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Hyperaccumulation of silver by *Amanita strobiliformis* and related species of the section *Lepidella*☆

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ABSTRACT

Two ectomycorrhizal macrofungal *Amanita* species of the section *Lepidella*, *A. strobiliformis* and *A. solitaria*, were found to hyperaccumulate silver (Ag). All samples were collected from non-argentiferous areas with background Ag content in soils (0.07–1.01 mg kg^{-1} Ag). The Ag contents of both *Amanita* species were mostly in the range of 200–700 mg kg^{-1} D.W. with the highest Ag content of 1253 mg kg^{-1} in one sample of *A. strobiliformis*. Silver concentrations in macrofungal fruit bodies were commonly 800–2500 times higher than in underlying soils. *A. strobiliformis* and *A. solitaria* are the first eukaryotic organisms known to hyperaccumulate Ag.

Introduction

Many macrofungal species are known to accumulate toxic heavy metals, metalloids or noble metals (Byrne *et al.* 1979; Kalač & Svoboda 2000; Borovička *et al.* 2005, 2006a,b; Borovička & Řanda 2007). An extraordinarily high ability of a plant or macrofungal species to accumulate a trace element in its tissues is called hyperaccumulation (Brooks 1998). This term was first defined by Brooks *et al.* (1977) 'to describe plants containing >1000 mg kg^{-1} Ni in dry material'. Detailed discussion on hyperaccumulators by Brooks (1998) adds that 'this amount of Ni represents a concentration about 100 times greater than values to be expected in non-accumulating plants growing on the same substrate', and is therefore a useful yardstick by which to define other hyperaccumulator species.

Despite the pronounced ability of macrofungi to accumulate various trace elements, hyperaccumulation has been reported only for arsenic (As); the ectomycorrhizal ascomycete *Sarcosphaera coronaria* regularly contains As at concentrations in the range of 100–7000 mg kg^{-1} D.W. (Stijve *et al.* 1990; Stijve 2003; Borovička 2004a).

The ability of macrofungi to accumulate Ag is a well-documented phenomenon (Schmitt *et al.* 1978; Byrne *et al.* 1979; Falandysz *et al.* 1994a,b,c). A literature search revealed that saprobic macrofungi usually have a higher Ag content (median 3.61 mg kg^{-1} Ag D.W.) than ectomycorrhizal fungi (median 0.65 mg kg^{-1} Ag D.W.) (Borovička 2004b). In the course of investigating trace element contents in ectomycorrhizal fungi collected from non-polluted areas, we have found unexpectedly high Ag contents of 479 and 1253 mg kg^{-1} D.W. in fruit

☆ This paper is dedicated to Tjakko Stijve on the occasion of his 70th birthday.

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bodies of *Amanita solitaria* (syn. *A. echinocephala*; Tulloss 2005b), and *A. strobiliformis*. In contrast, the Ag content of many other temperate *Amanita* species, including *Amanitopsis* (*A. caesarea, A. ceciliae, A. citrina, A. decipiens, A. lividopallescens, A. muscaria, A. pantherina, A. phalloides, A. regalis, A. rubescens, A. spissa*) did not exceed values typical for ectomycorrhizal fungi. Moreover, high selenium (Se) content was found in *A. strobiliformis*. The *Amanita* species (*Basidiomycota*, *Agaricales*, *Amanitaceae*) of the subgenus *Lepidella*, section *Lepidella* (Bas 1969; Horak 2005), are rather rare in Central Europe and usually occur on calcareous soils in warm hardwood forests and city parks in association with broad-leaved trees such as *Tilia*, *Carpinus*, *Corylus*, and *Quercus*, and occasionally with *Pinus*, *Fagus*, or *Betula* (Borovička 2006). The exceptional ability of *A. solitaria* and *A. strobiliformis* to accumulate Ag suggested by preliminary data prompted us to investigate the Ag content of a representative suite of these *Amanita* species.

Materials and methods

Sampling

Fruit bodies of *Amanita solitaria* (eight samples from two localities) and *A. strobiliformis* (26 samples from nine localities) were collected from their natural habitats over the period 2003–2005. In addition, herbarium specimens of two samples of *A. solitaria*, one of *A. strobiliformis* and two of an extremely rare species *A. vittadinii* were provided for analysis by the National Museum in Prague (herbarium numbers PRM 615688, 893693, 768625, 903169, and 903172, respectively). Except for samples B 202 and B 203 which originated from the Slovak Republic and UK, respectively, all samples came from the Czech Republic (Table 1). *Amanita* species were identified by J. Borovička. Surface soils (5–7 cm depth, excluding undecomposed plant litter) were sampled at most of the localities and analysed for total Ag content. Collections from Prague-Chuchle, Prague-Klíčov and Prague-Royal Garden have been deposited in the herbarium of the Mycological Department, National Museum, Prague (PRM 905506, PRM 905464, and PRM 857486, respectively).

Sample preparation

The fruit bodies were cleared of substrate debris using a stainless steel or plastic knife and rinsed with distilled water. They were cut into thin slices with a stainless steel knife, air-dried, and then dried to constant weight in an oven at 65 °C. Dry samples were pulverized and homogenized in a mill with stainless steel blades. Soil samples were dried to constant weight at 65 °C, homogenized in a mortar, sieved through a 1 mm polyamide screen and milled in an agate mill.

Analyses

Silver and Se concentrations were determined in 500 mg solid pelletized mushroom samples by using long-term instrumental neutron activation analysis (INAA) as has been described previously (Řanda & Kučera 2004).

In order to confirm the results for Ag obtained by INAA, three *Amanita* samples (B 153, B 188, B 194) were analysed by quadrupole based inductively-coupled plasma mass spectrometry (ICP-MS) (VG Elemental PQ3, UK). A mass of 0.2 g dry sample was dissolved in 5 ml HNO_3 (conc.) and 0.5 ml H_2O_2 (conc.) in a PTFE vessel (Savillex, Minetonka) on a hot plate (160 °C) overnight and evaporated to near dryness. The procedure was repeated and the residue was dissolved in 2 % (v/v) HNO_3. Analytical-grade acids (Merck) and deionised water were used to prepare the solutions. The quality of the analytical data and the procedure were verified using standard reference materials NIST 1575 (pine needles) and NIST 1515 (apple leaves).

Soil samples were analysed using radiochemical neutron activation analysis (RNAA). A 300 mg soil sample was irradiated for 2–3 h under the same conditions that were used for the fungi. After two weeks of radioactive decay, samples were placed in a glassy carbon crucible (Sigradur, HTW, Thierhaupten) and fused in the presence of an inactive carrier (10 mg Ag) with a $^{105+106}$Ag tracer (activity about 1 kBq), 2.5 g Na_2O_2 and 1 g anhydrous Na_2CO_3 for 3 min at 950 °C in an electric oven. After cooling, the resulting cake was dissolved in 10 ml water and centrifuged. The precipitate of hydroxides and carbonates was twice washed with several millilitres of 1 M NaOH and 0.5 M Na_2CO_3 and finally with distilled water. The precipitate was dissolved in a small amount of 7.2 M HNO_3, and several drops of 2.3 M HCl were added to precipitate AgCl. After centrifuging, the precipitate of AgCl was dissolved in 2 ml 6.9 M NH_4OH, centrifuged, the supernatant containing the Ag-complex was transferred to another cuvette and AgCl was precipitated with dilute HNO_3 and three drops of dilute HCl. The precipitate of AgCl was centrifuged, twice washed with distilled water and transferred on to polyethylene foil (25 mm diam), dried, weighed for the yield determination and heat-sealed for counting (see above). The yield was also determined using the radiotracer. Results from the two methods were compared and they were found to be within the range of 70–90 %.

Results and discussion

Silver and Se contents of *Amanita solitaria*, *A. strobiliformis* and *A. vittadinii* from recent and herbarium collections, are listed in Table 1 with the Ag content of underlying soils, calculated values of concentration factors, and indications of the bedrock. The Ag content in *Amanita* samples was commonly in hundreds of milligrams per kilogram; however, it varied within the quite large range of 5.90–1253 mg kg^{-1}. In order to confirm high values of Ag obtained by INAA, three *Amanita* samples were subjected to ICP-MS analysis. By using this analytical method, samples B 153, B 188a, and B 194c were found to contain 335, 908, and 785 mg kg^{-1} Ag, respectively. Considerably different figures obtained from ICP-MS analysis might be attributed to the high chlorine content of *A. strobiliformis* [1–2 %, results obtained by short-term INAA according to Řanda *et al.* (2005)], which may result in partial precipitation of insoluble AgCl. Nevertheless, ICP-MS confirmed the extraordinary capability of these *Amanita* species to accumulate Ag.

Table 1 – Silver and selenium contents (mg kg^{-1} D.W.) of *Amanita* species and underlying soils (Ag S_C)

Sample	[a]	*Amanita* sp.	Locality	[b]	Ag S_C	Silver	F_C	Selenium	Precision
B 201*	1961	*solitaria*	Libochovice n. Ohří	S	n.a.	9.80	-	4.72	(2)
B 203*	1990	*solitaria*	Norbury Park, UK	S	n.a.	7.08	-	0.68	(11)
B 200	2005	*solitaria*	Prague-Chuchle	S	0.92	784	852	14.2	(2)
B 209	2005	*solitaria*	Prague-Chuchle	S	0.92	489	532	1.49	(16)
B 210	2005	*solitaria*	Prague-Chuchle	S	0.92	326	354	1.28	(15)
B 211	2005	*solitaria*	Prague-Chuchle	S	0.92	586	637	1.59	(7)
B 217	2005	*solitaria*	Prague-Chuchle	S	0.92	633	688	1.69	(7)
B 218	2005	*solitaria*	Prague-Chuchle	S	0.92	443	482	1.95	(5)
B 70	2003	*solitaria*	Prague-Chuchle	S	0.92	479	521	1.03	(13)
B 177	2004	*solitaria*	Semice, Semická Hill	S	0.13	5.87	45	0.82	(7)
B 153	2004	*strobiliformis*	Solopysky	L	n.a.	472	-	8.22	(1)
B 202*	1984	*strobiliformis*	Šurany, Slovakia	S	n.a.	131	-	15.0	(1)
M 229	2005	*strobiliformis*	Kralupy n. Vlt.	S	0.08	148	1850	28.0	(1)
M 202	2005	*strobiliformis*	Libušín (Kladno)	S	0.09	33.8	376	15.5	(1)
B 207a	2005	*strobiliformis*	Markvarec	S	0.07	10.9	156	8.29	(2)
B 207b	2005	*strobiliformis*	Markvarec	S	0.07	8.50	121	6.52	(2)
B 152	2004	*strobiliformis*	Prague-Royal Garden	S	1.01	1253	1241	14.1	(1)
B 194a	2005	*strobiliformis*	Prague-Royal Garden	S	1.01	725	718	19.1	(2)
B 194b	2005	*strobiliformis*	Prague-Royal Garden	S	1.01	993	983	14.4	(3)
B 194c	2005	*strobiliformis*	Prague-Royal Garden	S	1.01	1096	1085	15.4	(1)
B 195	2005	*strobiliformis*	Prague-Klíčov	S	0.28	291	1039	29.9	(1)
B 196	2005	*strobiliformis*	Prague-Klíčov	S	0.28	215	768	28.3	(1)
B 197	2005	*strobiliformis*	Prague-Klíčov	S	0.28	289	1032	32.4	(1)
B 198	2005	*strobiliformis*	Prague-Klíčov	S	0.28	319	1139	26.7	(1)
B 204	2005	*strobiliformis*	Prague-Klíčov	S	0.28	311	1111	24.9	(1)
B 205	2005	*strobiliformis*	Prague-Klíčov	S	0.28	233	832	28.2	(1)
B 206	2005	*strobiliformis*	Prague-Klíčov	S	0.28	695	2482	36.8	(1)
B 208	2005	*strobiliformis*	Prague-Klíčov	S	0.28	262	936	16.1	(2)
B 212a	2005	*strobiliformis*	Prague-Klíčov	S	0.28	249	889	25.6	(1)
B 212b	2005	*strobiliformis*	Prague-Klíčov	S	0.28	259	925	24.4	(1)
B 213	2005	*strobiliformis*	Prague-Klíčov	S	0.28	317	1132	21.2	(1)
B 214	2005	*strobiliformis*	Prague-Klíčov	S	0.28	319	1139	24.1	(1)
B 188a	2004	*strobiliformis*	Prague-Střelecký Island	RFS	0.40	858	2145	18.7	(1)
B 188b	2004	*strobiliformis*	Prague-Střelecký Island	RFS	0.40	991	2478	18.3	(1)
B 188c	2004	*strobiliformis*	Prague-Střelecký Island	RFS	0.40	935	2338	18.5	(1)
B 193	2005	*strobiliformis*	Přerov	S	n.a.	91.7	-	17.1	(1)
B 199	2005	*strobiliformis*	Unknown	?	n.a.	802	-	16.5	(1)
B 219*	1980	*vittadinii*	Prague-Zbraslav	S	n.a.	70.0	-	2.86	(8)
B 220*	1980	*vittadinii*	Sinutec, Dlouhá Hill	V	n.a.	9.16	-	4.02	(4)

Soil analyses from composite sample collected at each locality. Precision (rel.%) is indicated in brackets. In case of Ag, precision was 1 %. Herbarium samples are indicated (*). n.a., not analysed.
F_C, concentration factor related to the total Ag content in underlying soil (Řanda & Kučera 2004).
a Year of collection.
b Type of bedrock: S, sedimentary (clastic); L, limestones and marbles; RFS, recent fluvial sediments; V, volcanic rocks.

The highest concentrations of Ag previously reported in mushrooms from non-argentiferous areas were found in saprobic *Agaricus* spp. — 150 mg kg^{-1} in *A. campestris* (Falandysz & Bona 1992) and 170 mg kg^{-1} in *A. bitorquis* (Cocchi & Vescovi 1997). However, these high concentrations (above 100 mg kg^{-1}) were unexpected. Stijve *et al.* (2001) investigated the Ag content of various sections of this genus and found the highest concentrations in *A. augustus* and allied species (7.5–78 mg kg^{-1}). A very high Ag content (995 mg kg^{-1}) was found in a single collection of *A. xanthodermus* from the tailings of a Ag mine (Řanda & Kučera 2004). Concentration factors of Ag in *A. campestris* were investigated by Falandysz & Danisiewicz (1995).

In non-argentiferous and unpolluted areas, soil Ag contents are very low. According to reviews by Adriano (2001) and Kabata-Pendias (2001), many studies have shown common Ag soil content to be below 1 mg kg^{-1} (<0.1–1 mg kg^{-1}). An average Ag content in the upper continental crust is 0.053 mg kg^{-1} (Rudnick & Gao 2003). The Ag concentrations found in top-soils from the localities visited (Table 1) were in accord with these values. It follows that Ag concentrations in most of *A. solitaria* and *A. strobiliformis* samples are 800–2500 times higher than soil concentrations indicating hyperaccumulation of this element.

The term 'hyperaccumulation' has been clearly defined only for certain elements such as cadmium (Cd), cobalt, copper, manganese, nickel, lead, and zinc (Greger 2004), but not for Ag. According to Greger (2004), Cd-hyperaccumulating plants should contain more than 100 mg kg^{-1} Cd in leaves. In view of the fact that in unpolluted soils, Cd and Ag have

similar contents (Adriano 2001; Kabata-Pendias 2001) we consider *A. solitaria* and *A. strobiliformis* to be Ag hyperaccumulators. Another definition uses the term 'hyperaccumulator' for a species containing at least 100 times higher concentrations of a particular element than other species growing over underlying substrate of the same characteristics (Brooks 1998). Considering the common Ag content in macrofungi, this definition seems to be applicable to both *Amanita* species as well. The status of *A. vittadinii* cannot be determined because of the low sample population.

It could be speculated that the differential ability to (hyper)accumulate Ag observed within species (Table 1) can be genetically disposed and thus absent in some genotypes. Significant divergence in metal accumulation within various genotypes and ecotypes has been observed among plant species (Greger & Landberg 1999; Österås *et al.* 2000). The variation in Ag content of fruit bodies within analysed *Amanita* species could also be caused by the fact that levels of Ag in soils are very low (Table 1) and the bioavailable amount of Ag is thus greatly limited. Low Ag concentrations in investigated *Amanita* species were found especially in places with soil Ag content below 0.1 mg kg^{-1}. A very highly significant correlation between soil Ag content and Ag content in *A. strobiliformis* fruit bodies was found ($r = 0.82$, $n = 23$, probability less than 0.001).

Among other factors influencing the trace elements content in macrofungi, especially the (total) time of presence of mycelium on site and the number of fruit bodies produced per season might play a significant role in Ag hyperaccumulation. If a high number of fruit bodies is produced in a particular locality, such as in Prague-Klíčov, their Ag content might be relatively low in comparison with localities where few fruit bodies are produced during the season, e.g. in Prague-Střelecký Island. Where growing, it appears that these mushroom species play a significant role in modifying soil Ag geochemistry.

On a molecular scale, the factors governing differential metal accumulation are unknown, but it appears that metal hyperaccumulation in vascular plants is an inadvertent consequence of an efficient mineral nutrient uptake system and metal translocation accompanied by efficient metal detoxification which is the feature underlying hyperaccumulation (Clemens *et al.* 2002). The only study addressing Ag speciation in macrofungi (cultivated *Agaricus bisporus*, champignon) indicated that the majority of Ag was contained as an Ag-protein complex (Byrne & Tušek-Žnidarič 1990). Its intermediate molecular weight of 8 000-10 000 Da would suggest that metallothioneins (MT) or MT-like species similar to those found in vascular plants (Kotrba *et al.* 1999) are involved in sequestration of Ag in the champignon mushroom.

It should be stressed that the ability of macrofungi to hyperaccumulate metals is apparently higher than that of most vascular plants. Metal-hyperaccumulating plants typically grow on substrates with high levels of accumulated elements such as mine tailings or serpentine soils (Brooks 1994) whereas Ag- and As-hyperaccumulating macrofungi were found in non-metalliferous unpolluted areas. The highest As content ever found in *Sarcosphaera coronaria*, 7090 mg kg^{-1} (Borovička 2004a), was detected in a specimen growing on dolomitic marble. The highest Ag content of 1253 mg kg^{-1} reported here was found in an *A. strobiliformis* specimen that came from a park in Prague with bedrock of Ordovician siltstones and shales.

To our knowledge, no Ag-hyperaccumulating eukaryotic organisms have been reported to date. However, Ag cations are microcidal at low concentrations and some bacteria can alleviate this toxicity through various processes (Hughes & Poole 1991). Pooley (1982) has shown that *Thiobacillus* spp. catalysing the bio-oxidation of sulphidic ores accumulated Ag_2S particles on cell surfaces. The amount of Ag accumulated per gram of dry biomass weight correlated with the Ag content of the sulphide mineral being leached and extremely high concentrations greater than 25 % were observed.

Besides its capability to hyperaccumlate Ag, *A. strobiliformis* accumulates substantial amounts of other elements, especially Se (Table 1; see also Vetter 2005). Muñoz et al. (2007) reported on the protective effect of Se against Cd and Ag toxicity in *Pleurotus ostreatus*. However, in *Amanita* species evaluated in this work, no significant correlation between Ag and Se contents has been found. The Se content in *A. strobiliformis* was considerably higher than that in *A. solitaria* and would have a chemotaxonomic significance. In addition to certain *Boletus* and *Albatrellus* species, *A. strobiliformis* can be a suitable species for investigation of Se speciation in macrofungi, which has already commenced (Šlejkovec *et al.* 2000; Huerta *et al.* 2005; Muñoz *et al.* 2006).

In conclusion, two ectomycorrhizal macrofungal species *A. strobiliformis* and *A. solitaria* were found to hyperaccumulate Ag. Silver concentrations in fruit bodies are up to 2500 times higher than those in underlying soils and the highest content was found in *A. strobiliformis* (1253 mg kg^{-1}). To our knowledge, these species represent the first example of Ag-hyperaccumulating eukaryotic organisms. Concentrations of Ag in the *Amanita* samples examined varied over a wide range and it could be hypothesized that the ability to hyperaccumulate Ag mainly depends on the total Ag content in soil, or the age of mycelium or genetic disposition. The mechanisms of accumulation and detoxification of Ag in hyperaccumulating *Amanita* species deserve further investigation. In seeking other Ag-hyperaccumulating *Amanita* species, it would be relevant to analyse the Ag content of Mediterranean species of the sections *Lepidella* and *Amidella* and *Amanita* species of the section *Lepidella* found in Africa, Asia, and in the Americas (Bas 1969; Pegler & Shah-Smith 1997; Bhatt *et al.* 2003; Tulloss 2005a).

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