SSI (Kerrigan *et al.*, 1992). This character is often used to preselect for homokaryons in spore prints. All commercial and most wild-collected strains have a secondary homothallic life cycle (Raper *et al.*, 1972; Xu *et al.*, 1998). Although homokaryotic status has been confirmed with genetic markers (Gao *et al.*, 2013), the low percentage of homokaryotic offspring is a significant drawback, slowing down the breeding work of *A. bisporus* (Sonnenberg *et al.*, 2017).

1.4.3 Vegetative and reproductive structures

A significant part of the fungal life cycle consists of vegetative growth where the fungus colonizes nutrient-rich areas to support its metabolism and general development (Watkinson *et al.*, 2001). A fungal colony generally consists of an interconnected network of branching hyphal cells spreading from a single point (Herman, 2009). The rigid composition of this cellular organization has important consequences for the way fungi can expand (Harris, 2009). In higher Basidiomycetes, great diversity in hyphal morphology exists (Molitoris *et al.*, 1996) that is related to the type of branching, cell wall thickness, and to the presence of aggregates inside cells or at their surface (Lohwag, 1941; Nobles, 1965; Donk, 1971). The mycelium of *A. bisporus* consists of strand-like mycelial cords (Molitoris *et al.*, 1996) that branch out through the growing medium.

Strand formation, as described by Mathew (1961) in Petri dish experiments, was found to proceed in two stages: in the first stage, several robust leading hypha branched outward from the food base or the inoculum disk at fairly wide intervals to form progressively thinner branches which grew away from or followed their parent hyphae. At first, growing away from the parent hypha, other branches were observed to change direction and grow alongside a larger hypha that they chanced to encounter. Fresh hyphae growing out from the food base tended to be smaller and made only limited outward growth. Some of these anastomosed at their tips with one of the leading hyphae or followed it in further growth. Others branched frequently and anastomosed among themselves to form a network near the food base. The second stage in strand development was characterized by numerous fine, thin-walled, aseptate hyphae as branches from the older regions of the main hyphae and their branches. These hyphae, assigned as 'tendril hyphae,' grew either forward or backward along the large hypha. In turn, the original tendril hyphae frequently branched to form yet finer tendrils, which grew around the larger hyphae, filling up interstices in the developing strands. Various types of hyphal anastomosis also helped consolidate the developing major strands, increasing in thickness with the accretion of minor strands.

Early growth of *A. bisporus* on sterile compost in dishes, as described by Straatsma *et al.* (1991), was characterized by slow- and flat-growing mycelium. Later, faster-growing sectors were formed, characterized by dense, fluffy mycelium consisting of radially oriented hyphae. Ultimately, sectors appeared all over the colonies' circumference

Importantly, a relatively stable characteristic of *A. bisporus* cultures is the presence of calcium oxalate (COC) crystals on hyphae (Buchalo, 1988). Practically, pH regulation or addition of calcium chloride to the growing medium of *A. bisporus* could stimulate the formation of COC crystals (Edwards, 1974) to benefit from their many roles reported in the literature, including: the provision of a mechanical barrier against bacteria, fungi, and arthropod attacks (Holdonrleder, 1982); disposal of accumulated toxic metabolites (Garibova *et al.*, 1982); storage of carbon for later utilization (Badalyan, 1993); maintenance of carbon/nitrogen balance through the elimination of excess carbon in a nitrogen-poor substrate (Akamatsu *et al.*, 1994); and many others.

During the commercial growing of *A. bisporus*, the first phase of mycelium growth starts by inoculating compost with cereal grains colonized with mushroom mycelium or spawn. In contrast, the second phase is started by stimulating fruit formation. In fact, changes in volatiles, cool temperatures, and low CO_2 initiate the formation of mushrooms. A model has been proposed by Eastwood *et al.* (2013) which involves three separate environmental factors at different stages of mushroom development:

1. The C8 volatile 1-octen-3-ol regulates the change from vegetative hyphae to the multicellular knots that give rise to mushrooms. Levels of 350 ppm are inhibitory. Once levels drop, the fruiting process starts.
2. Low temperatures allow the formation of the primordia. Only primordia that form below the surface of the casing turn into mushrooms. Smooth, undifferentiated primordia that appear on the casing surface – as occurs at 25°C – fail to develop further.
3. CO_2 levels determine the number of primordia that develop into mushrooms (generally 5–10%). High CO_2 levels (>3000 ppm) reduce the number of primordia that develop into mushrooms.

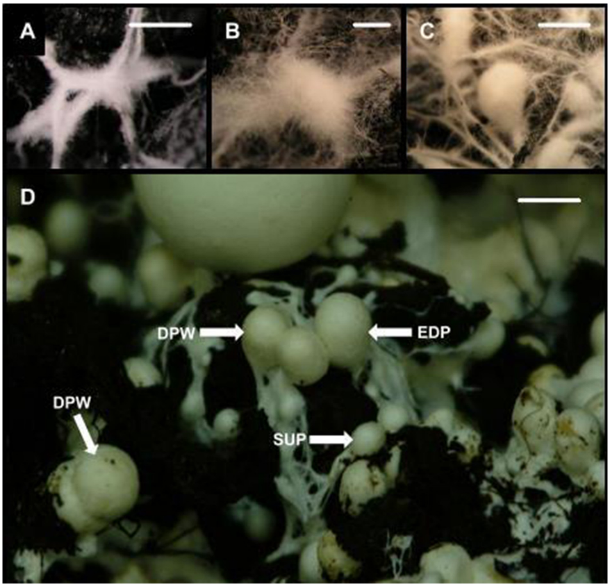

Fig. 1.2. Fruiting body development in *Agaricus bisporus*. (A) Fluffy mycelia cords; (B) Hyphal knots, scale bar A + B = 1 mm; (C) Fluffy undifferentiated primordia (approximately 95 h post-airing), scale bar = 2 mm; (D) approximately 200 h post-airing showing smooth undifferentiated primordia (SUP), elongated differentiated primordia (EDP), and differentiating primordia with waist (DPW), scale bar = 8 mm. Reproduced from Eastwood *et al*., 2013, with permission from Elsevier BV through PLSclear.

It was suggested that the detection of optimal conditions for reproductive growth is coordinated by the Spitzenkörper at the tip of an extending hypha, which serves as a signal trafficking organ (Harris, 2009). The earliest morphological sign of reproductive growth in *A. bisporus* is seen when mycelial cords exhibit heavy and localized branching referred to as 'primary nodules' or 'hyphal knots' (Wood, 1976; Kües and Liu, 2000; Kües, 2000; Umar and Van Griensven, 1997a, b). Moore (1994) speculated that in all multihyphal fungal structures, the ultimate morphogenetic regulatory structure may be the Reijnders hyphal knot – a little community comprising an induction hypha (or hyphal tip/compartment) – and the immediately surrounding hyphae (or tips/compartments) which can be brought under its influence. Larger scale morphogenesis could be coordinated by 'knot to knot' interactions (Straatsma *et al*., 2013).

The newly formed, short hyphae in these hyphal knots (Fig. 1.2) often have a globose and inflated cellular morphology and are embedded in a mucilaginous material. The primary hyphal knots (1–2 mm) then increase in size, through further hyphal growth and aggregation, forming compact secondary nodules (2–4 mm), commonly referred to as 'initial' or 'primordium' (Umar and Van Griensven, 1999; Kües, 2000; Eastwood *et al.*, 2013). Later, cap and stipe differentiation is initiated by cell proliferation; the histo-organogenetic stage occurs only late in the development of primordium and continues during the first stages of fruit body development. During the primordium's further development, the hyphal organization in this structure takes on its final mushroom-like characteristics. Hyphae that will form the stipe are predominantly oriented vertically, and those that will form the cap are oriented radially (Umar and Van Griensven, 1997c).

Clear signs of cap and stipe become visible at about 4–5 mm, but a velum connecting cap and stipe is not yet differentiated (Hammond and Nichols, 1975). Differentiated primordial structures then enlarge at a size of about 5–7 mm, called 'pinheads' (Eastwood *et al.*, 2013). At this stage (Stage 1), cell degeneration at the base of the young cap initiates a vertically positioned annular cavity (hymenial split), which eventually results in the beginnings of lamella formation. Hymenial split is then marked by an outer visible demarcation between cap and stipe in the differentiating primordium (Umar and Van Griensven, 1997c; Clémençon, 2004, 2012).

The cap with pileus margin and the beginning stipe with the 'bulbous' basal plectenchymal tissue beneath are then clearly distinguishable underneath the young outer skin (Eastwood *et al.*, 2013; Straatsma *et al.*, 2013). During the next stages, active structures further increase in size by both cell proliferation and cellular expansion. The hyphae at the cap's margin heavily branch and grow radially outwards to enlarge both the pileus and the cavity in size. With time, the enlarging downward-oriented cap margin bends round in direction toward the stipe and nestles to the partial veil evolving between cap and stipe (Kües and Navarro-Gonzalez, 2015). Lamellae grow in height by cell proliferation at their base attached to the pileus, and the partial veil becomes visible from the outside with further cap growth (Hammond and Nichols, 1975; de Groot *et al.*, 1997). When the cap is about 2–3 cm, its lower edges become closely connected to the stipe by a velum that remains closed and unstretched. This marks Stage 2, or 'button stage' (Hammond and Nichols, 1975; Hayes, 1978). Within the enclosed growing cap, the lamellae and mature gills are stained brown through a gradual darkening of cell saps by pink-red quinonoid pigments (Claydon, 1985). Stage 3 of development, or 'closed cups,' is reached when the cap is about 5 cm with a stretched but still closed velum. Stage 4, or 'cup opening stage,' is when the partial veil tears and Stage 5, 'open cup stage,' is when the veil is finally fully torn, and the gills become visible (Hammond and Nichols, 1975; Hayes, 1978).

The closed buttons already form basidiospores, as do the more advanced closed cups (Elliott, 1977). The basidia are born in a palisade-like layer called the 'hymenium' on the lower surface of the pileus, known as the 'hymenophore,' which appears in the forms of gills or lamellae. Basidia in *A. bisporus* do not mature synchronously. In mature gills, basidioles contain fused nuclei, but parts of the basidioles will successively replace any matured and, upon spore release, collapsed basidia. In contrast, many other basidioles appear to have only structural function commonly known as 'sterile paraphyzes' (Manocha, 1965; Saksena *et al.*, 1976; Allen *et al.*, 1992). Basidiospores are first released in Stages 4 and 5 (Kües and Navarro-Gonzalez, 2015).

Primordial development up to Stage 2 and then Stage 4 takes about 10 and 12 days, respectively (de Groot *et al.*, 1996, 1997; Morin *et al.*, 2012). During this time, stipe elongation occurs first at the lower part of the stipe to lift the developing mushroom from the substrate, and subsequently during mushroom maturation (from Stage 2 to Stage 4) by increasing proportionally with cap expansion, then by cell expansion through diffuse cell wall extension in the upper part of the stipe above the partial veil, but also by some cell proliferation (Kües and Navarro-Gonzalez, 2015). The stipe extends to about 2–3 times the length it is at the button stage. Around the extended stipe, at about two-thirds of its total height, a superior annulus or a velum tissue collar is left with an inferior ring somewhat visible below it. Both annuli mark the borders of attachment of the partial veil to the stipe (Gruen, 1963; Craig *et al.*, 1977).

Spore formation and shedding in *A. bisporus* continues for several more days ('spore-shedding stage') during which the flourishing cap may increase by further growth in diameter to over 20 cm: 'open flats' with a convex upper cap surface and flat gill surface (Stage 6); then 'flats' with the gill surface curving upwards (Stage 7; Hammond and Nichols, 1975). Growth can even happen after a sporophore is harvested at the button stage or a later stage (Gruen, 1963; Umar and Van Griensven, 1997b; Braaksma *et al.*, 1998) depending on nutrients provided by the stipe (Ajlouni *et al.*, 1992). Ultimately, the cap turns into the 'stage of senescence' in which cap tissues pigment and slowly degenerate, along with the mycelial cords (Burton *et al.*, 1997; Umar and Van Griensven, 1997b).

1.5 Nutritional and Medicinal Value of *Agaricus bisporus*

Nutritional information on foods is becoming increasingly important for both professionals in the food health areas and for consumers who show heightened concern about the nutritional quality of food, which makes up or could be introduced into their diets. *A. bisporus* is considered a valuable addition to the human diet, especially by health-conscious people. It is considered a substitute for meat with comparable nutritional value to many vegetables (Chang and Miles, 2004). Its nutritional status has been valorized based on its chemical composition.

The mushroom secretes enzymes to digest foodstuffs to get nutrients from organic matter in compost (Goyal *et al.*, 2006). As a result, its nutritional value largely depends on the compost's chemical composition (Gothwal *et al.*, 2012). As a matter of fact, the chemical composition data of cultivated *A. bisporus* mushrooms published by different authors working with even the same species are variable (Atila *et al.*, 2017). Observed differences, as extracted from early reports, may to some extent be explained by the analytical methods being used to determine the various mushroom components, or by other uncontrollable factors including the composition of the compost, mushroom strain, flush of mushroom culture, developmental/maturity stage of fruit body at harvest, what part of the mushroom is analyzed (cap or stipe), and mushroom size. It is important to note that postharvest treatments, processing, and cooking are effective determinants of mushroom proximate composition (Manzi *et al.*, 2001). Still, their effect will be discussed in later sections.

1.5.1 Energy

The calorific or energy value of a food is related to the number of calories (kcal) that it contains. It is calculated after determining the quantity of nutrients (carbohydrates 4 kcal/g, proteins 4 kcal/g, and lipids 9 kcal/g). Specifically, the button mushroom is one of the mushrooms with the lowest calories. Its energy value is even lower than many other vegetables such as broccoli, carrot, cauliflower, potato, onion, pea, pepper, squash, eggplant, and artichoke (Ramos, 2015). A calorific value ranging between 29 and 33 kcal/100 g was reported for the white button mushroom (Manzi *et al.*, 2001), and between 25.1 and 32.6 kcal/100 g for the brown mushroom (Reis *et al.*, 2012a).

1.5.2 Dry matter

When the nutritional value of mushrooms is evaluated, perhaps the most important factor is their dry matter/moisture content, which directly affects their nutrient content (Mattila *et al.*, 2002). The mushroom generally contains between 88% and 91% moisture (Crisan and Sands, 1978). Dry matter content is a basic indicator characterizing the raw material concerning the level of chemical constituents: carbohydrates, proteins, fiber, and minerals (Bernaś *et al.*, 2006). It is an important indicator of mushroom quality as it influences the mushroom shelf life and indicates its suitability for processing (Kałużewicz *et al.*, 2016).

In the literature, dry matter content of *A. bisporus* mushrooms ranged between 5.5–11.5% based on various factors, such as substrate and casing soil composition; species-, variety- and strain-related differences; the stage at which mushrooms were harvested; as well as the cap and stipe size at each mushroom flush (Table 1.2). With a general observation of reported values, one could assume that the strain plays a major role in influencing the dry matter content of *A. bisporus*. It varied differently when assessed on different strains of mushrooms at similar maturity stages or flushes (Tsai

Table 1.2. Dry matter content (%) in *Agaricus bisporus* mushrooms.

Source	Dry matter	Experiment conditions
Bąkowski *et al.*, 1986	7.1–11.5	Different strains (OCNOS-1, Somycel 11, Somycel 92, Somycel 653) and pileus diameter (25–40 mm, 40–50 mm)
Mattila *et al.*, 2002[a]	7.7–7.8	Local species (Finland) (white-brown)
Vetter, 2003	9.4–9.6	Different strains (var. 333 and var. 229)
Uliński and Szudyga, 2004	7.7–8.7	Three flushes of large-carpophore and medium-carpophore strains
Dikeman *et al.*, 2005	5.5–7.0	Different varieties (white, Crimini, Portabella) and maturity stages (immature, mature)
Tsai *et al.*, 2007[a]	8.0–10.7	Different maturity stages of MS strain: pinhead, veil intact (tight), veil intact (stretched), veil opened, gills exposed
Colak *et al.*, 2007	7.9–11.4	Different substrates and casing materials
Reis *et al.*, 2012a[a]	7.5–8.3	Local species (north-east Portugal) (white and Portabella)
Sobieralski *et al.*, 2011	9.3–11.2	Different strains of *A. bisporus*, *A. bitorquis* and cultivated species K26 (Poland)
Kałużewicz *et al.*, 2016	6.8–9.1	Different strains (Poland) of different pileus diameter (1.5–2.5 cm, 2.6–3.5 cm, 3.6–4.5 cm, and 4.6–5.5 cm) in three flushes

[a]Values were calculated by authors based on fresh weight; other data were calculated on dry weight basis.

et al., 2007; Kałużewicz *et al.*, 2016). In general, dry matter was higher in fruit bodies of large-fruiting strains at the three mushroom flushes (Uliński and Szudyga, 2004; Kałużewicz *et al.*, 2016).

1.5.3 Ash

'Ash' is what remains after the organic part of the mushroom has been oxidized through combustion. It is a measure of the total amount of minerals and salts in the mushroom (Ramos, 2015). Studies have shown that ash content ranged between 7.8 and 12.7% of dry weight in *A. bisporus* samples (Table 1.3).

1.5.4 Proteins and amino acids

Protein is the most critical component contributing to the nutritional value of food and is an important constituent of the dry matter of mushrooms (Miles and Chang, 1997). Average crude protein content in *A. bisporus* mushrooms may oscillate between 14.5% and 41.1% on a dry weight basis

Table 1.3. Ash content (% dry weight) in *Agaricus bisporus*.

Source	Ash content	Experiment conditions
Kurasawa *et al*., 1982	10–12	Different strains from the market
Cheung, 1997	10.3	From local market
Manzi *et al*., 2001	11.4	From local market
Mattila *et al*., 2002	10.0–10.1	Different strains
USDA, 2005	11.2–12.7	Different strains and growth stages
CSTJ, 2005	13.1	–
Goyal *et al*., 2006	9.17	–
Tsai *et al*., 2007	7.77–11	Different growth stages
Kalač, 2013	9.74–11.36	Different varieties
Vyas *et al*., 2013	9.7–9.9	Different types of compost

and 1.2 and 2.1% on a fresh weight basis (Table 1.4). In both cases, variations in reported values are due to different considerations: the first is related to analytical methods where different nitrogen to protein (NP) conversion factors were used to calculate crude protein content. The crude protein content of most foods is calculated from the nitrogen content using the conversion factor N × 6.25. Still, the Food and Agriculture Organization (FAO, 1970, 1972) has adopted the conversion factor N × 4.38 for mushrooms. In fact, 60–77% of the nitrogen in mushrooms is found in proteins, while relatively high amounts of non-protein nitrogen are present, largely in the chitin of the cell walls as well as in free amino acids and nucleic acids (Miles and Chang, 1997). On the other hand, NP conversion factors are particular for each mushroom species, and the use of a single factor may lead to errors in protein values. For instance, a conversion factor of 4.7% was used to calculate crude protein for *A. bisporus* in the study of Mattila *et al.* (2002). Moreover, time of harvest, compost type (Kosson and Bąkowski, 1984), compost supplementation by different nitrogen sources (Mami *et al.*, 2013), mushroom maturity stage (Dikeman *et al.*, 2005; Tsai *et al.*, 2007), and mushroom part exerted a considerable influence on reported values of crude protein content in *A. bisporus.* The effects of these factors varied with the mushroom strain.

A. bisporus contains all essential amino acids useful for human health, including methionine, threonine, valine, isoleucine, leucine, lysine, tyrosine, and phenylalanine (Atila *et al.*, 2017), as well as the non-essential amino acid cysteine, derived from methionine. Distinctively, amino acid composition in mushroom protein is more similar to animal protein than to vegetable protein, making them the ideal complement for vegetarian diets and a substitute for a meat diet (Muşzyńska *et al.*, 2013b; Ramos, 2015). The most common amino acid in *A. bisporus* is glutamic acid, while the most limited are sulfur amino acids, such as cysteine and methionine (Table 1.5.).

Table 1.4. Crude protein content (% dry weight) in *Agaricus bisporus* mushrooms.

Source	Crude protein	Analytical procedure	Experiment conditions
Kosson and Bąkowski, 1984	14.5–24.9	FAO, 1970, 1972	Different strains (strain 9, strain 53), mushroom sizes (<25 mm/25–40 mm, >40 mm cap and stipe), and compost types (chicken manure, horse manure)
Bąkowski *et al*., 1986	29.8–31.4	FAO, 1970, 1972	Different strains (OCNOS-1, Somycel 9, Somycel 11, Somycel 53)
Vetter, 2003	38.3–39.3	Hungarian standard and official methods	Different strains (var 333 and var 229)
Dikeman *et al*., 2005	26.3–31.4	AOAC, 1995	Different varieties (white, Crimini and Portabella) and maturity stages (immature, mature)
Goyal *et al*., 2006	24.4	AOAC, 1995	–
Tsai *et al*., 2007	21.2–27.4	AOAC, 1990	Different maturity stages: pinhead, veil intact (tight), veil intact (stretched), veil opened, gills exposed
Teklit, 2015[b]	41.1	AOAC, 1995	–
Mohiuddin *et al*., 2015[b]	17.7–24.7	Micro-Kjeldhal method	Different strains (Agora, Chinese can-1, Chinese can-2, Chinese can-3)
Reis *et al*., 2012a[a]	1.23–1.29	AOAC, 1995	Local varieties (Portugal) (white/Portabella)
Jaworska *et al*., 2015[a]	1.2	AOAC, 2005	–
Mattila *et al*., 2002[a]	2.07–2.09[c]	EC, 1998	Local varieties (Finland) (white/brown)

[a]Crude protein calculated on a fresh weight basis;
[b]Crude protein calculated using nitrogen to protein (NP) conversion factor NP = 6.24 (%N × 6.24), remaining data were calculated using NP = 4.38 (%N × 4.38);
[c]Crude protein calculated by authors using NP = 4.7 (%N × 4.7).

Table 1.5. Amino acid profile of *Agaricus bisporus* mushrooms.

Amino acids		Kosson and Bąkowski, 1984[a,c]	Manzi *et al.*, 1999[d]	Cherno *et al.*, 2013[d]		USDA, 2005[c]			Kim *et al.*, 2009[e]	Liu *et al.*, 2014[e]	Bąkowski *et al.*, 1986[b,c]			
				Cap	Stipe	White	Crimini	Portabella	Brown (strain KKU-02)		OCNOS-1	Somycel 653	Somycel 11	Somycel 92
Semi-essential	Histidine	2.1	2.8	2.8	2.8	1.8	2.7	1.7	1.7	0.8	1.6	1.4–1.8	1.6–1.9	1.9–2.2
	Arginine	3.4	8.0	4.9	4.8	2.5	4.9	2.7	0.4	1.5	3.7–3.8	3.2–3.6	3.8–4.1	4.4–4.7
Essential	Isoleucine	2.7	5.1	3.6	3.6	2.5	4.0	2.0	0.3	1.1	2.6–2.7	2.0–2.5	2.6–3.0	3.3–3.6
	Leucine	4.8	7.6	7.2	7.3	3.9	6.1	3.2	0.2	2.0	4.5–4.6	4.0–4.1	4.7–5.0	5.6–5.8
	Lysine	6.2	8.4	5.7	5.7	3.5	10.0	2.5	4.9	1.4	4.9–5.2	5.8–6.1	5.6–5.9	5.1–5.7
	Methionine	1.3	1.0	1.1	1.8	1.0	1.9	0.7	0.6	0.1	1.1	0.8–0.9	1.1–1.2	1.1–1.2
	Threonine	3.5	5.9	4.9	4.6	3.5	4.5	2.7	7.6	7.1	3.0–3.7	2.6–2.9	3.0–3.4	4.2
	Tryptophan	nd	2.2	1.2	1.4	1.1	2.2	1.2	nd	0.3	nd	nd	nd	nd
	Phenylalanine	5.3	4.7	4.2	4.2	2.8	3.9	2.2	0.3	2.8	2.8–3.1	2.5–3.2	2.7–2.8	3.4–3.8
	Valine	3.6	3.6	3.9	4.4	7.5	4.6	6.2	1.2	1.8	3.5–3.6	3.1–3.6	3.4–3.7	4.1–4.3
Non-essential	Alanine	4.7	5.8	5.7	5.7	6.4	7.5	4.2	0.4	8.8	4.9–5.3	3.9–4.6	4.8–5.5	4.8–5.1
	Aspartic acid	7.0	8.1	11.8	10.9	6.3	9.1	6.2	16.1	2.3	7.0–7.6	6.2–7.9	6.4–8.6	7.7–8.1
	Cysteine	nd	1.1	3.7	4.4	0.4	0.4	0.5	1.1	2.8	–	–	–	–
	Glutamic acid	14.5	16.2	20.0	18.1	11.0	17.0	11.0	17.9	18.6	15.3–18.2	12.9–13.8	14.8–17.7	15.1–18.0
	Glycine	3.4	3.6	5.0	5.7	3.0	4.4	2.5	5.9	1.2	3.6–3.8	2.9–3.1	3.4–3.8	3.7
	Proline	4.0	6.1	5.3	5.9	2.5	7.0	3.0	8.5	2.7	6.1–7.0	5.1–5.6	4.0–4.6	4.6–5.0
	Serine	3.7	5.2	5.8	5.9	3.0	4.5	2.7	11.1	3.6	3.1–3.4	2.5–2.9	3.1–3.7	3.6–4.3
	Tyrosine	2.3	4.2	3.4	2.7	1.4	2.2	1.7	0.2	0.9	2.1–2.7	2.1–2.2	2.1–2.4	2.7–3.0

nd: non-detectable
[a]Different strains (strain 9, strain 53), mushroom sizes (<25 mm/25–40 mm, >40 mm cap and stipe), and compost types (chicken manure, horse manure);
[b]Different strains and pileus diameter (25–40 mm, 40–50 mm);
[c]g/16g N;
[d]g/100 g total protein;
[e]g/kg dry weight.

Amino acids, as suggested by the name, contain an amino group (-NH_2) and a carboxylic acid group (-COOH; Oxtoby *et al.*, 2003). Consequently, the kind of nitrogen source introduced in compost may change the amino acid composition of *A. bisporus* (Kosson and Bąkowski, 1984). Supplementing compost with ammonium nitrate increased the aspartic acid, alanine, valine, and sulfur amino acid content of mushrooms. At the same time, it decreased both proline and arginine. Amino acid content may also change with successive flushes: an increase in proline and phenylalanine, and a decrease in aspartic acid, glutamic acid, lysine, arginine, and sulfur acids were found in each successive flush of mushrooms (Maggioni *et al.*, 1968). A decrease in tyrosine was also reported with successive flushes (Tsai *et al.*, 2007). The differences between the results of different reports are related to mushroom developmental stages, strains, and analytical methods.

1.5.5 Carbohydrates

Carbohydrates are present in fairly high amounts in mushrooms (OECD, 2007). According to Braaksma and Schaap (1996), mushroom total carbohydrate content is determined as follows:

$$\text{Carbohydrates} = 100 - (\text{water} + \text{ash} + \text{crude protein} + \text{crude fat content}) \quad (1.1)$$

The total carbohydrate content of *A. bisporus* ranges between 38.3–63.4 g/100 g on a dry weight basis, and 3.1–7.1 g/100 g on a fresh weight basis (Table 1.6).

However, the determination of carbohydrate content does not give enough information about carbohydrate composition in mushrooms. Specifically, mushroom carbohydrates include sugars, sugar alcohols, and

Table 1.6. Total carbohydrate content in *Agaricus bisporus* on dry weight (DW) basis and fresh weight (FW) basis.

Source	g/100 g DW	g/100 g FW	Notes
Abou Raya *et al.*, 2014	38.3–46.7	–	–
Ahlavat *et al.*, 2016	51.05	–	–
Gheibi *et al.*, 2006	–	4.5	–
Goyal *et al.*, 2006	53.1	–	–
Colak *et al.*, 2007	–	3.1–5.6	Different types of composts and casing soil
Reis *et al.*, 2012a	–	4.9–7.1	White/brown mushrooms
Liu *et al.*, 2014	63.4	–	–

sugar acids. Sugars are composed of monosaccharides, disaccharides, oligosaccharides, and polysaccharides. Polysaccharides are easily hydrolyzable (EHP) or hardly hydrolyzable (HHP). It was reported that EHPs dominate among mushroom carbohydrates, constituting around 64.7% of total carbohydrates. Monosaccharides found in varying amounts in their hydrolyzates are glucose, mannose, fucose, xylose, fructose, and galactose, where glucose or mannose were frequently the most dominant (Kim *et al.*, 2009; He *et al.*, 2012; Cherno *et al.*, 2013).

Disaccharides such as lactose and sucrose were detected in deficient amounts, sometimes non-detectable in *A. bisporus*. The mushroom also contains appreciable amounts of the disaccharide trehalose, usually at fairly constant levels around 1–3% of the dry weight (Hammond and Nichols, 1976, 1979; Ajlouni *et al.*, 1993). HHPs include chitin, glucans, and mannans (Cheung, 2010). The type of HHP depends on the mushroom type. For instance, chitin dominates in button mushroom, while glucan prevails in oyster mushroom (*Pleurotus ostreatus;* Chang and Miles, 2004; Andres and Baumann, 2012). Most of these polysaccharides are indigestible for humans; thus, they can be considered dietary fibers (Beelman *et al.*, 2003). In fact, dietary fiber includes components of cell walls, such as hemicelluloses (mannans) and non-starchy polysaccharides like chitin and β-glucans (Cheung, 2009; Maftoun *et al.*, 2015). Total dietary fibers in mushrooms, as the sum of intrinsic non-digestible carbohydrates (Vetter, 2007), were found to make up 40.5 g/100 g dry weight in *A. bisporus* (Ramos, 2015). Chitin is claimed to have advantageous and functional properties in the dietary fiber fraction of mushrooms (Beelman *et al.*, 2003; Dikeman *et al.*, 2005; Vetter, 2007), where it constitutes between 1.8–9.6 g/100 g dry weight (Manzi *et al.*, 2001; Dikeman *et al.*, 2005; Nitschke *et al.*, 2011). Chitin content of the cultivated mushroom is a characteristic of the species and seems to be independent of the cultivars (varieties). It is higher in the cap compared to the stipe (Vetter, 2007).

Cultivated button mushrooms do not present a very high β-glucans content (McCleary and Draga, 2016). The most common glucans extracted from *A. bisporus* are (1–>3), (1–>6)-β-glucans (Ren *et al.*, 2012). Among mannans, galactomannan was found in high concentrations in tested *A. bisporus* samples (Smiderle *et al.*, 2013). One interesting feature in the button mushroom is that it contains glycogen, a polysaccharide typical to the animal kingdom (Ramos, 2015). It is present in around 50–100 g/kg dry matter (Kalač, 2013). Finally, the content of complex carbohydrates and fiber shows that mushrooms are a very low glycemic index food (IG = 15), so their digestion is slower, and the sugar is released gradually. Therefore, they are recommended for people suffering from diabetes since they evolve a lower increase in postprandial glycemia (Ramos, 2015).

1.5.6 Sugar alcohols

Among sugars and sugar alcohols, mannitol dominates in *A. bisporus* (Baars *et al.*, 2016). It is the main form of carbon storage in the mushroom fruit body, and its level increases with maturation (Wannet *et al.*, 2000; Tsai *et al.*, 2007). It also varies with the mushroom part being analyzed, ranging between 10–18% in the gills, 30–49% in the cap, and 19–52% in the stipe (Hammond and Nichols, 1976; Ajlouni *et al.*, 1993). Mannitol may also act as an osmolyte in growing fruit bodies since mushrooms grown under salt stress accumulate larger amounts of mannitol than non-stressed mushrooms (Stoop and Mooibroek, 1998).

1.5.7 Organic acids

Various organic acids are found in fresh *A. bisporus* such as acetic, citric, formic, fumaric, lactic, malic, malonic, oxalic, and succinic acids (Stojkovic *et al.*, 2014; Glamočlija *et al.*, 2015). The latter is the most dominant in many *Agaricus* strains (Table 1.7.).

1.5.8 Fats

In general, the fat content of mushrooms is very low compared to proteins and carbohydrates (Abou Fayssal *et al.*, 2020; Alsanad *et al.*, 2021). Crude fat content ranges mostly between 1.6–4.0% of dry weight (Pedneault *et al.*, 2007; Tsai *et al.*, 2007; Shao *et al.*, 2010; Kalač, 2013; Ahlavat *et al.*, 2016) and rarely above 6% (Kalač, 2013). The fat content profile of *A. bisporus* is characterized by a higher concentration of mono- and polyunsaturated fatty acids than in saturated fatty acids (Rodrigues *et al.*, 2015), which increases its nutritional value. Total monounsaturated fatty acids ranged between 1.4–5.3%; the range of polyunsaturated fatty acids was 69.3–79.8% of total fatty acids (Shao *et al.*, 2010; Reis *et al.*, 2012a); while the range of total saturated fatty acids was 12.8–26.5% of total fatty acids (Shao *et al.*, 2010; Öztürk *et al.*, 2011; Reis *et al.*, 2012a; Abou Raya *et al.*, 2014; Goyal *et al.*, 2015). Around 26 fatty acids were detected by Reis *et al.* (2012a). Linoleic acid (18:2n-6) was dominant, followed by oleic acid (18:1) from unsaturated fatty acids, and palmitic (16:0) and stearic (18:0) acids from saturated fatty acids.

Caprylic acid (saturated fatty acid), and palmitoleic and linolenic acids (unsaturated fatty acids) were found present in lesser amounts in the mushroom (up to 5% of total fatty acids; Reis *et al.*, 2012a; Goyal *et al.*, 2015), and others such as capric, lauric, pentadecanoic, heptadecanoic, heneiocosylic, bhehenic, and lignoceric acids (saturated fatty acids), and elaidic, ecosadieonic, eicosenoic, gadoleic, nervonic, euric, asclepic, and hexadecatrienoic acids (unsaturated fatty acids) were found in less than 1% of total fatty acids (Mau *et al.*, 1991; Shao *et al.*, 2010; Öztürk *et al.*, 2011; Cherno *et al.*, 2013).

Table 1.7. Content of organic acids (mg/100 g dry weight) in fruiting bodies of cultivated *Agaricus bisporus* (first flush). From Gąsecka *et al*., 2018.

	Acetic	Citric	Formic	Fumaric	Lactic	Malic	Malonic	Oxalic	Succinic	Total
A. bisporus (brown), Hollander Spawn C9	$170.0^{c}\pm12.2$	$396.4^{c}\pm27.1$	$181.4^{c,d}\pm18.1$	$49.2^{b}\pm2.1$	$6806.6^{c}\pm271.9$	$45.3^{d}\pm1.9$	$216.4^{c,d}\pm18.2$	$713.8^{f,g}\pm18.9$	$5298.9^{e}\pm60.0$	13878.0^{b}
A. bisporus (white), Sylvan 767	$615.1^{b}\pm52.3$	nd	$2431.0^{a}\pm280.1$	$35.3^{b,c}\pm5.7$	$1853.2^{d,e}\pm165.2$	$397.9^{b}\pm29.4$	$1128.4^{a}\pm294.3$	$1317.9^{e}\pm151.2$	$2242.2^{h}\pm148.4$	10021.0^{c}
A. bisporus (white) Amycel 2600	$153.9^{c,d}\pm18.3$	nd	nd	$4.3^{d}\pm1.1$	$1259.3^{d,e}\pm270.2$	$68.0^{d}\pm4.2$	nd	$2023.2^{d}\pm153.3$	$11478.4^{a}\pm707.6$	14987.1^{d}
A. bisporus (white), Kanmy-cel 3–1	nd	nd	nd	$2.9^{d}\pm0.4$	$3091.3^{d}\pm160.2$	nd	$123.6^{c,d}\pm10.9$	$1427.6^{e}\pm38.9$	$7987.2^{d}\pm259.3$	12632.6^{b}
A. bisporus (white), Ital-Spawn F599	$139.8^{c,d}\pm17.2$	$460.9^{b}\pm30.9$	nd	$10.6^{c,d}\pm1.2$	$2889.7^{d}\pm349.8$	nd	$72.2^{d}\pm4.1$	$1928.8^{d}\pm87.8$	$8213.2^{c,d}\pm96.3$	13715.2^{d}

Continued

Table 1.7. Continued

	Acetic	Citric	Formic	Fumaric	Lactic	Malic	Malonic	Oxalic	Succinic	Total
A. bisporus (white), Kanmy-cel K2	nd	$259.9^{e}\pm28.7$	$1635.1^{b}\pm168.9$	nd	nd	$929.0^{a}\pm79.8$	$367.2^{b,c}\pm32.9$	$114.6^{h}\pm14.2$	$2727.3^{g,h}\pm248.9$	6033.1^{d}
A. bisporus (white), Sylvan A15	$1028.2^{a}\pm$ 41.2	$39.7^{f}\pm3.1$	$362.1^{c}\pm35.1$	$1.1^{d}\pm0.3$	nd	$37.9^{d}\pm1.9$	nd	$377.4^{g,h}\pm58.9$	$3951.9^{f}\pm415.1$	5798.3^{d}

nd: non-detectable.
Values followed by different letters in the same columns are statistically different at $P<0.05$ according to Tukey's test.

Table 1.8. Content (% of total fatty acids) of predominant fatty acids in *Agaricus bisporus* mushrooms.

	Saturated fatty acids		Unsaturated fatty acids	
Source	Palmitic acid	Stearic acid	Oleic acid	Linoleic acid
Mau *et al*., 1991[a]	12.1–12.0	3.3–3.7	1.7–1.8	77.7–78.6
Shao *et al*., 2010[b]	12.15–14.9	3.71–4.6	1.3–3.3	67.5–72.9
Öztürk *et al*., 2011[c]	13.3	3.7	6.07	67.3%
Reis *et al*., 2012a[a,d]	11.1–11.9	3.0–3.1	1.1–1.2	67.7–79.4%
Abou Raya *et al*., 2014	12.3	4.8	10.6	71.3%
Goyal *et al*., 2015	12.3	4.6	8.7	70.4%

[a]Different strains and different parts;
[b]Different strains and different stages of maturity;
[c]Different treatments – different type of supplement added on spawning and casing;
[d]White and brown mushroom.

Linoleic acid is an essential fatty acid for the human being; it is an omega 6 fatty acid that can be synthesized as the rest of the omega 6 and omega 3 fatty acids. Adding to its nutritional importance, its precursor function in mushrooms' volatile compounds should also be highlighted (Combet *et al.*, 2006; de Pinho *et al.*, 2008).

As shown in Table 1.8, mushroom composition of fatty acids varies with mushroom strain, variety, stage of maturity, what part of mushroom is analyzed, and substrate type. For instance, brown mushrooms had a higher content of linoleic acid than white mushrooms, higher levels in caps than in stems, and the levels increased with maturity (Shao *et al.*, 2010).

1.5.9 Vitamins

A. bisporus contains many vitamins, which presents it as a beneficial food to humans. Although the vitamin content varies depending on growing conditions (Muşzyńska *et al.*, 2017), it is agreed that *A. bisporus* is especially rich in the B-group vitamins (thiamine: B1, riboflavin: B2, niacin: B3, folates: B9, cobalamin: B12), mostly in niacin. It is also a good source of vitamin C. Reported amounts of vitamins B2, B3, and C in cultivated mushrooms were higher than those of vitamins B1, B5, B12, B9, and D, present in very small amounts and sometimes in traces (Mattila *et al.*, 2001; Simon *et al.*, 2011; Jaworska *et al.*, 2015; Roselló-Soto *et al.*, 2016).

Also identified in trace amounts in *A. bisporus* were α-tocopherol, β-tocopherol (Barros *et al.*, 2008; Jaworska *et al.*, 2015), γ-tocopherol, and δ-tocopherol (Reis *et al.*, 2012a) with vitamin E activity. Moreover, *A. bisporus* contains ergosterol, a precursor to vitamin D2 (Muşzyńska *et al.*, 2013a). The ultraviolet (UV) radiation from sunlight catalyzes a unique photochemical reaction whereby ergosterol is converted to vitamin D2 through a series of photochemical and thermal reactions, similar to the process by which vitamin D3 is produced by human skin (Altmeyer *et al.*, 1994). In some instances, the concentrations of vitamin D in *A. bisporus* (ergocalciferol: D2) rival those of vitamin D present in oily fish (cholecalciferol: D3; Simon *et al.*, 2011). The vitamin D2 content is commonly reported to be less than 1 μg/100 g fresh weight. Strains, cultivation, and illumination affects vitamin D2 content in mushrooms (Mattila *et al.*, 2001; Gąsecka *et al.*, 2018). Ergosterol content varied when mushrooms were exposed or not to light (Urbain and Jakobsen, 2015). It was found to be in the range of 39.5–56.7 mg/100 g fresh weight in cultivated white, brown, and Portabella mushrooms (Teichmann *et al.*, 2007).

Accordingly, experiments have been designed to enrich *A. bisporus* with vitamin D2 via irradiation with UV-B and UV-C light (Koyyalamudi *et al.*, 2009). Particularly, UV-B light was the most effective wavelength to stimulate vitamin D2 production in mushrooms (Jasinghe and Perera, 2006). These results seem to be promising in the prevention of vitamin D deficiencies. Some commercial mushroom growers, including Polish growers, have incorporated sources of UV light into their production processes, stimulating the production of vitamin D that occurs in mushrooms exposed to sunlight in their natural environment (Muşzyńska *et al.*, 2017). Detailed information about vitamins B, C, and D2 in *A. bisporus* is presented in Table 1.9.

1.5.10 Minerals

Mushrooms probably contain every mineral present in their growth substrate (Spaulding and Beelman, 2003). In general, four macro-elements (potassium: K, phosphorus: P, calcium: Ca, and magnesium: Mg) contribute 97–98% of the total mineral element concentration of *A. bisporus* (Vetter *et al.*, 2005). The reported content of micro-elements was often variable based on differences in the studied mushroom strains, varieties, what part of the mushroom is analyzed, method of cultivation, and substrate type.

Moreover, fungi possess an effective mechanism that enables them to take up some trace elements from the growth medium more readily (Lepsova and Mejstrik, 1988). Those elements are presented in Table 1.10 in different concentrations according to the experimental conditions. Studies on elemental composition and distribution of fruiting bodies of *A. bisporus* generally reveal caps as higher accumulators than stipes (Vetter and Lelley, 2004).

Mushrooms are characterized by their capacity to collect and accumulate metals (Muşzyńska *et al.*, 2018). It has been proven in the wild that accumulation of heavy metals in macrofungi is affected by environmental factors, including soil (amount of organic matter, pH, and metal concentrations) and fungal factors (species of mushroom, morphological part of the

Table 1.9. Vitamin content in *Agaricus bisporus*.

Source	Vit B1mg/100 g	Vit B2mg/100 g	Vit B3mg/100 g	Vit B9μg/100 g	Vit B12μg/100 g	Vit Cmg/100 g	Vit D2μg/100 g
Mattila *et al.*, 2001[a,d]	0.05	0.33–0.39	3.4–4.1	35.0–46.0	0.05–0.06	1.3–1.6	<0.02
Jaworska *et al.*, 2015[e]	0.9	5.19–5.89	22.6–24.4	nt	nt	nt	nt
Roselló-Soto *et al.*, 2016[d]	0.03–0.19	0.04–0.62	3.6	17.0	0.04	2.1	0.2
Simon *et al.*, 2011[b,e]	nt	2.89–3.79	33.8–40.8	nt	nt	<14.0	0.9–10.1
Çağlarirmak, 2009[c]	0.07–0.13	nt	2.7–4.3	0.07–0.1	nt	3.0–10.1	nt

nt: non-tested vitamin.
[a]Means for white and brown mushroom;
[b]Means for medium-sized mushrooms;
[c]Means from different flushes and harvests of *A. bisporus* (brown);
[d]Means provided on fresh weight basis;
[e]Means provided on dry weight basis.

Table 1.10. Mineral composition of *Agaricus bisporus* (mg/kg on dry weight basis).

	Vetter, 1994[a]				Vetter, 2003[b]		Mattila *et al*., 2001[c]		Muşzyńska *et al*., 2017[d]	
	Compost		Wheat straw							
Mineral	Cap	Stipe	Cap	Stipe	Strain 333	Strain 229	White	Brown	Review	Range
Potassium	41132.00	35534.00	47370.00	45657.00	38105.000	39566.00	47300.000	46000.000	35000–45200	35000–47370
Phosphorus	14311.00	9694.00	18810.00	12782.00	11235.000	10430.00	12700.000	12900.000	9690–17300	9690–18180
Calcium	2829.00	2372.00	2377.00	1228.00	888.000	860.00	250.000	130.000	460–990	130–2829
Magnesium	1236.00	906.00	1446.00	1064.00	1099.000	1115.00	1300.000	1410.000	1150.5–2275	906–2275
Sodium	762.00	859.00	597.00	678.00	861.000	849.00	420.000	440.000	760–860	420–861
Iron	78.50	75.80	128.00	100.20	49.900	44.50	48.000	28.000	200–400	28–400
Aluminum	70.00	40.10	74.00	46.60	21.200	18.60	nm	nm	nm	18.6–74
Zinc	93.00	81.40	70.10	50.10	60.500	62.40	66.000	47.000	54.81–112.75	47–112.75
Copper	61.50	41.50	37.50	25.70	57.700	64.70	29.000	35.000	25–125	25–125
Boron	25.20	17.80	2.50	2.65	3.730	3.57	nm	nm	nm	2.5–25.2
Manganese	8.24	6.35	8.44	6.09	5.700	6.03	5.500	5.100	nm	5.1–8.44
Strontium	9.82	9.37	9.67	7.90	6.700	7.47	nm	nm	0.01–0.04	0.01–9.82
Barium	2.30	2.39	2.67	1.89	2.370	2.12	nm	nm	2.06–7.71	1.89–7.71
Cadmium	0.20	0.24	0.22	0.26	0.220	0.12	0.036	0.096	0.02–0.09	0.02–0.26
Cobalt	0.00	0.09	0.00	0.00	<0.002	0.09	nm	nm	nm	0–0.09
Chromium	1.10	1.04	1.40	1.13	0.730	0.85	nm	nm	0.34–0.64	0.3–1.4
Molybdenum	0.34	0.05	0.47	0.53	nm	nm	nm	nm	nm	0.05–0.53
Nickel	1.42	1.35	1.70	1.34	0.350	0.73	nm	nm	0.10–0.78	0.1–1.7
Vanadium	0.00	0.08	0.11	0.03	<0.050	<0.05	nm	nm	nm	0–0.11
Selenium	nm	nm	nm	nm	1.880	3.75	1.400	3.200	0.053–0.15	0.053–3.75

Continued

Table 1.10. Continued

	Vetter, 1994[a]				Vetter, 2003[b]		Mattila *et al*., 2001[c]		Muşzyńska *et al*., 2017[d]	
	Compost		Wheat straw							
Mineral	Cap	Stipe	Cap	Stipe	Strain 333	Strain 229	White	Brown	Review	Range
Arsenic	0.00	0.00	0.00	0.00	<0.050	<0.05	nm	nm	nm	<0.05
Mercury	nm	nm	nm	nm	0.102	0.08	nm	nm	nm	0.08–0.102
Lead	nm	nm	nm	nm	nm	nm	0.180	0.035	0.03–0.15	0.03–0.18

nm: non-measured mineral.
[a]Variation of mineral content between cap and stipe, and between different culture methods (on compost and on wheat straw);
[b]Variation of minerals among two different strains (333 and 229);
[c]Variation of minerals among two different varieties (white and brown);
[d]Review from Bernaś *et al*., 2006; Kalač, 2010; Kalembasa *et al*., 2012; Muşzyńska *et al*., 2015.

fruiting body, development stage, and age of mycelium; Garcia *et al.*, 1998; Kalač and Svoboda, 2000). However, heavy metal content in mushrooms grown on non-contaminated composts are usually low (OECD, 2007). The levels of metals found in cultivated *A. bisporus* are considerably lower than in those growing wild (Kalač and Svoboda, 2000). For instance, uptake of selenium (Se; Gergely *et al.*, 2006) and mercury (Hg) is much lower in cultivated *A. bisporus* than in wild relatives (OECD, 2007). Accordingly, Werner and Beelman (2002) developed a method to increase the Se content in *A. bisporus* fruiting bodies by growing the mushroom on substrates fortified with Se either as an inorganic salt or as selenized yeasts. The aim was to produce a 'new' organic source of Se which serves as an ingredient in developing functional food products or dietary supplements.

Some reports suggested higher metal concentrations in younger fruiting bodies. This is explained by the transport of metals from mycelium to the fruiting body during fructification. During the following increase of the fruit body mass, the metal concentration decreases (Kalač and Svoboda, 2000). The acceptable concentration of heavy metal content in the fruiting bodies of edible species has been established based on the binding regulations of the Commission of the European Communities (Commission Regulation (EC) No. 1881/2006) on maximum levels of chemical and biological contamination which can be present in food (cultivated mushrooms; Muşzyńska *et al.*, 2018).

1.5.11 Phenols

A. bisporus is rich in phenolic compounds, which are aromatic hydroxylated compounds with one or more aromatic rings having one or more hydroxyl groups. They include flavonoids and phenolic acids (Palacios *et al.*, 2011). The phenolic compound content in *A. bisporus* depends on the *A. bisporus* strain, environmental factors, harvest conditions, and detection methods (Table 1.11). Gąsecka *et al.* (2018) reported a higher phenolic content in brown than in white varieties of *A. bisporus*. Moreover, discoloration of button mushrooms is believed to be due to the differences found in the total amount of phenolic compounds and the diverse functional groups present (Dubost *et al.*, 2007). Specifically, several phenolic compounds found in *A. bisporus* mushrooms such as tyrosine, glutaminyl-4-hydroxybenzene (GHB), glutaminyl-3,4,-dihydroxybenzene (GDHB), and L-3,4-dihydroxyphenylalanine (L-DOPA) are responsible for enzymatic browning at postharvest stage. GHB is present in every part of the fruiting bodies at higher concentrations than other phenolic compounds (Oka *et al.*, 1981; Choi and Sapers, 1994). Detected phenolic acids via ethanolic/methanolic extraction methods were gallic acid, protocatechuic acid, catechin, caffeic acid, ferulic acid, myricetin (Liu *et al.*, 2013), pyrogallol, naringin (Kim *et al.*, 2008), chlorogenic acid, p-coumaric acid, p-hydroxybenzoic acid, homogentisic acid (Palacios *et al.*, 2011), cinnamic

Table 1.11. Total phenolic content in *Agaricus bisporus* extracts (mg gallic acid equivalence (GAE) per g dry weight)

Source	Extraction method	Total phenolic content
Ramirez-Anguiano *et al*., 2007	Methanolic	4.5
Dubost *et al*., 2007[a]	Ethanolic	8.0–10.7
Palacios *et al*., 2011	Methanolic	3.4
Liu *et al*., 2013	Ethanolic	6.18
Bubueanu *et al*., 2015	Methanolic/ hydroalcoholic[b]	4.6–5.2
Alisaphić *et al*., 2015[a]	Ethanolic	6.4–7.6
Gąsecka *et al*., 2018[c]	Methanolic	1.3–7.6

[a]White/brown mushroom;
[b]No significant difference in results obtained by both methods of extraction;
[c]Different strains of white and brown *A. bisporus*.

acid (Reis *et al.*, 2012b), syringic acid, and trans-cinnamic acid (Gąsecka *et al.*, 2018).

1.5.12 Flavonoids

Flavonoid presence in *A. bisporus* is ambiguous. It was claimed that flavonoids are not present in mushrooms because the latter do not have the main enzymes involved in their metabolic pathway, and no significant absorption was noticed from fruiting bodies cultivated in flavonoid-enriched substrates or from mycelia grown on flavonoid-supplemented laboratory media (Gil-Ramírez *et al.*, 2016). Neverthless, Mattila *et al.* (2001), Kim *et al.* (2008), and Palacios *et al.* (2011) reported few amounts of flavonoids in tested mushrooms. However, a later review published by Gil-Ramírez *et al.* (2016) speculated the flavonoids identified in several mushroom species using liquid chromatography diode array detection (DAD) and liquid chromatography–mass spectrometry (MS) might be due to sampling contaminations or other pitfalls within the utilized protocols.

1.5.13 Flavor and aroma

Flavor and taste represent the most important quality attributes of cultivated mushrooms (Atila *et al.*, 2017). Mushrooms give umami or palatable tastes or the perception of satisfaction, which is an overall food flavor sensation linked to volatile and non-volatile compounds (Smiderle *et al.*, 2013). The terpenes, lactones, amino acids, and carbohydrates in mushrooms determine a range of special aromas and flavor properties to their fruiting body and mycelial biomass (Smiderle *et al.*, 2013).

Specifically, the peculiar umami taste is primarily contributed to mushrooms by the free amino acids, 5'-nucleotides, and organic acids as nonvolatile flavor substances (Tsai *et al.*, 2008), the concentrations of which differ with cultivated mushroom species (Li *et al.*, 2014) as well as in different parts of the mushroom (Cho *et al.*, 2010). Komata (1969) classified the free amino acids in edible mushrooms into four groups based on their taste characteristics. The first group, being the monosodium glutamate-like (MSG-like) components, includes aspartic and glutamic acids. The second comprises sweet taste amino acids, like alanine, glycine, serine, and threonine. The third encompasses bitter amino acids, such as arginine, histidine, isoleucine, leucine, methionine, phenylalanine, and valine, and the fourth group contains tasteless free amino acids, like lysine and tyrosine. Among free amino acids, the MSG-like may be responsible for the natural taste of mushrooms (Beluhan and Ranogajec, 2011), and together with other sweet components could mask the mushrooms' bitterness (Tsai *et al.*, 2007; Liu *et al.*, 2014). According to Atila *et al.* (2017), the high amounts of sugars and polyols, especially mannitol, would give rise to a sweet perception rather than a typical mushroom taste.

Compounds of fungal aroma stimulate the appetite and give mushroom dishes a characteristic flavor. The main substances responsible for the aroma of most edible mushrooms are octavalent carbonate alcohols and carbonyl compounds, among them 1-octanol, 3-octanol, 3-octanon, 1-caprynol-3-ol, 1-octynol-3-ol, 2-octynol-3-ol, and 1-caprynol-3-on (Mau *et al.*, 1993; Breheret *et al.*, 1997).

Taşkin *et al.* (2013) identified a total of 28 aroma compounds of *A. bisporus*. Alcohols were detected to be major compounds, and 1-octen-3-ol was found to be the major alcohol (Atila *et al.*, 2017) that dominates in the fructifications of *A. bisporus* (Mau *et al.*, 1992). The aroma of mushrooms also depends on some other elements, such as nitrogen, phosphorus, potassium, sulfur, iron, and zinc, and also on auto-oxidation of unsaturated fatty acids (Grzybowski, 1978).

1.5.14 Toxicants

Allergenicity due to consumption of *A. bisporus* is relatively rare. In the very few allergy cases reported, the cause was the low molecular weight compound mannitol (OECD, 2007). Sometimes, allergy was induced by the compost, the mushroom tissues, or very often spores or basidiocarps (Venturini *et al.*, 2005). *Agaricus*-related occupational allergy is manifested as asthma, dermatitis, and hand eczema (Korstanje and van de Staak, 1990; Kanerva *et al.*, 1998). Agaritine has been identified in the mushroom together with other presumed precursors for its biosynthesis (Ross *et al.*, 1982; Chauhan *et al.*, 1984). Agaritine detection can be an indicator of the likely presence of potentially toxic phenylhydrazines which are normally low in *A. bisporus* (OECD, 2007).

1.5.15 Medicinal importance

The use of mushrooms as a functional food for maintaining health is becoming more notable throughout the world. *A. bisporus* contains bioactive compounds which exhibit anti-inflammatory, immunomodulating, and anticancer properties. Biologically active compounds are affected by differences in strain, substrate, and age of mushrooms (Miles and Chang, 1997). Among the biologically active substances present in mushrooms, phenolics have attracted much attention due to their superb properties as antioxidant, anti-inflammatory, or antitumor agents (Puttaraju *et al.*, 2006). Further, phenolic compounds such as gallic acid, protocatechuic acid, catechin, caffeic acid, ferulic acid, and myricetin provide the button mushroom the properties of a natural antioxidant (Liu *et al.*, 2013). Other potential antioxidant components such as carotene and tocopherols might also contribute to the total antioxidant activity of ethanolic extract of *A. bisporus* (Liu *et al.*, 2013).

Moreover, antioxidant activity and vitamin D2 content were proposed as interesting components for the development of *A. bisporus* as a nutraceutical (Muna *et al.*, 2015). The antioxidant activity and antioxidant levels of brown and white button mushrooms were correlated with their ergosterol content (Shao *et al.*, 2010), culture conditions, and substrate type (de Román *et al.*, 2006). Ergothioneine (amino acid) from *A. bisporus* mushrooms is bioavailable and its consumption is associated with an attenuated postprandial triglyceride response (Weigand-Heller *et al.*, 2012).

Furthermore, high content of serotonin was obtained in the extracts of *A. bisporus* fruiting bodies *in vivo* and *in vitro* (Muşzyńska *et al.*, 2011, 2014). Serotonin is a long-known compound playing the role of a regulator of sleep, body temperature, mood, maturation, and regeneration, and is an inhibitor of cell aging, thereby contributing to the general strengthening of the immune system and used as an antidepressant. Antioxidant reactions of serotonin and its ability to prevent Alzheimer's disease were referred to by Hasegawa *et al.* (2005).

Anti-inflammatory and antinociceptive (formaline-induced antinociception) effects of fucogalactans, fucomanogalactans, and mannogalactans isolated from *A. bisporus* var. *hortensis* were proved by Komura *et al.* (2010) and Ruthes *et al.* (2013). *A. bisporus* has potential health benefits for improving mucosal immunity (Jeong *et al.*, 2010). Mushroom powder has shown a beneficial effect on the intestine (Kawakami *et al.*, 2016). In an experiment on rats, the intake of fruiting bodies of *A. bisporus* regulated antiglycemic and anticholesterolemic responses and had a positive influence on lipid metabolism and liver function (Jeong *et al.*, 2010). On quails, it positively affected cholesterol, high-density lipoprotein (HDL), and low-density lipoprotein (LDL; Zheng *et al.*, 2005).

Major unsaturated fatty acid constituents (linoleic acid, and conjugated linoleic acid: CLA) that suppress aromatase activity and estrogen biosynthesis are responsible for the potential anti-breast cancer activity of the mushroom (Winer *et al.*, 2002; Chen *et al.*, 2006; Savoie *et al.*, 2008; Dhamodharan and Mirunalini, 2010). Mushrooms are characterized by high amounts of α- and β-glucans with an immune stimulatory effect, the reason why they are potentially used in anticancer drugs and against Human Immunodeficiency Virus (HIV; Bahl, 1987; Prasad *et al.*, 2015). Further, Zhang *et al.* (2014) reported that brown mushroom polysaccharides possessed strong immunostimulatory and antitumor bioactivity, both *in vivo* and *in vitro*. Consumption of fruit juice enriched with α-glucans from *A. bisporus* lipolysaccharide induced tumor necrosis factor (TNFα) production by 69% (Atila *et al.*, 2017).

Extracts from *A. bisporus* have been shown to inhibit cell proliferation of HL-60 leukemia cells and other leukemia human cell lines via the induction of apoptosis (Jagadish *et al.*, 2009). *A. bisporus* lectins (ABL) are interesting potential agents for cancer therapy (Yu *et al.*, 1993), and might be useful in eye surgery for glaucoma or increased intraocular pressure (van den Brandt *et al.*, 2003). The potential use of *A. bisporus* stipes as natural antimicrobial agents was suggested by Ndungutse *et al.* (2015). Specifically, the mushroom protein extracts revealed antimicrobial activity against some bacteria, particularly *Staphylococcus aureus* and methicillin-resistant *S. aureus* (Houshdar Tehrani *et al.*, 2012), yeasts, and dermatophytes (Abah and Abah, 2010; Akyüz *et al.*, 2010).

Mineral composition of *A. bisporus* mushroom also provides medicinal advantages. For instance, accumulated selenium has a possible role in preventing cancer through antioxidant protection and/or increased immune function. Trials have shown the benefits of selenium in reducing liver, prostate, lung, and colon cancers (Spolara *et al.*, 2006). The low sodium concentrations in mushrooms also make them a good source for special diets for people with hypertension (Manzi *et al.*, 1999; Mattila *et al.*, 2001).

Nanotechnology, conducted at the nanoscale (with about 1 to 100 nanometers), has an additional role in increasing the benefits from *A. bisporus*. Owaid and Ibraheem (2017) developed the methanolic nanoparticles of *A. bisporus* that have various advantages in treating cancer as well as viral, bacterial, and fungal diseases. This type of nanoparticle synthesis with edible mushrooms is economic and suitable to apply in nanomedicine worldwide (Majumder, 2017; Owaid and Ibraheem, 2017).

1.6 Global Mushroom Production and Trade

1.6.1 Most popular species

With the increase in mushroom cultivation and diversity, people have slowly realized that they prefer certain mushroom species over others. According to a study by Miles and Chang (1997), the top ten most popular species at the time were *A. bisporus/bitorquis*, *Lentinula edodes*, *Pleurotus* spp., *Auricularia* spp., *Volvariella volvacea*, *Flammulina velutipes*, *Tremella fuciformis*, *Hypsizygus marmoreus*, *Pholiota nameko*, and *Grifola frondosa*. These species were ranked from the most popular to the least popular. The leading rank of *A. bisporus* was maintained in the year 2010, according to Royse (2014), who stated that 85% of the global production of mushroom in 2010 comprised five major species. Chang and Miles (2004), Feeney *et al.* (2014), and Patyshakuliyeva (2015) also stated that *A. bisporus* is the most widely cultivated and the most economically important cultivated mushroom species. In a more recent study, however, Royse *et al.* (2016) stated that *Lentinus edodes* is now the world's leading cultivated edible mushroom with about 22% of the world's supply. *Lentinula* and four other genera (*Pleurotus*, *Auricularia*, *Agaricus*, and *Flammulina*) now account for 85% of the world's total supply of cultivated edible mushrooms, according to the authors. The research also stated that *A. bisporus* had become the fourth mushroom species cultivated globally, constituting 15% of the global production (34 × 106 t) of edible mushrooms. Many authors have quoted these findings, such as Salmones *et al.* (2018) and Collela *et al.* (2019).

1.6.2 Market share in global trade

According to the FAO (2018), between the years of 2006 and 2016, mushrooms (including truffles) had the fifth highest average annual market growth rate following quinoa, gum (natural), blueberries, and ginger. In 2013, the mushroom industry was valued at US$63 billion (Royse *et al.*, 2016). The mushroom market share in that year was mainly divided between North America, Europe, and Pacific Asia (Mushroom Market Research Report, 2015). The production, consumption, and global trade of mushrooms have grown tremendously over the past few decades. In 2015, the Mushroom Market Research Report indicated that the mushroom market was projected to grow at a compound annual growth rate of 9.5% between the years of 2014 and 2019. The report also compared the market share of each mushroom species in 2014 and the estimated projections of these shares in the year 2019.

In the year 2020, Mushroom Market Research Report 1 projected that the mushroom market would grow from a value of US$16.7 billion in 2020 to reach a value of US$20.4 billion by 2025, at a compound annual growth rate of 4%. They explained that this growth was due to the crop's multiple health benefits, increased per capita consumption, cost-effectiveness, and increased interest of people in vegan diets and 'clean eating.' They also estimated that *A. bisporus* will continue to dominate the global market and that the Asian-Pacific market will account for the largest market share in 2025 due to its higher per capita mushroom consumption in comparison to other areas (Mushroom Market Research Report 1, 2020). Although it appeared to contain much insightful information in its abstract, this report was not accessible to the authors of this chapter (purchase cost: around

US$5000), which seems to be the case for most market growth projection estimates. As credible as that data might seem, however, upon analyzing the abstract of other costly pay-for-view reports, which are very similar in content to this one and published via the same online platform, there was a lot of contradiction in the information presented there. For instance, Mushroom Market Research Report 2 (2020) forecasted the mushroom market's growth between the years 2019 and 2024 and found the expected compound annual growth rate to be at 8% and not at 4% as the previous report had stated. Another huge contradiction exists between the mushroom market value stated in the first report and that stated in other reports. Mushroom Market Research Report 3 (2020) states that the global mushroom market is expected to grow from US$25,475.27 million in 2019 to US$40,943.85 million by the end of 2025, at a compound annual growth rate of 8.22%. Further contradictions to this information can also be seen in scientific articles. For instance, Chang (2006) stated in his article published in the International Journal of Medicinal Mushrooms that in the year 2005, the market value of the mushroom industry was estimated to be at US$45 billion. In an article by Sharma (2019), the author cited a different Mushroom Market Research Report which had very contradicting information to the three research reports mentioned above, even though it was projecting the growth of mushroom in a very closely similar time period (2018–2024).

1.6.3 Leading producers

Global production of mushrooms has increased exponentially in the last century, especially since the mid-1990s (Royse, 2014). According to the Statistics Division of the Food and Agriculture Organization (FAOSTAT), there has been a steady increase in producing countries over the past 70 years. For instance, only 40 countries contributed to the international mushroom production (including truffles) in the year 1961. However, in 2018 FAOSTAT stated that the number of internationally producing countries increased to 76 (FAOSTAT, 2020). Table 1.12 lists the FAOSTAT top ten countries producing mushrooms (including truffles) in 1961, 1980, 2000, and 2018 and the yearly production per country (in tons).

As shown in Table 1.12, China and the USA are the leading countries in mushroom production worldwide. Interestingly, the increase in the amount of production by all the aforementioned countries is exponential. It was described by Royse (2014) to be phenomenal, stating that the increase in production that happened to meet the growing demand for mushroom is a performance seldom duplicated in agriculture today. He based his astonishment on comparing the production data between the years 1978 and 2012, realizing that it has increased in that time period from 1 billion kg to 27 billion kg. As stated earlier, *A. bisporus* was the leading species of mushroom in the global market for a long time. Royse (2014)

Table 1.12. Top ten ranking countries in mushroom production (FAOSTAT, 2020).

Rank	Year 1961	Production (tons)	Year 1980	Production (tons)	Year 2000	Production (tons)	Year 2018	Production (tons)
#1	China	302,784	China	426,159	China	2,408,227	China	6,675,364
#2	China, mainland	300,000	China, mainland	350,000	China, mainland	2,400,000	China, mainland	6,664,606
#3	USA	50,000	USA	213,200	USA	383,830	USA	416,050
#4	Japan	35,000	France	152,224	The Netherlands	265,000	The Netherlands	300,000
#5	France	32,342	Japan	79,900	France	203,861	Poland	280,232
#6	UK	20,000	China, Taiwan Province	76,159	Poland	109,409	Spain	166,250
#7	Germany	10,530	UK	61,300	UK	89,900	Canada	138,412
#8	Canada	7,800	The Netherlands	60,000	Canada	80,241	UK	98,500
#9	Italy	6,464	Germany	47,373	Italy	72,492	France	83,013
#10	Poland	5,087	Italy	41,500	Japan	67,224	Iran	81,406

detailed each country's contribution to the global production of *A. bisporus* in the year 2010, where China was the foremost producer, followed by the USA and The Netherlands.

China annually supplies over 30 million t or 87% of the global mushroom supply (Royse *et al*., 2016). *A. bisporus* production amounted to about 70% of China's total yearly edible mushroom production in 2003 (Owaid *et al*., 2017). However, a decade later in 2013, China's production of *A. bisporus* only accounted for 54% (2.37 billion kg) of the world's production of this species. Royse *et al.* (2016) identified certain trends in *A. bisporus* production and trade in some countries. For instance, in the few years prior to 2013, the production of *A. bisporus* in China had gradually moved northwards in the country where the climatic conditions were more favorable and the raw materials for mushroom production were more available. In the USA, there was an 11.7% increase in *A. bisporus* production between 2006 and 2015, where the white variety grew in production by 10.1% and the brown variety grew by 24.3%. In the year 2013, Poland was the world's third largest producer of *A. bisporus*, which is a rank usually occupied by other Europian countries such as The Netherlands.

Salmones *et al.* (2018) stated that the national production of *A. bisporus* in Mexico in the year 2014 amounted to 93.7% of total national edible mushroom production of the country, cementing Mexico's position as the largest Latin American producing country of *A. bisporus*. It must be noted here, however, that *A. bisporus* is not the most produced crop in all countries. For instance, in Brazil, *A. bisporus* production amounts only to 33% of the country's total annual mushroom production (Collela *et al*., 2019). It is worth mentioning that Royse (2014) stated that there is a lot of contradiction in the information that is available regarding mushroom statistics (production, consumption, etc.). The author gave an example that showed a huge difference between the production statistics provided by FAOSTAT (2020) and the Chinese Edible Fungi Association (Li, 2012). This indicates a lack of statistics that specify the exact amounts of mushrooms produced and the top producing countries per species. As a result, there should be some global efforts to compile reliable global mushroom data and present it correctly for further market research purposes.

1.6.4 Major consumers

With the increase in the human population over the last 15 years came a simultaneous increase in per capita consumption of mushrooms, from about 1 kg/year to 4 kg/year (Royse, 2014). According to Koopman and Laney (2010), the major consumers of mushroom in 2007, when there was a global consumption of 3.3 million t of mushroom (Table 1.13), were China (38%), the European Union (31%), followed by USA (14%). Other major consumers of mushroom in that year were Canada (3%), Japan (2%), and Russia (2%). Each country's consumption of mushrooms, however, comes

Table 1.13. Mushrooms: global production, exports, imports, and apparent consumption in 2007 (Koopman and Laney, 2010).

Country	Production (tons)	Exports (tons)	Imports (tons)	Consumption (tons)	Ratio of imports to consumption
China	1,605,000	379,110	661	1,226,551	0.1
European Union	1,009,821	10,066	31,914	1,031,669	3.1
USA	390,000	437	62,257	451,820	13.8
Canada	81,500	457	17,878	98,921	18.1
Japan	67,000	66	12,712	79,646	16.0
Russia	5,700	19	60,857	66,538	91.5
Australia	42,000	8	4,825	46,817	10.3
India	48,000	2,835	3	45,168	0.0
Korea	28,500	19	9,501	37,982	25.0
Iran	28,000	0	0	28,000	0.0
Vietnam	18,000	0	0	18,000	0.0
Indonesia	30,000	18,234	1,473	13,239	11.1
Switzerland	7,500	2	4,381	11,879	37.0
Ukraine	5,000	78	5,053	9,975	50.7
Thailand	10,000	736	350	9,614	3.6
New Zealand	8,500	5	343	8,838	3.9
South Africa	8,500	158	359	8,701	4.1
Belarus	6,800	0	0	6,800	0.0
All other	26,846	9,271	58,562	76,137	87.9
Total	3,426,667	421,501	271,129	3,276,295	

from a combination of export and import. Almost all of the mushroom supply of China and the European Union were from domestic production. The USA, Canada, Japan, and Australia also relied on imports as an important source for mushroom acquisition. That was still more pronounced in the USA in the year 2016 as their mushroom supply in that year was about 440.326 t of mushroom, of which 12% were imported, and only 1% was exported, amounting to a 1.4 kg of mushroom consumed per capita (Robinson *et al.*, 2018).

There is not a globally compiled available database on the consumption of *A. bisporus*. However, some countries have collected statistics on their own level regarding their import/export trends of this crop. For instance, according to Bulam *et al.* (2018), Turkey's exportation of *A. bisporus* is much higher than its importation, making the crop a significant one. In fact, between 2007 and 2017, Turkey earned about US$7 million from the foreign trade of fresh and processed mushroom products. According to the Turkish Statistical Institute (TUIK, 2018), *A. bisporus* in Turkey in the year 2017 was imported from China, UK, Holland, Italy, and India, and exported to many countries such as Germany, Cyprus, Iraq, Syria, etc. Interestingly, Barmon *et al.* (2012) have determined that the consumption of *A. bisporus* in Bangladesh is very dependent on income level. Precisely, 77% of its consumers in Bangladesh were from the upper-income class, 37% were middle-income, and only 13% were low-income. In The Netherlands on the other hand, Royse *et al.* (2016) found that 90% of the country's production of *A. bisporus* is exported, 60% of which are exported frozen or canned, while the remaining 30% are exported as fresh. Newer and global databases on the topic of *A. bisporus* consumption and global import/export trends were not available when writing this chapter.

1.6.5 Marketed forms of mushrooms

Generally speaking, mushroom is traded as either fresh or processed. Processed mushrooms can be dried, frozen, pickled, powdered, canned, etc. (Raut, 2019; Chandirasekaran *et al.*, 2020). Currently, fresh mushrooms are dominating the market; however, the processed mushroom market is projected to grow at a faster pace due to an increase in people's demand for ready-to-eat products (Raut, 2019). Chandirasekaran *et al.* (2020) also projected an increase in the consumption of processed foods over fresh foods even though his data showed that the market is currently dominated by fresh mushroom consumption. The author suspects that the reason for this trend is because the producers and sellers are facing many issues with the perishability and short shelf life of fresh mushrooms, which can be resolved when the mushrooms are processed into other forms. The preference of the market toward fresh foods was previously established in an article by Mayett *et al.* (2006) in which they found that 75.5% of Mexican consumers ate fresh mushrooms while 21.3% ate canned mushrooms. The remaining consumption portion was of wild mushrooms (3.2%). In a more recent study by Boin and Nunes (2017), however, the authors tested the consumption patterns in a sample of 925 subjects in Portugal and found that people preferred the consumption of canned mushrooms over fresh. None the less, the contradiction between the two aforementioned research articles could be explained by the fact that different populations could have different preferences in terms of mushroom consumption and varying exposure to different market forms of the crop. It is clearly seen in both of these articles, however, that between the different forms of processed mushrooms, those canned are the most preferred for consumption.

Various market forms of mushrooms (fresh or processed) contribute differently to the global market value of the crop. In a study by Wakchaure (2011), the author compiled market research data between the years 1970 and 2010 regarding the contribution of different mushroom market forms to their global market value. The findings suggested that during these four decades, processed (canned and dried) exports of mushroom steadily increased from 0.049 to 0.683 million t, while fresh mushroom exports increased from 0.014 to 0.482 million t. According to Koopman and Laney (2010), in the year 2008, global exports of fresh mushrooms were about 34.802 million t, with Canada and the USA being the largest exporters of that year and mainly exporting items to each other. In the same year, the global import of fresh mushroom amounted to 90.879 million t, mainly carried out by Russia and the USA. On the other hand, the global exports of canned mushroom in 2008 amounted to 458.137 million t, with China being responsible for 87% of this. In the same year, the global import of canned mushrooms was 292.267 million t, mainly by Russia and the USA, similar to the global import of fresh mushrooms. So, these two latter countries were the main importers of fresh and canned mushrooms in 2008.

Wakchaure (2011) examined the consumption of canned mushroom in the USA and found that at the beginning of the time period between 1970 and 2010, 75% of people's consumption of mushroom was of the canned variety, shifting to only at 15% at the end of this period. This suggested that people's preferences had shifted into other market forms of mushroom, especially fresh. Finally, the author listed the countries with the highest canned mushroom importation, including Germany, Russia, the USA, and Japan. It was also revealed that most of these canned mushrooms were produced in China, The Netherlands, and Spain.

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