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Chemotaxonomic interest of volatile components in *Lepista inversa* and *Lepista flaccida* distinction

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Abstract – Wild *Lepista inversa* and *L. flaccida* were investigated for volatile constituents by gas chromatography-mass spectrometry (GC-MS). More than 40 compounds were identified with this technique from diethyl ether extracts as aliphatic alcohols, aldehydes and cetones as well as numerous aromatic compounds. Chlorinated compounds only detected in *L. inversa* samples clearly differentiated them from those obtained from *L. flaccida.* However, the chemotaxonomic value of these secondary metabolites to distinguish these two related clitocyboid species has to be checked with the litter incidence.

Basidiomycota / chlorinated volatile compound / GC-MS analysis / *Lepisteae* / solvent extraction / *Tricholomataceae*

Résumé – Des sporophores sauvages de *Lepista inversa* et de *L. flaccida* ont été étudiés par chromatographie en phase gazeuse couplée à la spectrométrie de masse (CG-SM) pour leur contenu en composés volatils. A partir d'extraits éthérés, plus de 40 composés ont été identifiés par cette technique d'analyse, tels que des alcools, des aldéhydes, des cétones ainsi que de nombreux composés aromatiques. Des composés chlorés, uniquement détectés dans les échantillons de *L. inversa* les différencient clairement de ceux issus de *L. flaccida*. L'intérêt chimiotaxonomique de ces métabolites secondaires pour distinguer ces deux très proches espèces clitocyboïdes doit cependant être précisé par rapport à l'éventuelle influence de la litière.

Analyse CG-SM / Basidiomycota / composé volatil chloré / extraction par solvant / *Lepisteae* / *Tricholomataceae*

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INTRODUCTION

Many reports deal with sporophore odours of Basidiomycota (Claus; 1978; Moreau, 2002). The aroma chemistry of mushrooms investigated through volatile components can be of interest for both discovery of original "natural" label for flavouring compounds and chemotaxonomic investigation. Previous reviews placed the volatile fraction as being the major contributor to characterize mushroom flavour (Hanssen, 1982; Maga, 1981; Mau *et al.,* 1994, 1997). The broad spectrum of volatile components identified in mushroom species is about 150 and represents a wide variety of natural compound classes (Abraham & Berger, 1994; Audouin *et al.*, 1989; Breheret *et al.*, 1999; Fons *et al.*, 2003; McAfee & Taylor, 1999; Rapior *et al.*, 1997, 2003).

Few data are reported on the chemical composition of *Lepista* species. First, the sterols, triterpenes and fatty acids were determined for *L. nuda* and *L. nebularis* (Dembitsky *et al.*, 1993; Morelli *et al.*, 1981; Régérat *et al.*, 1976; Senatore, 1992). Bioactive diterpenoids (lepistal, lepistol) on human leukaemic cells were then identified from fermentation of *L. sordida* (Mazur *et al.*, 1996). Specific nucleosides as clitocine (Kubo *et al.*, 1986) and nebularine (Löfgren & Lüning, 1954) were identified in *L. inversa* and *L. nebularis*, respectively and mainly investigated for their cytotoxic properties (Moss *et al.*, 1988; Secrist *et al.*, 1994). Recently, a crude methanolic extract of *L. inversa* was reported to be active on various cancer cell lines (Bézivin *et al.*, 2002) and clitocine was thought to be the major active compound on L1210 mice leukaemia *in vivo* (Bézivin *et al.*, 2003).

Little is known in terms of volatile composition from sporophores of *Lepista* species. Low concentrations of 1-octen-3-ol as well as of glutamic acid were first observed in *L. nuda* fruiting-bodies (Disjkstra, 1976). In the 1990's, more than 30 volatile components including bisabolane derivatives (lepistirones) were identified from submerged cultures of *L. irina* (Strong-scented Blewit), edible mushroom with a typical "iris oil" or "orange blossoms" flavour (Abraham *et al.*, 1991; Krings *et al.,* 1995). At the same time, linalool seems to be a key compound in *L. nuda* (Wood Blewit) and *L. nebularis* (Clouded Agaric) odours (Audouin *et al.*, 1989; Breheret *et al.*, 1997a, b). Moreover, Noël-Suberville *et al.* (1996) reported a correlation between fatty acid content and C_8-derivative effluents (1-octen-3-ol, 1-octen-3-one, 3-octanone) in *L. nuda*: the gills are the major compartments for the metabolic interconversion of linoleic acid into 1-octen-3-ol ("mushroom alcohol"). Recently, major and minor volatile compounds contributing to the overall smell of *L. nebularis* were identified from frozen and fresh materials, respectively (Rapior *et al.*, 1996, 2003).

In the present study, *L. inversa* and related *L. flaccida* were investigated for apolar and low polar compounds from diethyl ether extracts by Gas Chromatography-Mass Spectrometry (GC-MS). The volatile compositions were compared and the chemotaxonomic value of some constituents was discussed therein.

MATERIALS AND METHODS

Wild sporophores representing a combination of young and old basidiocarps of either *Lepista inversa* (Scop.) Patouillard (Tawny Funnel Cap) or *L. flaccida* (Sow.:Fr.) Patouillard were collected under *Picea* species (fall of 1999 and

2002) and under *Quercus* species (2000 and 2003), near Rennes and L'Espérou (France), respectively. After identification by two of us (JB and SR), soil particles and the lower part of the stipe were cautiously discarded for both species; the clean fungal materials were cut into small pieces and then frozen at –18°C.

Solvent extraction was performed with diethyl ether (w/4v) directly added to the frozen mushrooms – without thawing – to stop enzymatic activity and then left in the darkness for 15 days. The organic extracts were gently concentrated to a small volume (0.5 mL) under nitrogen stream and analysed (1.0 µL) in duplicate by Gas Chromatography-Mass Spectrometry (GC-MS).

GC-MS analyses were carried out using a gas chromatograph Hewlett-Packard (5890) and a mass selective detector Hewlett-Packard (5971) with a potential of 70 eV for ionization by electron impact. Solvent extract analyses were performed using a 25 m × 0.20 µm × 0.13 µm dimethylpolysiloxane BPX5 (Macherey-Nagel) fused silica capillary column. The injector and detector temperatures were 200°C and 270°C, respectively. The column was temperature programmed as follows: 50°C (2 min) to 230°C (3°C/min). The carrier gas was helium with a constant flow rate set close to 0.9 mL/min. All volatile components were identified by comparison with mass spectral library NBS (MacLafferty & Stauffer, 1989), literature spectra (Adams, 1995; Jennings & Shibamoto, 1980; National Institute of Standard and Technology, 1994) and our own data bank.

RESULTS

The yields of residue for the diethyl ether *Lepista* extracts were about 2% of the fresh sporophores. Using GC-MS analyses, 32 and 20 volatile components were identified from *L. inversa* and *L. flaccida*, respectively (Table I). Most of these natural substances belong to various but usual classes of chemical products biosynthesized from the lipidic, shikimic and terpenic pathways. The common classes of compounds encountered in mushrooms are present as hexa- to undeca-carbon derivatives at different oxidized stages, i.e., 1-octanol, 3-octanone, (E)-2-octenal, and non-aromatic carboxylic acids (2-methylbutyric acid, hexanoic acid...) as well as aromatic derivatives (benzoic acid, phenylacetaldehyde...) and terpenic compounds (nerolidol).

The two related clitocyboid species have different volatile profiles. The *L. inversa* volatile fraction was characterized by three chlorinated molecules (RI = 1193, 1315 and 1423) as well as phenylacetic acid. None of the natural chlorinated metabolites detected from *L. inversa* were present when GC-MS analysis was carried out on *L. flaccida*; aromatic compounds derived from the shikimic pathway at various oxidized stages, i.e., benzaldehyde, *p*-hydroxybenzaldehyde, phenylacetaldehyde and phenylacetic acid, were found to be the major compounds for the latter species.

DISCUSSION

L. inversa (Tawny Funnel Cap) was described as possessing a mushroom-like odour (Bon, 1988; Borgarino & Hurtado, 2001); no specific odour was repor-

Table I. Volatile components (percentage) of *Lepista inversa and L. flaccida.*

Volatile compounds	*RI*[a]	*L. inversa*	*L. flaccida*
γ-Butyrolactone	795	0.4[b]	
Hexanal	797	1.9	0.3
Octane	800	0.3	
3-Methylbutyric acid	836		2.2
2-Methylbutyric acid	842	0.9	0.3
(E)-2-Hexenal	850	6.1	
Benzaldehyde	954	1.1	43.0
1-Octen-3-one	970	0.3	
1-Octen-3-ol	975	1.5	
3-Octanone	979	0.6	
2,3-Octanedione	985		0.2
2-Pentylfurane	990	0.3	0.1
3-Octanol	992	0.4	
Benzyl alcohol	1022		0.2
Phenylacetaldehyde	1037	1.6	24.0
(E)-2-Octenal	1060	0.5	3.0
1-Octanol	1069	0.6	
Nonanal	1100	1.6	0.3
Hexyl isobutyrate	1147	2.1	
3-Methylthiopropionic acid	1150	4.4	
Heptanoic acid	1152		0.3
(E)-2-Nonenal	1157	0.5	
Clitolactone[c]	1193	35.4	
(E,E)-2,4-Nonadienal	1214	0.6	
Nonanoic acid	1260	1.4	0.4
2-Undecanone	1295	2.4	
(E)-2-Decenal	1254	0.7	
Phenylacetic acid	1279	23.5	1.6
(Z,E)-2,4-Decadienal	1298	1.0	
Benzoic acid	1305	0.2	2.1
Chlorinated I[c]	1315	0.5	
(E,E)-2,4-Decadienal	1325	1.3	
Decanoic acid	1357		1.1
(E)-2-Undecenal	1358	0.3	
p-Hydroxybenzaldehyde	1414		13.5
Chlorinated II[c]	1423	4.5	
Cinnamic acid	1455	0.7	
Phenylacetamide	1510		0.2
(E)-Nerolidol	1560	0.5	
p-Hydroxybenzoic acid	1660		2.4
N-*p*-Ethoxyphenylacetamide	1703		1.2
Myristic acid	1765		2.0

[a] Retention Indices due to the GC column used.
[b] Relative percentage of the volatile compounds based on the GC-MS chromatographic area.
[c] Mass spectra of the three chlorinated compounds: m/z (%).
Clitolactone [5-(chloromethyl)-3-methyl-2(*5H*)-furanone]: 97(100), 41(85), 39(55), 69(41), 49(14), 51(11), 146(8), 148(3), 117(4), 119 (2), 110(2).
RI = 1315: 147(100), 39(83), 149(35), 67(32), 49(25), 51(18), 74(23), 83(22), 102(20), 41(16), 160(11), 76(8), 130(5), 104(5), 162(3), 132(2), 178(1).
RI = 1423: 132(100), 39(90), 69(40), 75(37), 134(33), 131(31), 104(28), 133(23), 50(23), 49(21), 51(18), 64(11), 77(10), 41(7), 106(5), 148(2).

ted for *L. flaccida* (Bon, 1997). Unlike Romagnesi (1971) and Malençon and Bertault (1975), it might be noted that Moser (1983) and Bon (1997) as well as Courtecuisse and Duhem (2000) distinguished *L. inversa* from *L. flaccida* on the basis of macro and micromorphological descriptions, and environmental conditions (Gymnosperms and Angiosperms substrates, respectively). Considering these two species found in North America where *L. flaccida* appears to be the most common species growing on humus under conifers (spruce) as well as hardwoods, Bigelow (1985) mainly distinguished them on macroscopical characters, particularly as the gills of *L. flaccida* do not become rufescent with age while Pomerleau (1980) reported only one species as *Lepista inversa* (Fr.) Pat. (= *Clitocybe flaccida* (Fr.) Kum.) under both hardwoods and softwoods.

According to Courtecuisse and Duhem (2000), both clitocyboid species belong to the *Tricholomataceae, Tricholomatoideae,* tribe *Lepisteae,* genus *Lepista* (Fr.) W.G. Smith, subgenus *Lepista*, section *Inversae*. It should be mentioned that *L. inversa*, and *L. flaccida* indeed, could be confused with species responsible for the acromelalgic syndrome as toxic *Clitocybe ameonolens* and *C. acromelalga* (Konno *et al.*, 1988; Moreau *et al.*, 2001; Saviuc, 2000; Saviuc *et al.*, 2001, 2003).

Although *L. inversa* and *L. flaccida* have similar odours, many differences were found with regard to their volatile pattern. The major compounds found in *L. flaccida* were aromatic aldehydes, i.e., benzaldehyde (43%), phenylacetaldehyde (24%) and *p*-hydroxybenzaldehyde (13.5%) while a chlorinated compound (clitolactone, 35.4%) along with phenylacetic acid (23.5%) were predominant for *L. inversa*. This major chlorinated metabolite was recently identified as a banana slug antifeedant by Wood *et al.* (2004).

The *L. inversa* volatile composition also appears to be more varied than that of *L. flaccida* but neither this observation nor the nature of shikimic derivatives are an unequivocal feature to distinguish them considering natural variations according to stage of development and sampling. Conversely, presence of three chlorinated compounds (more than 40.4%, Table I) in the volatile fraction of *L. inversa* is of interest in this way. Considering little information of their mass spectra, no chemical structure can be suggested by the authors to the chlorinated compounds I and II. Nevertheless, the similarity between mass spectra from the three metabolites lead us to think that the chlorinated components I and II have also a lactonic structure. Thus, the three chlorinated metabolites probably could come from a nonprotein amino acid such as those reported by De Jong and Field (1997).

To our knowledge, these chlorinated natural substances could be of major interest for the chemotaxonomic distinction between *L. inversa* and *L. flaccida*, which is controversially identified as a distinct mushroom. Three chlorinated components including clitolactone were detected from *Lepista inversa* (Scop.) Patouillard growing under coniferous trees in two French locations over two years (Rennes and L'Espérou). Moreover, according to our GC-MS analyses over two years, *Lepista flaccida* (Sow.:Fr.) Patouillard growing under deciduous trees in two French locations has no chlorinated metabolites (Table I) while recent investigation on volatiles from *Clitocybe flaccida* (Fries) Kummer growing "in combination with conifers in western North America" (Wood *et al.*, 2004) demonstrates presence of clitolactone. Different characteristics distinguish humus from softwoods (*Picea*) and hardwoods (*Quercus*); the lowest pH values of natural substrates were particularly reported for softwoods (Scheikl, 1994). A low pH of humus/litter in coniferous forest could explain the transformation from a nonprotein amino acid precursor such as 2-amino-2-methyl-5-chloro-4-pentenoic acid to 5-(chlorome-

thyl)-3-methyl-2(5*H*)-furanone (clitolactone) for the French *Lepista inversa* or the American *Clitocybe flaccida* species, both specimens growing under spruce.

Occurrence of natural chlorinated compounds was previously detected in Basidiomycota strains. Some wood- and forest litter-degrading fungi are well known to produce chlorinated anisyl metabolites (De Jong *et al.*, 1994; Field and Wijnberg, 2003). This feature has particularly been depicted for *L. nuda* that has ability to biosynthesise organically bound halogens in culture or in field conditions as in coniferous forest (Hjelm *et al.*, 1996, 1999). Moreover, *L. nuda* and three *Clitocybe* species were shown to produce low to moderate amounts of aromatic chlorometabolites among 55% of the 191 fungal strains screened for adsorbable organic halogen production (Verhagen *et al.*, 1996). Only some aliphatic chlorinated structures have been previously found in Basidiomycota, i.e., pinicoloform from *Resinicium pinicola* (Becker *et al.*, 1994), scorodonine from *Marasmius scorodonius,* lepiochlorine from *Lepiota* sp. (Field *et al.*, 1995), along with two aminochloropentenoic acids and two aminochlorohexenoic acids found in some *Amanita* species (*in* Field *et al.*, 1995; Ohta *et al.*, 1995). Recently, Wood *et al.* (2003) identified 3-chloroindole from *Hygrophorus paupertinus*.

Overall, our findings underlined intraspecific variability in the chlorinated volatile profile for *L. inversa* and *L. flaccida* resulting probably from the fungus/litter combination. It should be noted that correlation between the amanitin distribution and the chemical composition of substrate was statistically validated for *Galerina marginata* (Batsch) Kühner (Enjalbert *et al.,* 2004). However, relationship between either the pH or the chemical composition of the litter and the expression of chlorinated metabolites from *Lepista* or *Clitocybe* species should be ascertained.

On the other hand, with regard to flavour production as well as bioactive molecule production, higher fungi represent an alternative to traditional plant sources. The remarkable metabolic diversity of Basidiomycota obtained through biotechnological processes (without using specific precursors) offers immediate industrial applications (Abraham & Berger, 1994; Giacinti-Martinie, 1999). Extended screenings of mushroom volatiles may lead to improvement in the spectrum of natural-labeled odorous components to be mostly used in food agro-industry as additives, preservatives or bioactive substances.

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REFERENCES

ABRAHAM W.R., HANSSEN H.P. & URBASCH I., 1991 — Lepistirones, major volatile metabolites from liquid cultures of *Lepista irina* (Basidiomycotina). *Zeitschrift fur Naturforschung* 46c: 169-171.

ABRAHAM W.R. & BERGER R.G., 1994 — Higher fungi for generating aroma components through novel biotechnologies. *Journal of Agricultural and Food Chemistry* 42: 2344-2348.

ADAMS R.P., 1995 — *Identification of essential oil components by gas chromatography-mass spectroscopy*. Allured Publishing Corporation, Carol Stream, 469 p.

AUDOUIN P., VIDAL J.P. & RICHARD H., 1989 — Volatiles from aroma of some edible mushrooms: Morel (*Morchella conica*), Wood Blewitt (*Lepista nuda*), Clouded

Agaric (*Clitocybe nebularis*), and false chanterelle (*Hygrophoropsis aurantiaca*). *Sciences des Aliments* 9: 185-193.

BECKER U., ANKE T. & STERNER O., 1994 — A novel halogenated compound possessing antibiotic and cytotoxic activities isolated from the fungus *Resinicium pinicola* (J. Erkiss.) Erkiss. & Hjortst. *Zeitschrift für Naturforschung* 49c: 772-774.

BEZIVIN C., LOHEZIC F., SAULEAU P., AMOROS M. & BOUSTIE J., 2002 — Cytotoxic activity of Tricholomatales on murine and human cancer cell lines. *Pharmaceutical Biology* 40: 196-199.

BEZIVIN C, DELCROS J.G., FORTIN H., AMOROS M. & BOUSTIE J., 2003 — Toxicity and antitumor activity of a crude extract from *Lepista inversa* (Scop.:Fr.) Pat. (*Agaricomycetideae*): a preliminary study. *International Journal of Medicinal Mushrooms* 5: 25-30.

BIGELOW H.E., 1985 — North American Species of *Clitocybe*. Part II. *Nova Hedwigia Beihefte, Beihefte* 81: 334-338.

BON M., 1988 — *Champignons d'Europe occidentale*. Arthaud, Paris, 268 p.

BON M., 1997 — Flore mycologique d'Europe. Les Clitocybes, Omphales et ressemblants. *Tricholomataceae*. Part 2. *Clitocyboideae*. *Documents Mycologiques, Mémoire Hors Série* n° 4: 1-181.

BORGARINO D. & HURTADO C., 2001 — Champignons de Provence (Haute Provence, Provence et Midi méditerranéen). Edisud, Aix-en-Provence, 439 p.

BREHERET S., TALOU T., RAPIOR S. & BESSIÈRE J.M., 1997a — Composés volatils : un outil pour la chimiotaxinomie des Basidiomycètes. *Cryptogamie, Mycologie* 18: 111-114.

BREHERET S., TALOU T., RAPIOR S. & BESSIÈRE J.M., 1997b — Monoterpenes in the aromas of fresh wild mushrooms (Basidiomycetes). *Journal of Agricultural and Food Chemistry* 45: 831-836.

BREHERET S., TALOU T., RAPIOR S. & BESSIÈRE J.M., 1999 — Geosmin, a sesquiterpenoid compound responsible for the musty-earthy odor of *Cortinarius herculeus*, *Cystoderma amianthinum*, and *C. carcharias*. *Mycologia* 91: 117-120.

CLAUS G., 1978 — Des odeurs en mycologie. *Documents mycologiques* 8 (30-31): 31-63.

COURTECUISSE R. & DUHEM B., 2000 — *Guide des champignons de France et d'Europe*. Delachaux et Niestlé, Lausanne, 476 p.

DE JONG E., FIELD J.A., SPINNLER H., WIJNBERG J.B.P.A. & DE BONT J.A.M., 1994 — Significant biogenesis of chlorinated aromatics by Fungi in natural environments. *Applied and Environmental Microbiology* 60: 264-270.

DE JONG E. & FIELD J.A., 1997 — Sulfur tuft and turkey tail: Biosynthesis and biodegradation of organohalogens by Basidiomycetes. *Annual Review of Microbiology* 51: 375-414.

DEMBITSKY V.M., REZANKA. T. & SHUBINA E., 1993 — Chemical constituents of some higher fungi. I. Fatty acid and phospholipid compositions of Basidiomycetes. *Cryptogamic Botany* 3: 373-377.

DIJKSTRA F.Y., 1976 — Studies on mushroom flavours. 3. Some flavour compounds in fresh, canned and dried edible mushrooms. *Zeitschrift für Lebensmittel-Untersuchung und -Forschung* 160: 401-405.

ENJALBERT F., CASSANAS G., RAPIOR S., RENAULT C. & CHAUMONT J.P., 2004 — Amatoxins in wood-rotting *Galerina marginata*. *Mycologia* 96: 720-729.

FIELD J.A., FRANK J.M., VERHAGEN J.M. & DE JONG E., 1995 — Natural organohalogen production by Basidiomycetes. *Trends in Biotechnology* 13: 451-456.

FIELD J.A. & WIJNBERG J. B.P.A., 2003 — An update on organohalogen metabolites produced by Basidiomycetes. *In:* Gribble G. W. (Ed.) *The Handbook of Environmental Chemistry* 3 (Part P). Springer Verlag, Berlin, pp. 103-119.

FONS F., RAPIOR S., EYSSARTIER G. & BESSIÈRE J.M., 2003 — Les substances volatiles dans les genres *Cantharellus*, *Craterellus* et *Hydnum*. *Cryptogamie, Mycologie* 24: 367-376.

GIACINTI-MARTINIE G., 1999 — *Étude de quelques Macromycètes : aspects aromatique et fonctionnel*. Diplôme de Recherche Universitaire, Institut national polytechnique de Toulouse – École nationale supérieure de chimie de Toulouse, 220 p.

HANSSEN H.P., 1982 — Pilzaromen - Aromen aus Pilzen? *Deutsche Lebensmittel-Rundschau* 78: 435-440.

HJELM O., BOREN H. & ÖBERG G., 1996 — Analysis of halogenated organic compounds in coniferous forest soil from a *Lepista nuda* (Wood Blewitt) fairy ring. *Chemosphere* 32: 1719-1728.

HJELM O., JOHANSSON E. & ÖBERG G., 1999 — Production of organically bound halogens by the litter-degrading fungus *Lepista nuda. Soil Biology and Biochemistry* 31: 1509-1515.

JENNINGS W. & SHIBAMOTO T., 1980 — *Qualitative analysis of flavor and fragrance volatiles by Glass Capillary Gas Chromatography*. Academic Press, New York, 472 p.

KONNO K., HASHIMOTO K., OHFUNE Y., SHIRAHAMA H. & MATSUMOTO T., 1988 — Acromelic acids A and B. Potent neuroexcitatory amino acids isolated from *Clitocybe acromelalga. Journal of American Society* 110: 4807-4815.

KRINGS U., ABRAHAM B.G. & BERGER R.G., 1995 — Plant impact volatiles from higher fungi: A biotechnological perspective. *Perfumer & Flavorist* 20: 79-85.

KUBO I., KIM M., WOOD W.F. & NAOKI H., 1986 — Clitocine: a new insecticidal nucleoside from *Clitocybe inversa. Tetrahedron letters* 27: 4277-4280.

LÖFGREN N. & LÜNING B., 1954 — The isolation of nebularine and the determination of its structure. *Acta Chemica Scandinavica* 8: 670-680.

McAFEE B.J. & TAYLOR A., 1999 — A review of the volatile metabolites of fungi found on wood substrates. *Natural Toxins* 7: 283-303.

McLAFFERTY F.W. & STAUFFER D.B., 1989 — *The Wiley NBS Registry of mass spectral data*. Wiley & Sons, New York, 256 p.

MAGA J.A., 1981 — Mushroom flavor. *Journal of Agricultural and Food Chemistry* 29: 1-4.

MALENCON G. & BERTAULT R., 1975 — *Flore des champignons supérieurs du Maroc*. Tome II. Editions marocaine et internationales, Rabat, 541 p.

MAU J., BEELMAN R.B. & ZIEGLER G.R., 1994 — Aroma and flavor components of cultivated mushrooms. *In*: Charalambous G. (Ed.), *Spices, Herbs and Edible Fungi*. Elsevier, Amsterdam, pp. 657-684.

MAU J.L., CHYAU C.C., LI J.Y. & TSENG Y.H., 1997 — Flavor compounds in Straw Mushrooms *Volvariella volvacea* harvested at different stages of maturity. *Journal of Agricultural and Food Chemistry* 45: 4726-4729.

MAZUR X., BECKER U., ANKE T. & STERNER O., 1996 — Two new bioactive diterpenes from *Lepista sordida. Phytochemistry* 43: 405-407.

MOREAU P.A., COURTECUISSE R., GUEZ D., GARCIN R., NEVILLE P., SAVIUC P. & SEIGLE-MURANDI F., 2001 — Analyse taxinomique d'une espèce toxique : *Clitocybe amoenolens* Malençon. *Cryptogamie, Mycologie* 22: 1-23.

MOREAU P.A., 2002 — Les odeurs des champignons : un monde à découvrir. *La Garance voyageuse* 61: 33-41.

MORELLI I., PISTELLI L. & CATALANO S., 1981 — Some constituents of *Clitocybe nebularis* and of *Hydnum repandum. Fitoterapia* 52: 45-47.

MOSER M., 1983 — *Keys to Agarics and Boleti (Polyporales, Boletales, Agaricales, Russulales)*. Ed. Roger Philips, London, 535 p.

MOSS R.J., PETRIE C.R., MEYER R.B., DEE NORD L., WILLIS R.C., SMITH R.A., LARSON S.B., KINI G.D. & ROBINS R.K., 1988 — Synthesis, intramolecular hydrogen bonding, and biochemical studies of clitocine, a naturally occurring exocyclic amino nucleoside. *Journal of Medicinal Chemistry* 31: 786-790.

NATIONAL INSTITUTE OF STANDARD AND TECHNOLOGY, 1994 — *PC version of the NIST / EPA / NIH Mass Spectra Database*, version 4.5, U.S., Department of Commerce. Gaithersburg, Maryland.

NOEL-SUBERVILLE C., CRUZ C., GUINBERTEAU J. & MONTURY M., 1996 — Correlation between fatty acid content and aromatic compound release in Fresh Blewit (*Lepista nuda*). *Journal of Agricultural and Food Chemistry* 44: 1180-1183.

OHTA T., TAKAHASHI A., MATSUDA M., KAMO S., AGATSUMA T. & NOZOE S., 1995 — Russuphelol, a novel optically active chlorohydroquinone tetramer from the mushroom *Russula subnigricans. Tetrahedron Letters* 36: 5223-5226.

POMERLEAU R., 1980 — *Flore des champignons au Québec.* Ed. La Presse, Ottawa, p 317.

RAPIOR S., CAVALIE S., CROZE P., ANDARY C., PELISSIER Y. & BESSIÈRE J.M., 1996 — Volatile components of ten frozen mushrooms (Basidiomycetes). *Journal of Essential Oil Research* 8: 63-66.

RAPIOR S., BREHERET S., TALOU T. & BESSIÈRE J.M., 1997 — Volatile flavor constituents of fresh *Marasmius alliaceus* (Garlic *Marasmius*). *Journal of Agricultural and Food Chemistry* 45: 820-825.

RAPIOR S., FONS F. & BESSIÈRE J.M., 2003 — Volatile flavor constituents of *Lepista nebularis*. *Cryptogamie, Mycologie* 24: 159-166.

REGERAT F., POURRAT H. & POURRAT A., 1976 — Study of ergosterol in the carpophores of several Macromycetes. *Annales Pharmaceutiques françaises* 34: 231-235.

ROMAGNESI H., 1971 — *Petit atlas des champignons.* Tome 2. Bordas, Paris, 348 p.

SAVIUC P., 2000 — Champignons : *Lepista inversa* a un sosie toxique. *Les nouvelles pharmaceutiques* 204: 14.

SAVIUC P.F., DANEL V.C., MOREAU P.A., GUEZ D.R., CLAUSTRE A.M., CARPENTIER P.H., MALLARET M.P. & DUCLUZEAU R., 2001 — Erythromelalgia and mushroom poisoning. *Journal of Toxicology - Clinical Toxicology* 39: 403-407.

SAVIUC P., FLESCH F. & DANEL V., 2003 — *Intoxications par les champignons : syndromes majeurs.* Encyclopédie Médico-Chirurgicale. Toxicologie Pathologie Professionnelle. Elsevier, Paris, 16-077-A-10. 10 p.

SCHEIKL M., 1994 — Electrometric measurement of the surface pH value of wood types. *Holzforschung und Holzverwertung* 46: 105-108.

SENATORE F., 1992 — Chemical constituents of some mushrooms. *Journal of Science and Food Agriculture* 58: 499-503.

SECRIST J.A., SHORTNACY-FOWLER A., BENNETT L. & MONTGOMERY J. A., 1994 — Synthesis and biological evaluation of 8-substituted derivatives of nebularine (9-β-ribofuranosylpurine). *Nucleosides & Nucleotides* 13: 1017-1029.

VERHAGEN F.J.M., SWARTS H.J., KUYPER T.W., WIJNBERG J.B.P.A. & FIELD J. A., 1996 — The ubiquity of natural adsorbable organic halogen production among Basidiomycetes. *Applied Microbiology & Biotechnology* 45: 710-718.

WOOD W.F., SMITH J., WAYMAN K. & LARGENT D.L., 2003 — Indole and 3-chloroindole: the source of the disagreeable odor of *Hygrophorus paupertinus*. *Mycologia* 95: 807-808.

WOOD W.F., CLARK T.J., BRADSHAW D.E., FOY B.D., LARGENT D.L. & THOMPSON B.L., 2004 — Clitolactone: a banana slug antifeedant from *Clitocybe flaccida*. *Mycologia* 96: 23-25.