Octenol, the fungal compound you didn't know you love (and possibly hate?)

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Abstract: Octenol is the eight-carbon compound that provides the "mushroomy" flavor of many popular edible fungi. You can find it in a wide range of mushrooms: *Agaricus* spp., Morels, Oyster mushrooms, and many others. The biological roles of octenol include insect attraction or repulsion and inhibition of various microbes. Octenol also occurs in plants and in the breath and sweat of mammals, even humans. Production of this eight-carbon alcohol is a fascinating aspect of mushroom biology that deserves both culinary appreciation and scientific interest.

Keywords: semiochemical, flavor, aroma, 1-oct-en-3-ol, oct-1-en-3-ol, mushroom alcohol

Edible mushrooms produce many compounds that form the flavors that we enjoy. Alone and in combination, these are the chemicals that attract gastronomes (and repel mycophobes). Octenol is perhaps the leading example. Also known as 1-oct-en-3-ol, oct-1-en-3-ol, mushroom alcohol, or matsutake alcohol, it often predominates in edibles with its quintessential "mushroomy" taste. For example, while over 150 volatile compounds are found in Button Mushrooms (*Agaricus bisporus*; Figure 1), octenol is a main determinant of its flavor (Moliszewska, 2016).

Octenol was originally discovered in crushed Matsutake mushrooms (*Tricholoma matsutake*) in 1936 when S. Murahashi called it "matsutake alcohol" (Murahashi, 1936). It also occurs in a wide range of other organisms. Aromatic herbs such as Oregano (*Origanum vulgare*), Amla (*Phyllanthus emblica*), Barbed Skullcap (*Scutellaria barbata*), and Lemon Balm (*Melissa officinalis*) produce this compound (Nurzyńska-Wierdak et al., 2014; Xiong et al., 2017). On top of all of that, you can find it in the sweat and breath of mammals, including humans (more on that later).

Characteristics

From its name, you can tell that octenol is an eight-carbon alkene. That means it's a hydrocarbon with a double-bond lurking somewhere in a group of eight linked carbon atoms (if it was "oct***a***nol" it wouldn't have any double bonds between the carbons). You can also tell it's an alcohol (the "-ol" refers to an oxygen-hydrogen or "-OH" group tacked on to one of the carbons; Figure 2). In

Table 1. Some popular edible mushrooms containing octenol.

Common name	Genus	Species	Reference(s)
Black Trumpet	*Craterellus*	*cornucopiodes*	Fons et al., 2003
Blewit	*Collybia*	*nuda*	Noël-Suberville et al., 1996
Button Mushroom	*Agaricus*	*bisporus*	Moliszewska, 2016
Chanterelle	*Cantharellus*	*cibarius*	Fons et al., 2003; Zhou et al., 2015
Fairy Ring Mushroom	*Marasmius*	*oreades*	Vidal et al., 1986
Hedgehog Mushroom	*Hydnum*	*repandum*	Fons et al., 2003
Hen-of-the-woods	*Grifola*	*frondosa*	Zhou et al., 2015
King Bolete	*Boletus*	*edulis*	Zhou et al., 2015; Zhang et al., 2020
King Oyster Mushroom	*Pleurotus*	*eryngii*	Zhou et al., 2015
Landscape Morel	*Morchella*	*importuna*	Tietal and Mesaphy, 2017
Lion's Mane	*Hericium*	*erinaceus*	Zhou et al., 2015
Matsutake	*Tricholoma*	*matsutake*	Lee et al., 2020
Oyster Mushroom	*Pleurotus*	*ostreatus*	Zawirska-Wojtasiak, 2009
Paddy-Straw Mushroom	*Volvaria*	*volvacea*	Mau et al., 1997
Shaggy Mane	*Coprinus*	*comatus*	Dijkstra and Wikén, 1976
Shiitake	*Lentinula*	*edodes*	Dermiki et al., 2013; Zhou et al., 2015
White Truffle	*Tuber*	*magnatum*	Mustafa et al., 2020
Yellow Legs	*Craterellus*	*tubaeformis*	Fons et al., 2003

Figure 1. Fruiting bodies of *Agaricus bisporus* (white and brown types) about to contribute their octenol content to a pasta sauce.

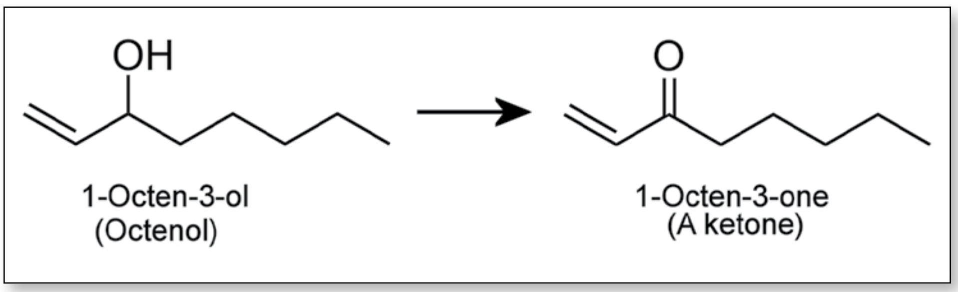

Figure 2. The chemical structure of octenol (1-octen-3-ol) and its ketone derivative (1-octen-3-one). Carbon atoms (not shown) are positioned where line segments (chemical bonds) join, or where they end. Each carbon atom is linked to four other atoms, in this case usually two or three other hydrogen atoms (not shown). Otherwise, oxygen atoms are indicated by "O" and hydrogen by "H."

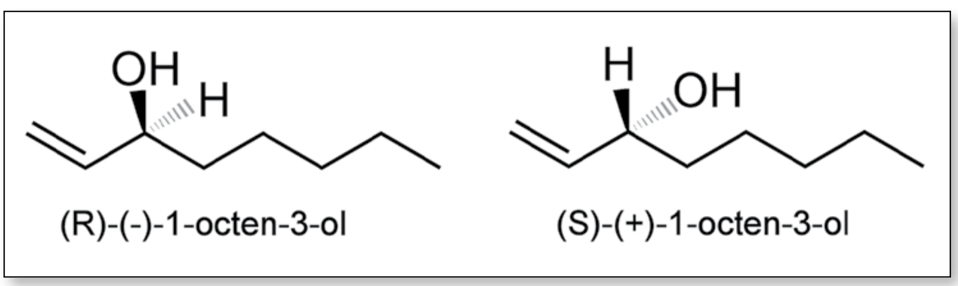

Figure 3. The enantiomers of octenol. The dark triangular bond coming upward from the second carbon should be imagined as slanting out toward the viewer. The grey stippled triangular bond should be imagined as slanting back and away from the viewer. The "(-)" in the "(R)" enantiomer indicates that it is levorotatory (rotates polarized light counterclockwise). The "(+) in the "(S)" enantiomer indicates that it is dextrorotatory (rotates polarized light clockwise).

pure form, it's a clear, aromatic liquid that boils between 84–85ºC and is only slightly soluble in water. Unsurprisingly, the strong odor of the compound has resulted in its use in various flavor and perfume products (Environmental Protection Agency, 2003).

Acute doses of octenol can cause mild eye and respiratory irritation, headaches, or nausea (Wålinder et al., 2008). Laboratory experiments with fruit flies have shown that octenol can damage the insect's dopamine physiology and nervous system. This might be concerning for people chronically exposed to mold-infested buildings and may also have implications for risks related to Parkinson's Disease (Inamdar et al., 2013). The actual significance or degree of risk to humans remains unquantified and has not been demonstrated.

If you eat mushrooms, the chances are pretty good that you regularly consume octenol. It is found in many popular edibles, including (but not limited to) those found in Table 1.

Dynamics

So where does the compound come from? In *T. matsutake*, octenol is produced when enzymes (lipoxygenases and peroxide lyases) oxidize linoleic acid, an omega-6 fatty acid essential in human diets (Lee et al., 2020). Octenol concentrations in mushrooms like Matsutake can be very dynamic, because enzymatic activity is necessary for its production. Research on American Matsutake (*T. magnivelare*) has shown that production in that species only occurs when cells are damaged (Wood and Lefevre, 2007). On the other hand, there is an 85% *reduction* of octenol levels when *Marasmius oreades* mushrooms are dried (Vidal et al., 1986). Drying also reduces volatile components like octenol in *Boletus edulis* (Zhang et al., 2020) and *Morchella importuna* (Tu et al., 2018). Concentrations of volatiles (in general) can also change as fruiting bodies develop, something that has been noticed in morels (Tietal and Mesaphy, 2022).

Other factors can also have an impact on octenol levels. A Ukrainian study of *Pleurotus ostreatus* found that production of volatiles and mushroom-like aroma increased when mushrooms were cultivated on sunflower husks vs. barley straw (Vlasenko et al., 2018). A study of Wood Ear (*Auricularia auricula*) found regional differences in levels of octenol and other flavor compounds (Fu et al., 2020).

Variations

Octenol is chiral (a compound with asymmetrical structures, where the mirror images don't match). Its mirror images are called enantiomers. Naturally occurring octenol is often the "R" type enantiomer (Figure 3). In octenol, the R form causes polarized light to rotate counterclockwise, making it "levorotatory." This is the form that is most attractive to many mosquito species (Grant and Dickens, 2011). The "S" enantiomer also exists (Figure 3). It is dextrorotatory, causing polarized

Figure 4. Photomicrograph of a ca. 6-mm-long Common House Mosquito (*Culex pipiens*?; *Culicidae*) specimen from the Pacific Forestry Centre Arthropod Reference Collection. Mosquitoes are attracted to octenol present in human perspiration.

light to rotate clockwise. The S form is a preferred attractant for some fungus-colonizing beetles (Thakeow et al., 2008). For humans, the R form is associated with a fruity, mushroom-like taste, while the S form has grassy, moldy notes. Even within the same fungal genus, the ratio of the two forms can be contrasting. For example, Oyster Mushroom (*P. ostreatus*) and Pink Oyster Mushroom (*P. djamor*) produce relatively high amounts of optically pure R form (over 90%) compared to an even mix of the R and S forms in the Golden Oyster Mushroom (*P. citrinopileatus*) (Zawirska-Wojtasiak et al., 2009).

As if all of that wasn't enough, octenol has a related ketone derivative (1-octen-3-one) that often accompanies it as a sort of secret, highly effective sidekick. This ketone derivative occurs at relatively low levels in *A. bisporus*, but it's actually more potent than octenol and can have a much larger impact on flavor (Aisala et al., 2019; Moliszewska, 2016). The ketone's lower odor threshold probably stems from changes to that alcoholic "-OH" group that sticks out in octenol.

Figure 5. A commercially produced bait package containing octenol. Among other brands, the product is used to lure biting insects into traps.

When the group and its carbon neighbor both shed a hydrogen, the remaining double-bonded oxygen (Figure 1) is likely more reactive to receptors in your nose and mouth, making it more smelly and tasty.

Octenol as an attractant

Now we come to reason some of you may (knowingly or unknowingly) hate octenol. The compound attracts insect pests. Animal breath and perspiration contains octenol, and insect pests are able to detect it to hone in on sources of plant nectar or animal blood. Researchers searching for tsetse fly attractants in Africa found that cattle odors contain octenol, and that it attracts the tsetse flies (Hall et al., 1984). You can also find the volatile compound in human perspiration (made by human enzymes, not skin microbes). Human-produced octenol has actually received a fair bit of study, because it attracts mosquitoes (Figure 4), including species that are malaria vectors (Cork and Park, 1996). This brings up an interesting factoid for your next scientific trivia contest: chemical repellents like DEET (N,N-diethyl-meta-toluamide) block octenol receptors, thereby inhibiting your attractiveness to mosquitoes (Bohbot and Dickens, 2010).

A wide variety of commercial products (Figure 5) use octenol as a chemical lure to attract and trap mosquitoes, black flies, no-see-ums, etc. (Figure 4).

Octenol has also been shown to attract fungivorous (fungus-eating) beetles, specifically Darkling Beetles, Pleasing Fungus Beetles, and Minute Tree Fungus Beetles (Figure 6; Drilling and Dettner, 2009).

Octenol as a repellent and inhibitor

The biological effects of octenol are multi-faceted, and this is where its ecological role becomes both complicated and fascinating. Consider, for example, the Mushroom Phorid Fly (*Megaselia halterata*), a pest of mushroom cultivation. Higher concentrations of octenol (in compost) may actually repel these flies—but only the females (Pfeil and Mumma, 1993). In another twist, fungivorous larvae of the Fruit Fly (*Drosophila melanogaster*) are attracted to octenol (Figure 7) along with an entomopathogenic (insect-infecting) nematode, *Steinernema diaprepesi.* However, larvae of the non-fungivorous Root Weevil (*Diaprepes abbreviatus*) avoid octenol, thereby also avoiding the nematode and reducing their infection levels. This kind of Jekyll-and-Hyde behavior can even be seen in the same insect species. For example, species of mosquitoes attracted by octenol also have larvae killed by it (Chaiphongpachara et al., 2019).

You probably won't be surprised to learn that octenol also has antimicrobial properties. It shows strong inhibition of bacteria, especially Gram-positive bacteria like *Staphylococcus aureus* and *Bacillus subtilis.* Octenol inhibits growth and/or spore germination of fungi, for example *Fusarium* spp. (Xiong et al., 2017) and *Penicillium* spp. (Yin et al., 2019).

Conclusions

In fungi, octenol is an intriguing compound tied to gastronomic appreciation and a variety of ecological interactions. But it's really only the tip of the iceberg when it comes to secondary compounds in mushrooms. Perhaps you favor nucleotides that provide the complex, umami-flavored goodness of Hen-of-the-Woods or Black Trumpets. Or you might prefer the methyl cinnamate that spices up Matsutake, or maybe the wild mix of different compounds that provide the apricot-like notes in Chanterelle aromas. The literature on flavors and odors in edible mushrooms

Figure 6. Photomicrograph of a ca. 2-mm-long Minute Tree Fungus Beetle (*Cis soror*; *Ciidae*) specimen from the Pacific Forestry Centre Arthropod Reference Collection. This beetle was collected from a Cinnabar Polypore (*Pycnoporus cinnabarinus*) fruiting body. The Ciidae are attracted by octenol and most members of the genus inhabit and consume fungi (*Polyporaceae*, rarely also *Corticiaceae*).

collects a bewildering array of hundreds of different compounds, all with different appeal and potentially different ecological roles. In fact, we make good use of this diversity every time we use aromas to help identify mushrooms. There is still much to learn (and appreciate) about this aspect of mycology.

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Figure 7. If you have Fruit Flies (*Drosophila melanogaster*; *Drosophilidae*) in your kitchen during canning season, you can perform this experiment. Lay out slices of banana (upper left) and octenol-producing mushrooms and after a short time compare the attractive power of the baits. In this case, the flies are clearly excited by the banana slices. However, the arrows show three who prefer the apricot-like scent of the Pacific Golden Chanterelle (*Cantharellus formosus*, lower left). Meanwhile, two have shown interest in the Button Mushroom (*Agaricus bisporus*, lower right).

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