Antioxidant and anti-quorum sensing properties of edible mushrooms

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Summary
This study investigated the free radical-scavenging activity (*RSA*) using 2,2-diphenyl-1-picrylhydrazyl (DPPH) radical, total phenolic content and the potential of anti-quorum sensing (anti-*QS*) properties of *Agaricus bisporus* (white button mushroom), *Clitocybe nuda* (wood blewit), *Lactarius volemus* (weeping milk cap), *Macrolepiota procera* (parasol mushroom) and *Xerocomellus chrysenteron* (red cracking bolete) water extracts. The anti-*QS* activity of mushroom extracts was determined by a chemiluminescent reporter strain *E. coli* JM109 (containing a recombinant pSB 1142 plasmid) in white microtitre plates. All five water extracts showed significant antioxidant activity (in the range of 68.5–90.5 %) and anti-*QS* activity (594–5 772 relative light units RLU for *P. aeruginosa* 119 and 4–531 RLU for *P. aeruginosa* 44).

Keywords
mushroom; 2,2-diphenyl-1-picrylhydrazyl; phenolics; radical-scavenging activity; quorum sensing

Edible mushrooms are appreciated as a valuable source of food, not only for their unique taste, but also for their nutritional, chemical and antibacterial qualities [1, 2]. In this sense, mushrooms have been valued as functional food as well as a valuable source for the development of natural medicines and nutraceuticals.

The mushrooms with antioxidant effect prevent from the diseases by protecting cells from damage and apoptosis. Thus consuming a diet rich in mushrooms with antioxidant properties provides health-protective effects. Mushrooms have a long record of use in the treatment of some health problems in countries of Asia, America, Africa, Russia and Europe. They were used fresh or as a dried powder form or a macerate. In the case of using mushrooms as a health-protective material, information on their properties is required [3].

Mushrooms are known as an unfailing source of biologically active compounds, such as carbohydrates, proteins, vitamins and minerals. Fruiting bodies, spores and mycelia accumulate a wide spectrum of bioactive metabolites with immunomodulatory, cardiovascular system-modulating, liver-protective, anti-inflammatory, antidiabetic, antitumour, antioxidant, antimicrobial, antiviral and anti-infective and otherwise beneficious properties from a health perspective [4–7]. The antioxidant properties of extracts obtained from mushrooms contain active compounds, such as phenolic derivatives, flavonoids [8], β-carotenes, lycopenes [9], ascorbic acid analogues, terpenes, steroids, anthraquinones, quinolones and benzoic acid derivatives, but also metabolites such as formic acid, oxalic acid and high molecular weight compounds, for example peptides, proteins and nucleic acids. Ascorbic acid and β-glucans, polysaccharides typical for mushrooms, exhibit antioxidant, antibacterial, antiviral anticarcinogenic and anti-inflammatory activities [2, 10–12]. Bioactive compounds play an effective role in the prevention of cardiovascular problems, the reduction of blood cholesterol levels and on treatment of illnesses such various cancers and diabetes [13]. Antioxidants are chemical compounds that protect cells from the damage caused by unstable molecules known as free radicals. They include a wide range of structures, for example polyhydroxyphe-

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nols, flavonoids, ascorbic acid, tocopherol or carotenoids.

Since inhibition of quorum sensing (*QS*) does not target bacterial growth, inhibitors do not exert a selective pressure on bacterial populations and, consequently, they have emerged as a promising alternative to antibiotics and biocides. *QS* disruption can be achieved by interfering with *QS* signalling pathways, or intercepting with the signal molecules [14, 15]. Enzymes that inactivate *QS* signals are called quorum quenching enzymes (such as acyl-homoserine lactonase, acylases), while chemicals that disrupt *QS* pathways and reduce the expression of *QS*-controlled genes are called *QS* inhibitors. Natural products, in particular extracts and supernatants, are a major source of chemical diversity and are promissing agents, which are able to control *QS*. Supernatant from lactobacilli was found to inhibit *QS* [16].

In that context, flavonoids and phenolic compounds, have been revealed as potential inhibitors of biofilm formation and the production of virulence factors in the pathogenic bacteria by interfering with *QS* mechanisms [17]. Gram-negative bacteria use a *QS* system mediated by diffusible signalling molecules of the *N*-acyl homoserine lactones family [18]. Although bacterial-fungal interactions are largely documented [19, 20], there are relatively few reports on *QS* inhibition by mushroom metabolites or extracts [21].

In the present study, five mushroom water extracts (*Agaricus bisporus* – white button mushroom, *Clitocybe nuda* – wood blewit, *Lactarius volemus* – weeping milk cap, *Macrolepiota procera* – parasol mushroom and *Xerocomellus chrysenteron* – red cracking bolete) were screened for their antioxidant properties and anti-*QS* activity.

MATERIALS AND METHODS

Mushrooms

Five edible mushrooms (*Agaricus bisporus, Clitocybe nuda, Lactarius volemus, Macrolepiota procera* and *Xerocomellus chrysenteron)* were studied regarding their antioxidant properties using 2,2-diphenyl-1-picrylhydrazyl (DPPH) radical, the half maximal inhibitory concentration (IC_{50}) of extracts and total phenolic content (*TPC*). Mushrooms were purchased in local markets in Košice (Slovakia).

Chemicals and characterization techniques

Chemicals were purchased from Sigma Aldrich (St. Louis, Missouri, USA), Fisher Scientific (Hampton, New Hampshire, USA), Lachner (Neratovice, Czech Republic) and Mikrochem (Pezinok, Slovakia) and were used without further purification. For determination of antioxidant activity, IC_{50} and *TPC*, UV-Vis spectrophotometer Libra S 12 (Biochrom, Cambridge, United Kingdom) with optical path of beam of 1 cm was used.

Evaluation of DPPH-scavenging activity

Preparation of extracts

An amount of 100 mg of dried and homogenized mushrooms was suspended in 2 ml of distilled water. Extractions proceeded at 8 °C with mixing for 24 h. After heating to room temperature, extracts were filtered off and the filtrates were used for further analysis.

DPPH assay

To 250 μl of water extract, 2 ml of 0.2 mmol·l^{-1} methanolic solution of DPPH radical (Sigma Aldrich) were added. The mixture was incubated for 30 min in the dark at room temperature. After incubation, the decrease of absorbance at 517 nm was evaluated. The control sample was a solution of 0.2 mmol·l^{-1} DPPH with 250 μl of methanol. As reference standards for evaluation of ascorbic acid equivalents (*AAE*), L-ascorbic acid (Lachner) calibration solutions with concentration of 10, 20, 40, 60, 80, 100, 200 and 400 μg·ml^{-1} in methanol (Mikrochem) were used. The radical-scavenging activity (*RSA*) using the DPPH radical was determined according to Brand-Williams et al. [22] spectrophotometrically at 517 nm against a blank. *RSA* was determined as a percentage of the radical DPPH inhibition with respect to the decrease in absorption of control using the formula:

$$RSA = \frac{(A_0 - A_x)}{A_0} \cdot 100 \quad (1)$$

where A_x is the absorbance of the solution containing the sample, and A_0 is the absorbance of the control sample.

Determination of half-maximum inhibitory concentration

The extracts concentration providing 50% inhibition of DPPH radical (IC_{50}) was determined according to Atanassova et al. [23]. To 2 ml of 0.2 mmol·l^{-1} DPPH solution, 50, 100, 150, 200, 250 and 300 μl of mushroom extracts were added. The mixtures were incubated in the dark at room temperature for 30 min and then absorbance at 517 nm was measured. From the obtained data, calibration lines were constructed for all extracts and from the equation line, the concentration of extracted compounds corresponding to 50% inhibition of DPPH radical was determined.

Determination of total phenolic content

TPC was determined spectrophotometrically by a modified method of WATERHOUSE [24] using Folin-Ciocalteu reagent (Sigma Aldrich).

The standard solutions of gallic acid (Fisher Scientific) were prepared at concentrations of 0, 50, 100, 150, 250, 500, 750 and 1000 $mg \cdot l^{-1}$ in distilled water. Distilled water was used as a blank.

Volumes of 20 μl of standard solutions of gallic acid and mushroom extracts were pipetted into the test tubes. To individual solutions, 1.6 ml of distilled water and 100 μl of Folin-Ciocalteu reagent were added, then the solutions were mixed and left for 5 min at room temperature to react. Then, 300 μl of 10% Na_2CO_3 (Mikrochem) water solution was added. The solutions were mixed and incubated for 2 h in the dark at room temperature. Absorbance at 765 nm was measured for all solutions compared to the blank sample without gallic acid. The data obtained from gallic acid standard solutions were used for construction of a calibration line. From equation line, the amount of *TPC* for all the extracts was determined as grams of the gallic acid equivalent (GAE) per kilogram of dry weight (DW) of mushrooms.

Bacterial strains

The microorganisms used in this study were selected for their high production of *N*-acylhomoserine lactones. The clinical isolate *Pseudomonas aeruginosa* 44 originating from bovine lungs was obtained from Veterinary and Food Institute (Dolný Kubín, Slovakia) and human clinical strain *P. aeruginosa* 119 was obtained from Medy (Košice, Slovakia). Supernatants from *P. aeruginosa* strains were used as natural sources of long-chain *N*-acylhomoserine lactones as signal molecules with a C_{10}–C_{14} acyl chain. The bacterial *QS*-reporter strain used in this study was a long-chain (C_{10}–C_{14}) *N*-acylhomoserine lactone reporter strain *Escherichia coli* JM109, containing the plasmid pSB1142 carrying *P. aeruginosa* genes *lasR* and *lasI* fused to *luxCDABE*. The strain was kindly provided by Dr. M. Fletcher from University of Nottingham (Nottingham, United Kingdom) and was cultured at 37 °C on brain heart infusion (BHI) agar (Oxoid, Basingstoke, United Kingdom) with 20 $\mu g \cdot ml^{-1}$ tetracycline.

Tab. 1. Radical-scavenging activity of mushroom water extracts.

Mushroom	*RSA* [%]	*AAE* [$mg \cdot l^{-1}$]
Agaricus bisporus	88.2 ± 0.1	183.78 ± 2.63
Clitocybe nuda	90.5 ± 0.2	147.70 ± 3.76
Lactarius volemus	80.2 ± 1.2	368.89 ± 25.85
Macrolepiota procera	88.1 ± 2.1	191.00 ± 43.46
Xerocomellus chrysenteron	68.5 ± 1.6	592.11 ± 26.50

t (expressed as mean ± standard deviation, as percentage of DPPH radical-scavenging effect). *AAE* – ascorbic acid equivalents are expressed as mean ± standard deviation, as milligrams per litre of extract.

Preparation of the supernatant preparation as a source of *N*-acyl homoserine lactones

Cell-free supernatants of *P. aeruginosa* overnight culture were collected by centrifugation (6720 ×*g*, 10 min) followed by filtration (0.22 μm pore size, syringe filter from Techno Plastic Products, Trasadingen, Switzerland). The clarified supernatant was stored at 4 °C.

Quorum sensing inhibition assay

Inhibition of *QS* by fungal extracts with the reporter strain *E. coli* pSB1142/JM109 was quantitatively analysed using the microtitre plate method method described by WANG et al. [25] with some modifications. Briefly, an overnight-grown culture was inoculated into BHI broth (Oxoid) to reach the density equivalent to McFarland standard 0.5, supplemented with 50 μl of *P. aeruginosa* supernatant in a white 96-well microtiter immunoplate (SPL Life Sciences, Gyeonggi-do, Korea). Wells contained 10 μl of fungal extracts and were incubated at 37 °C for 24 h. Luminescence was measured using Synergy HT Multi-Mode Microplate Reader (BioTek, Winooski, Vermont, USA) and imaged with a Fusion Fx (Vilber, Collégien, France). Light output was reported as relative light units (RLU) divided by optical density.

Statistical analysis

All assays were performed in eight replicates and mean as well as standard deviation were calculated. One-way ANOVA and Tukey's test were used to compare data utilizing Statistica 9.0 software (StatSoft, Tulsa, Oklahoma, USA).

RESULTS AND DISCUSSION

The antioxidant activity of water extracts of mushrooms was evaluated on the basis of scavenging activity with DPPH radicals and the phenolic as well as flavonoid contents. The scavenging effect on DPPH radicals of all extracts is shown in Tab. 1. As can be seen, the best *RSA* had *Clitocybe nuda* (90.5 %), followed by *Agaricus bisporus* (88.2 %), *Macrolepiota procera* (88.1 %), *Lactarius volemus* (80.2 %) and, finally, *Xerocomellus chrysenteron* (68.5 %). *RSA* on DPPH radicals of

all the mushroom extracts slowly increased along the amount of extract until it reached a final plateau, as can be seen in Fig. 1. *RSA* values were compared with L-ascorbic acid as a standard. All the mushroom extracts had lower *RSA* than the standard, but all of them had significant uptake effect compared to the values of *AAE* (Tab. 1).

The IC_{50} values were determined for all the mushroom extracts as the weight of the dry sample that caused 50% inhibition of *RSA* with the free radical DPPH. All mushroom extracts showed significantly low IC_{50} values (Tab. 2). The lowest value was determined for *Agaricus bisporus* as 0.339 mg of dried weight of water extractable substances. Moderate values were determined for *Macrolepiota procera* (0.948 mg), followed by *Clitocybe nuda* (1.041 mg) and *Xerocomellus chrysenteron* (1.134 mg). The highest value, but still documenting that the extract was considerable as an antioxidant, was determined for *Lactarius volemus* (1.993 mg).

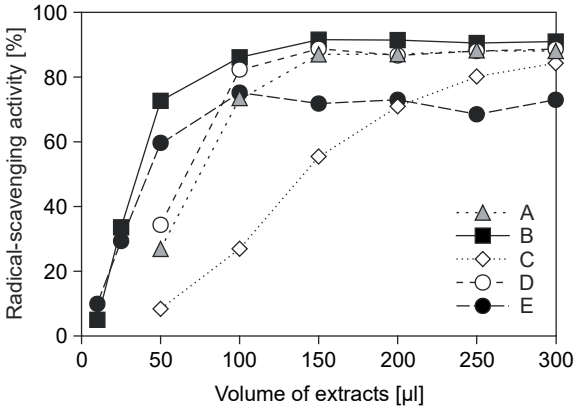

Fig. 1. DPPH radical-scavenging activity of water extracts due to amount of extracts.

A – *Agaricus bisporus,* B – *Clitocybe nuda,* C – *Lactarius volemus,* D – *Macrolepiota procera,* E – *Xerocomellus chrysenteron.*

Tab. 2. The half-maximum inhibitory concentration values of mushroom water extracts and water-extractable substances.

Mushroom	IC_{50} [mg]	*WES* [mg·ml^{-1}]
Agaricus bisporus	0.339	26.861 ± 2.563
Clitocybe nuda	1.041	28.902 ± 1.998
Lactarius volemus	1.993	13.554 ± 0.687
Macrolepiota procera	0.948	14.367 ± 1.177
Xerocomellus chrysenteron	1.134	20.340 ± 1.707

IC_{50} – half-maximum inhibitory concentration (values are expressed as dried weight of water-extractable substances inhibiting 50 % of DPPH radicals). *WES* – water-extractable substances are expressed as mean ± standard deviation in milligrams per millilitre of extracts.

Tab. 3. Total phenolic content in water extracts of mushrooms.

Mushroom	*TPC* [g·kg^{-1}]
Agaricus bisporus	1.753 ± 0.087
Clitocybe nuda	1.642 ± 0.060
Lactarius volemus	1.870 ± 0.153
Macrolepiota procera	2.429 ± 0.119
Xerocomellus chrysenteron	2.516 ± 0.218

TPC – total phenolic content (expressed as mean ± standard deviation in grams of gallic acid equivalents per kilogram of mushrooms on dry weight basis).

Total phenolic content

It is well known that the phenolic compounds are secondary metabolites, which are generally considered as antioxidants blocking free radicals activated due to oxidative stress or environmental pollution. They also have a protective effect on living organisms [26]. Phenolic compounds present in human diet provide health benefits associated with reduction of risk of chronical diseases. Studies showed that the phenolics of mushrooms, similar to phenolics of other plants, may directly provide an antioxidant effect and correlation between scavenging activity and *TPC* was also observed [27–29].

In Tab. 3, *TPC* values as gallic acid equivalents per kilogram of mushrooms are shown. The highest *TPC* content was recorded in *Xerocomellus chrysenteron* (2.516 g·kg^{-1}). Similar content was determined for *Macrolepiota procera* (2.429 g·kg^{-1}), followed by *Lactarius volemus* (1.870 g·kg^{-1}) and *Agaricus bisporus* (1.753 g·kg^{-1}). Finally, the lowest content was determined for *Clitocybe nuda* (1.642 g·kg^{-1}). These results confirmed the fact that *TPC* fluctuates within a range depending on the mushroom species, growth substrate or medium, and with polarity of the solvent used for extraction [30, 31]. THILLAIMAHARANI [32] used methanol, ethanol, ethyl acetate and chloroform for the extraction of phenolic compounds. In their study, *TPC* fluctuated in the range of 0.85 g·kg^{-1} DW in chloroform to 6.25 g·kg^{-1} DW in ethanol. Water is, from the polarity point of view, optimal extraction agent for phenolic compounds. In our study, *TPC* of the mushrooms was determined to fall in the range from 253.52 mg·l^{-1} (*Lactarius volemus*) to 511.86 mg·l^{-1} (*Xerocomellus chrysenteron*), which was in concordance with current knowledge [31]. *Agaricus bisporus* species (white button, crimini and portabella) were previously found to

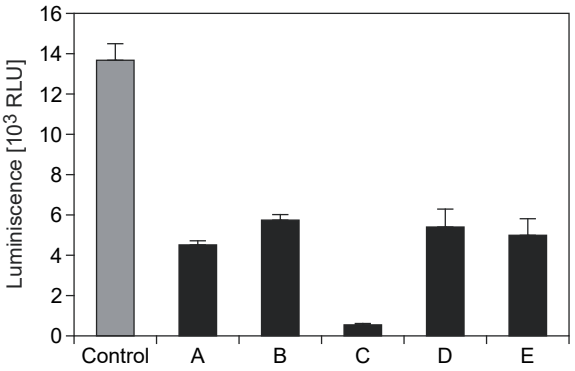

Fig. 2. Inhibition of quorum sensing activity of *Pseudomonas aeruginosa* 119 by mushroom extracts.

Mean values ± standard deviation are presented.
A – *Agaricus bisporus,* B – *Clitocybe nuda,* C – *Lactarius volemus,* D – *Macrolepiota procera,* E – *Xerocomellus chrysenteron.*

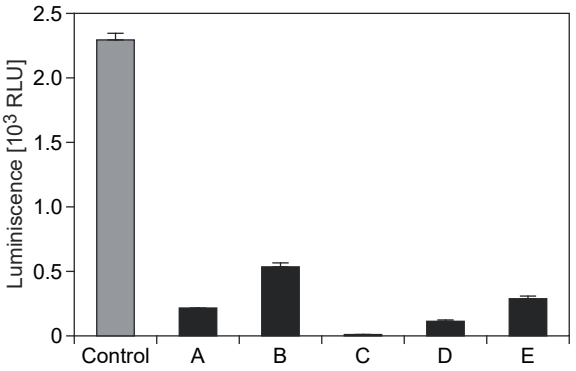

Fig. 3. Inhibition of quorum sensing activity of *Pseudomonas aeruginosa* 44 by mushroom extracts.

Mean values ± standard deviation are presented.
A – *Agaricus bisporus,* B – *Clitocybe nuda,* C – *Lactarius volemus,* D – *Macrolepiota procera,* E – *Xerocomellus chrysenteron.*

contain significant amounts of *TPC*, the contents ranging from 8.0 g·kg^{-1} to 10.7 g·kg^{-1} DW [29].

Quorum sensing inhibition tests

The extracts from five mushrooms were tested as *QS* inhibitors using a reporter strain *E. coli* JM109 with pSB1142 plasmid. All mushroom extracts showed significant anti-*QS* activity against the microorganisms tested ($p < 0.001$) without affecting the bacterial growth. Anti-*QS* activity values were similar for both tested bacterial strains, as shown in Fig. 2 for *P. aeruginosa* 119) and in Fig. 3 for *P. aeruginosa* 44. The untreated control of *P. aeruginosa* 119 reached 13706 RLU, while exposed to *Xerocomellus chrystenseron* extracted reached values of 5029 RLU, *Lactarius volemus* 594 RLU, *Agaricus bisporus* 4540 RLU, *Clitocybe nuda* 5772 RLU and *Macrolepiota procera* 5443 RLU. The value of 2299 RLU was observed for the control of *P. aeruginosa* 44, while lower values were recorded for the extracts of *Xerocomellus chrystenseron* (289 RLU), *Lactarius volemus* (4 RLU), *Agaricus bisporus* (207 RLU), *Clitocybe nuda* (531 RLU) and *Macrolepiota procera* (114 RLU).

Similar observations were made previously by other authors using different experimental setups to determine anti-*QS* activity of *Lactarius* sp. and *Amanita rubescens* extracts against *Chromobacterium violaceum* [33]. Other study on ethanolic extracts of *Agaricus bisporus* and *A. bitorquis* showed anti-*QS* activity against *P. aeruginosa*, the activity being found to be associated with the content of phenolic compounds and organic acids [34]. Soković et al. [35] also reported anti-*QS* activity of an *Agaricus blazei* hot water extract with the same bacteria. A natural source of *N*-acyl-L-homoserine lactones (AHL) was examinated for the AHL-degrading capacity of *Bacillus cereus* and results showed better degradation, in comparison to the synthetic AHL, the natural source being also cheaper [36].

This is a pioneer study since, as far as we know, there are no reports on the anti-*QS* activity of the extracts of mushrooms *Macrolepiota procera*, *Clitocybe nuda* and *Leccinellum crocipodium* against *P. aeruginosa* involved in the study. Nevertheless, further studies are required to elucidate the mechanism of action.

CONCLUSIONS

Extracts from mushrooms are complex mixtures of various chemical compounds. This study showed that the highest *RSA* had the water extract from *Clitocybe nuda*, which is a novel information. High *RSA* values were determined also in water extracts of other studied mushrooms. High *RSA* values of mushrooms extracts were connected with high *TPC* values. The results suggest that *QS* inhibition by *Lactarius volemus*, *Agaricus bisporus*, *Clitocybe nuda*, *Macrolepiota procera* and *Leccinellum crocipodium* extracts is probably associated with *TPC*. Another interesting outcome of this study was the development of a modified method for the determination of anti-*QS* activity.

Acknowledgements

This study was supported by project ITMS 262 2022 0204 (Probiotech).

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Received 13 July 2018; 1st revised 8 November 2018; accepted 19 November 2018; published online 28 March 2019.