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MINI REVIEW

Volatile sensation: The chemical ecology of the earthy odorant geosmin

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Abstract

Geosmin may be the most familiar volatile compound, as it lends the earthy smell to soil. The compound is a member of the largest family of natural products, the terpenoids. The broad distribution of geosmin among bacteria in both terrestrial and aquatic environments suggests that this compound has an important ecological function, for example, as a signal (attractant or repellent) or as a protective specialized metabolite against biotic and abiotic stresses. While geosmin is part of our everyday life, scientists still do not understand the exact biological function of this omnipresent natural product. This minireview summarizes the current general observations regarding geosmin in prokaryotes and introduces new insights into its biosynthesis and regulation, as well as its biological roles in terrestrial and aquatic environments.

INTRODUCTION

The sense of smell evokes the strongest memory of all the senses and is largely based on the perception of volatile organic compounds (VOCs). While VOCs are part and parcel of our lives, we know very little about their biological function. One enigmatic experience is the feeling of well-being that is generated by a walk in the forest. That smell is caused by geosmin, a sesquiterpene discovered in 1965, whose name is derived from the Greek words ‘gê’—earth and ‘osmê’—odour. Geosmin is abundant in nature and mainly produced by Actinobacteria (Gerber, 1967; Gerber & Lechevalier, 1965; Schoeller et al., 2002) and myxobacteria (Dickschat et al., 2004; Schulz et al., 2004; Trowitsch et al., 1981) in soil, and by cyanobacteria in aquatic systems (Izaguirre et al., 1982; Safferman et al., 1967). Geosmin also occurs in ascomycete fungi (Kikuchi et al., 1981; Larsen & Frisvad, 1995; Mattheis & Roberts, 1992), in Basidiomycota (Breheret et al., 1999), in amoebae (Hayes et al., 1991), in liverwort (Spoerle et al., 1991), in

mosses (Saritas et al., 2001), in maize where it serves as a possible attractant of the corn earworm *Heliothis zea* (Flath et al., 1978), and in the defence secretions of the polydesmid millipede *Niponia nodulosa* (Omura et al., 2002). It has also been reported from different foodstuff including beetroot (Acree et al., 1976), dry beans (Buttery et al., 1976), rainbow trout (Persson, 1980), molluscs (Hsieh et al., 1988) and shrimps (Lovell & Broce, 1985), and is a constituent of garden soil (Buttery & Garibaldi, 1976).

Geosmin is a member of the largest family of natural compounds, the terpenoids (Avalos et al., 2022). Many of these compounds are highly odour-active. The human nose can detect geosmin at less than five parts per trillion, equivalent to one teaspoon in 200 Olympic swimming pools, yet we do not understand its exact biological function. The widespread distribution of geosmin synthase genes across microbial life in seemingly unrelated microorganisms such as Actinobacteria, myxobacteria, cyanobacteria and fungi suggests that geosmin has an important ecological role in their lifecycle. A

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whole-genome-based phylogenetic study on *Streptomyces* species and comparison of the distribution of terpene synthase genes among them revealed that geosmin synthases were the most widely distributed, as they were present in all except one of the *Streptomyces* species analysed (Martín-Sánchez et al., 2019). The phylogenetic analysis of geosmin synthases were not congruent with the phylogeny of the *Streptomyces* species pointing to horizontal gene transfer as mechanisms involved in the distribution of geosmin biosynthesis. Geosmin also plays an important role in biotechnology, as the smell we associate with the pleasant smell of soil creates an off-flavour in water, wine and freshwater fish products that producers struggle to eliminate.

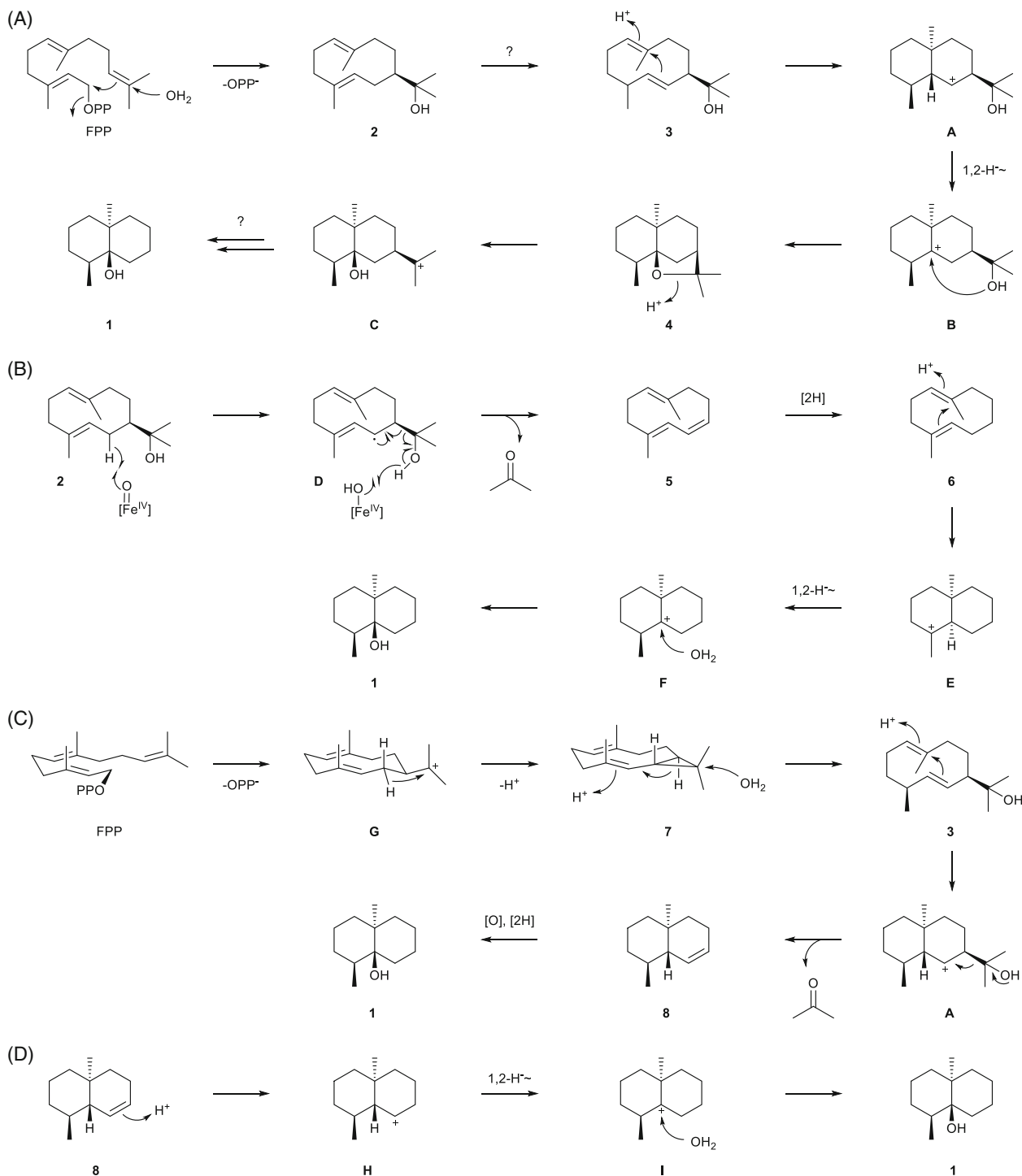
This minireview summarizes the current knowledge regarding geosmin and offers new insights into its biosynthesis and regulation as well as its possible biological and ecological roles in terrestrial and aquatic environments. As mentioned above, geosmin is not only produced by prokaryotes, but also by many other organisms. This review will focus specifically on geosmin from prokaryotic sources, whereby we will only briefly touch on its role in the biology of other organisms.

BIOSYNTHESIS OF GEOSMIN

After its discovery (Gerber & Lechevalier, 1965) and structural identification (Gerber, 1968), the biosynthesis of geosmin (**1**, Scheme 1) was a long-standing debate. Speculations that geosmin could be a degraded eudesmane sesquiterpene with a lost isopropyl group (Gerber, 1968) were first addressed experimentally by feeding radioactive labelled precursors to *Streptomyces antibioticus*. While [1-¹⁴C]acetate and [2-¹⁴C]acetate were incorporated into geosmin, [methyl-¹⁴C]methionine was not, which was interpreted in favour of an isoprenoid pathway to geosmin (Bentley & Meganathan, 1981). Several years later, a series of structurally related sesquiterpenes including (1(10)*E*,5*E*)-germacradien-11-ol (**3**) and dihydroagarofuran (**4**) were isolated from the geosmin producer *Streptomyces citreus*, culminating in a first detailed biosynthetic hypothesis in which these cometabolites were speculated to be intermediates, but neither the formation of **3** from hedycaryol (**2**) nor the loss of the isopropyl group were explained satisfyingly (Scheme 1A, Pollak & Berger, 1996). The terpenoid origin of geosmin was finally confirmed by feeding of the terpene precursors (5,5-²H₂)-1-desoxy-D-xylulose to *Streptomyces* sp. JP50 and (4,4,6,6,6-²H₅)mevalolactone to the liverwort *Fossombronia pussilla* (Spiteller et al., 2002), while feeding experiments using ¹³C-labelled NaHCO₃ established the biogenetic origin of geosmin in the cyanobacterium *Calothrix* (Höckelmann & Jüttner, 2004). First mechanistic proposals for the loss of the isopropyl group suggested oxidative cleavage with formation of

acetone (Scheme 1B, Spiteller et al., 2002) or a retro-Prins fragmentation during terpene cyclisation to the octalin derivative **8**, followed by double bond reduction and oxidative installation of the hydroxy function (Scheme 1C, Cane & Watt, 2003). Feeding experiments with (²H₁₀)leucine and (4,4,6,6,6-²H₅)mevalolactone to *Myxococcus xanthus* demonstrated retainment of the bridgehead hydrogen in the octalin, in disagreement with oxidative introduction of the alcohol function in **8**. Instead, geosmin biosynthesis proceeds without redox chemistry through a typical cationic terpene cyclisation cascade (Dickschat et al., 2005). The cascade proceeds through 1,10-cyclisation of FPP to cation **G**, deprotonation with cyclopropanation to isolepidozene (**7**), reprotonation induced ring opening with attack of water to **3**, and another reprotonation induced cyclisation to **A** and retro-Prins fragmentation to **8** (Scheme 1C, Cane & Watt, 2003). The downstream steps include a sequence of protonation to **H**, 1,2-hydride shift to **I** and attack of water to yield **1** (Scheme 1D, Dickschat et al., 2005).

Gene replacement experiments in *Streptomyces coelicolor* finally identified the gene for geosmin synthase, a bifunctional two-domain terpene synthase (Gust et al., 2003). Replacement of the N-terminal domain abolished geosmin biosynthesis, while replacement of the C-terminal domain had no apparent effect on geosmin production. At the same time, the protein function was established through the enzymatic conversion of FPP in vitro, showing that the full length geosmin synthase and also the N-terminal domain alone yielded (1(10)*E*,5*E*)-germacradien-11-ol (**3**), while the C-terminal domain initially did not show a catalytic effect towards FPP (Cane & Watt, 2003). Shortly later, incubation experiments with recombinant proteins revealed that the geosmin synthases from *S. coelicolor*, *S. avermitilis* and the cyanobacterium *Nostoc punctiforme* can, in fact, convert FPP into geosmin (Cane et al., 2006; Giglio et al., 2008; Jiang et al., 2006). Detailed investigation of the enzyme from *S. coelicolor* through incubation experiments with the individual domains of the geosmin synthase combined with site-directed mutagenesis revealed that the N-terminal domain converts FPP into **3**, while the C-terminal domain catalyses the downstream reaction from **3** to **1** (Jiang et al., 2007). The geosmin synthase mechanism was further established by the detection of deuterated acetone formed from a deuterated FPP precursor (Jiang & Cane, 2008) and the structural verification of octalin **8** through total synthesis (Nawrath et al., 2008). A crystal structure of full-length geosmin synthase is not available, but the N-terminal domain has been crystallized, showing the typical α -helical fold and active site architecture of type I terpene synthases (Harris et al., 2015). The whole biosynthetic pathway starting from acetic acid, including the mevalonate pathway, the biosynthesis of FPP and its cyclisation to geosmin, has been reconstituted in vitro (Dirkmann et al., 2018).



SCHEME 1 Biosynthesis of geosmin. (A) First hypothesis by Pollak and Berger (1996), (B) biosynthetic model by Spiteller et al. (2002) involving oxidative side chain cleavage, (C) refined model by Cane and Watt (2003) through side chain cleavage by retro-Prins reaction and subsequent redox transformations, and (D) biosynthetic model by Dickschat et al. (2005) proposing substitution of the redox transformations from 8 to 1 by a cationic cascade. The today generally accepted mechanism proceeds through the steps from FPP to 8 as in (C), followed by the steps from 8 to 1 as in (D).

While the pathway in bacteria is well established, such detailed knowledge about geosmin biosynthesis in other organisms is lacking. Deletion of a gene encoding a cytochrome P450 in *Penicillium expansum* abolished geosmin biosynthesis (Siddique et al., 2012), but

the direct involvement of this enzyme remains to be demonstrated. Another recent study reported on a candidate fungal gene (*ges1*) in *Tricholoma vaccinum* that encodes a terpene synthase involved in geosmin biosynthesis (Abdulsalam et al., 2021).

However, knockdown of *ges1* through RNAi resulted in strongly reduced gene expression levels but only slightly lower geosmin production (Abdulsalam et al., 2022). Further functional characterization will be required to gain evidence for the function of *ges1*. Recently, a terpene synthase for (1(10)*E*,5*E*)-germacradien-11-ol (**3**) was discovered from *Aspergillus ustus*, suggesting that this compound may also be an intermediate in fungal geosmin biosynthesis, but the conversion of **3** into geosmin has not been shown (Peter et al., 2022). Taken together, the molecular basis for geosmin biosynthesis in fungi is currently unclear. The detection of geosmin in aseptically grown beet roots was taken as an evidence that beet roots are capable of endogenous geosmin biosynthesis (Lu et al., 2003), but also for this organism characterization of plant genes and enzymes are lacking.

A few studies have addressed the regulation of geosmin biosynthesis. Early investigations showed an increased geosmin production in *Streptomyces albidoflavus* in the presence of copper (Dionigi, 1996). Geosmin biosynthesis correlates to sporulation in *Streptomyces*, as evidenced by the fact that non-sporulating strains are unable to produce the compound (Schoeller et al., 2002). ChIP-seq experiments showed that the gene for geosmin synthase (*geoA*) in *Streptomyces venezuelae* is under the direct control of the sporulation-specific transcription factor WhiH (Becher et al., 2020). Notably, the geosmin synthase gene in *Streptomyces peucetius* is silent, but becomes activated after deletion of the biosynthetic gene cluster for doxorubicin (Singh et al., 2009). Doxorubicin is a DNA-degrading compound, and its biosynthesis inhibits development of the producer strain (Hulst et al., 2022). Since geosmin is produced in particular during sporulation, this likely explains why wild-type *S. peucetius* does not produce the compound, while the well-sporulating mutant does. In cyanobacteria, transcription of the geosmin synthase gene is not light-dependent, but is downregulated at the same time of growth cessation in laboratory cultures (Giglio et al., 2011).

Similar to other bacterial secondary metabolites produced by bacteria, geosmin biosynthesis is influenced by carbon source utilization and by trace elements. For example, mannitol as a carbon source promoted maximum geosmin production in *Streptomyces halstedii*, and also the trace elements zinc, iron and copper had a profound effect on geosmin production in the same strain (Schrader & Blevins, 2001).

BIOLOGICAL ROLE OF GEOSMIN IN TERRESTRIAL SYSTEMS

As an abundant chemical compound in soil, geosmin may have an important influence on terrestrial organisms. Recently, it was reported that geosmin acts as a

warning signal that repels the bacterial predator *Caenorhabditis elegans* (bacteriophagous nematode) and reduced contact between the worms and the geosmin-producing bacteria *S. coelicolor* (Zaroubi et al., 2022). Geosmin itself was not toxic to *C. elegans* but reduced grazing on *S. coelicolor*.

Geosmin and other terpenes may play a role in controlling the activity of protists, which are known predators of soil bacteria, including *Streptomyces*. Geosmin was tested as a pure compound against *Tetramitus*, where the total number of protists was reduced by observing a lower amount of inactive forms of the protist compared to the control, while the number of active protists remained the same (Avalos, 2019). This suggests a role for geosmin in inhibition of protist proliferation and as an antipredator compound.

Geosmin is important for the ecology and, in particular, the behaviour of insects. A stinging assay revealed that geosmin strongly suppresses the defensive behaviour of honeybees. Interestingly, this suppression was only observed at very low geosmin concentrations, while the effect was not observed at high concentrations (Scarano et al., 2021). Fire ants (*Solenopsis invicta*) preferentially start forming new nests in actinobacteria-rich soil, and this attraction was mediated by geosmin, resulting in a higher survival rate of the queen (Huang et al., 2020).

Geosmin may be attractive to one insect while repellent to another. For example, in *Aedes aegypti*, geosmin is a strong attractant and mediates egg-laying site selection (Melo et al., 2020), while in the fruit fly, *Drosophila melanogaster*, geosmin creates aversion, even in the presence of compounds that by themselves act as attractants (Stensmyr et al., 2012). The different response of insects to geosmin could be related to their ecological niche and lifestyle. The fruit fly, as its name suggests, feeds on decaying or fermented fruit, a process carried out by yeasts present in the fruit. Decaying fruits, however, may also be inhabited by fungi and bacteria which produce toxic compounds in addition to geosmin. Fruit flies, thus, use geosmin to detect the presence of harmful microbes (Stensmyr et al., 2012). On the other hand, the larvae of the mosquito *A. aegypti* feed on cyanobacteria which in turn makes the smell of geosmin attractive to the female mosquitoes to lay their eggs on (Melo et al., 2020). Both insects detect geosmin in a very sensitive manner, yet, their response is opposite. Despite the difference, both responses seem to be more ecologically related to the nutrient sources needed by the two organisms and may indicate an adaptation of the insects towards their environment.

While these examples relate to insects that respond to a chemical cue induced by geosmin, it is likely that, in nature, these cues originate from a microbial source. For example, geosmin attracts springtails to sporulating *Streptomyces* colonies. Springtails are known to be

'omnivorous' and can feed on a wide range of microorganisms as well as plants. A recent study by Becher et al. (2020) showed that the attraction of springtails towards *Streptomyces* is mediated by the volatile terpene compounds geosmin and the related 2-methylisoborneol. In *Streptomyces*, the production of these molecules is correlated with the onset of sporulation. The springtail feeds on the *Streptomyces* colonies; however, this also results in an advantage to the bacteria itself as it helps to disseminate the streptomycete spores via the faecal pellets of the springtail and through adherence to its hydrophobic cuticle (Becher et al., 2020). In *Streptomyces*, the production of geosmin is connected to the developmental life cycle of these bacteria, with the peak of geosmin production corresponding to the onset of sporulation (Becher et al., 2020).

The production of geosmin during a specific phase in the bacterial development has been suggested to be a fitness benefit. In *Myxococcus xanthus*, geosmin concentration increased during the exponential phase, peaked during the early stationary phase and decreased thereafter (Zaroubi et al., 2022). *M. xanthus* is a predatory bacterium, which suggests that geosmin could be of help when looking for prey (Zaroubi et al., 2022). Transcriptomics studies also showed expression of geosmin genes during the 'predasome' (when the predator encounters a prey), suggesting that this metabolite may participate in predation. The role of geosmin as a chemical signal is becoming increasingly evident; nevertheless, further exploration is required.

As a highly abundant terpenoid in soil, being produced by a wide range of microorganisms, it is logical to assume that geosmin may have a direct effect on plant physiology. The effect of geosmin was tested on plant seed germination using 15 kinds of seeds from the *Brassicaceae* family. The germination of all kinds of seeds was inhibited by geosmin, with 50% inhibition at a concentration of 7.5 mg L^{-1} (Ogura et al., 2000). Many germination inhibitors act by means of toxicity, killing the seeds, such as cyanide, a respiratory inhibitor. However, geosmin did not kill the seeds as the germination was restored once the exposure to geosmin was removed and the seeds were stratified or treated with the plant hormone gibberellin A. These studies suggest that geosmin can indeed act as a plant growth-regulating substance, primarily acting during seed germination and early plant life. Additional experiments on the role of geosmin on plant root development and root architecture are eagerly awaited.

GEOSMIN IN AQUATIC SYSTEMS

Cyanobacteria and Actinobacteria are often associated with geosmin production in aquatic environments (Clerc et al., 2021; Izaguirre & Taylor, 2004; Jüttner &

Watson, 2007; Klausen et al., 2005; Suurnäkki et al., 2015). The marine bacterium *Myxococcus fulvus*, a Deltaproteobacterium, also possesses a geosmin synthase gene, although its ability to produce the compound remains to be verified (Churro et al., 2020). Cyanobacteria or blue-green algae are organisms that thrive in aquatic environments; the water bodies and global warming result in algal blooms that cause an unpleasant smell in water and are also associated with toxicity because algal blooms are prolific producers of cyanotoxins (Freeman, 2010; Graham et al., 2010). Geosmin-producing cyanobacteria are abundantly found in freshwater reservoirs, where geosmin odour impacts the water quality, while only a few strains were isolated from brackish water (Churro et al., 2020; Persson, 1980). The limited reports of geosmin producers from brackish water and marine environments may be due to the low practical interest since seawater is rarely a source of drinking water (Jüttner & Watson, 2007).

Geosmin synthesis in aquatic producers is affected by various factors, including light availability, water flow and temperature (Espinosa et al., 2020; Shen et al., 2022). It was proposed that in aquatic environments, the geosmin bioactivity level may not be efficient in diffuse planktonic communities (Watson, 2003). After all, aquatic geosmin producers are mainly biofilm-forming benthos and epiphytes, and biofilm formation may support the geosmin action at microscale levels (Jüttner & Watson, 2007; Watson, 2003; Watson & Ridal, 2004). Furthermore, putative actinobacterial and cyanobacterial geosmin synthase encoding genes could be detected in subseafloor sediment samples (Schmidt et al., 2023).

Many questions remain on the biological and ecological roles of geosmin in aquatic environments. However, several reports demonstrate that geosmin has algicidal activity (Ikawa et al., 2001; Ozaki et al., 2008), affects metabolism and development of higher aquatic organisms (Nakajima et al., 1996; Zhou et al., 2020, 2023), and is released when producer cells are grazed by zooplankton (Durrer et al., 1999). This evidence indicates that geosmin may act as a repellent compound in microbial competition and herbivore deterrence (Fink, 2007; Saha & Fink, 2022; Wang et al., 2015). The studies described often used a high concentration of geosmin, which is unlikely to be found in a natural environment (Nakajima et al., 1996; reviewed by Watson, 2003). However, the hydrophobicity of this molecule may cause it to accumulate and reach higher concentrations in local areas where biofilms and cyanobacterial scums occur. Additionally, geosmin serves as a freshwater guiding signal during glass eel migration. Eels have a very sensitive sense of smell and seem to perceive odours on a greater scale than what can be measured in studies. Eel's perception of fresh water and possibly of geosmin is also dependent on salinity

gradients in the water (Kroes et al., 2020; Tosi & Sola, 1993). Geosmin was also proposed as the attractant for Bedouins' camels searching for freshwater sources in the desert. The ability of African elephants to detect geosmin was demonstrated, indicating that this compound also serves as an olfactory cue for water source location (Wood et al., 2022).

GEOSMIN IN WATER AND FOOD CONTAMINATION

As mentioned above, geosmin acts as a pollutant of water, which is mainly associated with production by cyanobacteria, though Actinobacteria also contribute to its accumulation. A study performed in Italy throughout the four different seasons showed that cyanobacteria counts were highly correlated with the increased odour in spring and summer, while an increased count in Actinobacteria correlated to a higher odour in autumn and winter (Lanciotti et al., 2003). Since actinobacteria are also common soil bacteria, the terrestrial production of geosmin could end up in water sources by washing or runoff.

A study of *Oreochromis niloticus* or Nile tilapia raised in net cages in Brazilian freshwater farms showed a high composition of cyanobacteria and Actinobacteria in digesta, intestinal mucous, and on the skin of fish as well as in the water. The study points to the intestinal tract as the main source of geosmin-producing bacteria (Lukassen et al., 2019).

Besides water, products such as wine and liquors also suffer from the presence of this earthy odour. In wines, the so-called cork taint involves the presence of geosmin among other contaminant compounds. In Chinese liquor, geosmin is found during the fermentation process where Daqu, the fermentation starter, is used. In both alcoholic beverages, the origin of geosmin seems to be microbial; in wine, it is hypothesised that it originates from microorganisms grown on the grapes, especially if stored in humid places. In Chinese liquor, *Streptomyces* strains were identified and isolated in the Daqu (Cravero, 2020; Darriet et al., 2000; Du & Xu, 2012).

The biotech industry has invested significantly in approaches to remove geosmin. While geosmin is not toxic at the concentrations found in the environment (Burgos et al., 2014), the association of geosmin to toxins produced by organisms such as cyanobacteria and the low perception threshold of 5 ng/L (Cravero, 2020) as well as the demand for clean, odourless water, necessitates the removal of the compound. Several techniques have been developed, such as the application of powdered activated carbon, coagulation, sedimentation, membrane filtration and chlorination, but since geosmin is difficult to oxidize (the only functional group is a tertiary alcohol), its full removal

from water remains challenging (Cook et al., 2001, Mustapha et al., 2021). Biodegradation of geosmin has also gained attention as an alternative to remove this compound. Bacterial communities able to degrade geosmin have been tested where bacteria belonging to the genus *Methylobacterium* and also bacteria from the family Oxalobacteraceae have shown promising results (Xue et al., 2012). Another biological approach to the removal of geosmin was the infection of geosmin-producing *Streptomyces* with streptophages. The infected streptomycetes were not able to produce geosmin anymore (Jonns et al., 2017). Bioremediation is a more natural alternative for the removal of geosmin. However, it seems that the combination of conventional techniques (physicochemical and biological) with advanced oxidation processes, such as ozonation or UV/photocatalyst, would provide a more effective solution for the removal of the odorous geosmin (Mustapha et al., 2021).

FUTURE RESEARCH DIRECTIONS AND OUTSTANDING QUESTIONS

The broad distribution of geosmin synthases among bacteria in both terrestrial and aquatic environments suggests that geosmin has an important ecological function as a signal (strong attractant or repellent) (Melo et al., 2020; Stensmyr et al., 2012) or as protective specialized metabolite against biotic and abiotic stresses (Figure 1). Geosmin does not seem to be involved in the basic cellular physiology. As discussed above, in *Streptomyces* the production of geosmin is linked to sporulation (Becher et al., 2020). However, the deletion of *geoA* does not affect sporulation, and it is therefore logical to assume that geosmin plays a more ecological role, such as promoting spore dispersal. The genes encoding geosmin synthases in myxobacteria, cyanobacteria and Actinobacteria are homologous (Wang et al., 2015), consistent with the idea that they may have a common ancestor. Considering the large evolutionary distance between the microorganisms, horizontal gene transfer likely contributed to the spreading of the gene for geosmin synthase.

Mammals and insects can detect geosmin at extremely low concentrations. While geosmin-sensitive receptors are known from insects, such a receptor has not been discovered in mammals so far, and hence we cannot reconstruct the evolutionary history of human sensitivity to this compound. It was proposed that geosmin could have allowed our ancestors and other animals to find water in arid environments.

Geosmin may also provide information about water availability to plants; however, so far, there is no study that has explored the effect of geosmin on plants and plant root development. Geosmin was detected in beet but not in other root vegetables. While it was originally

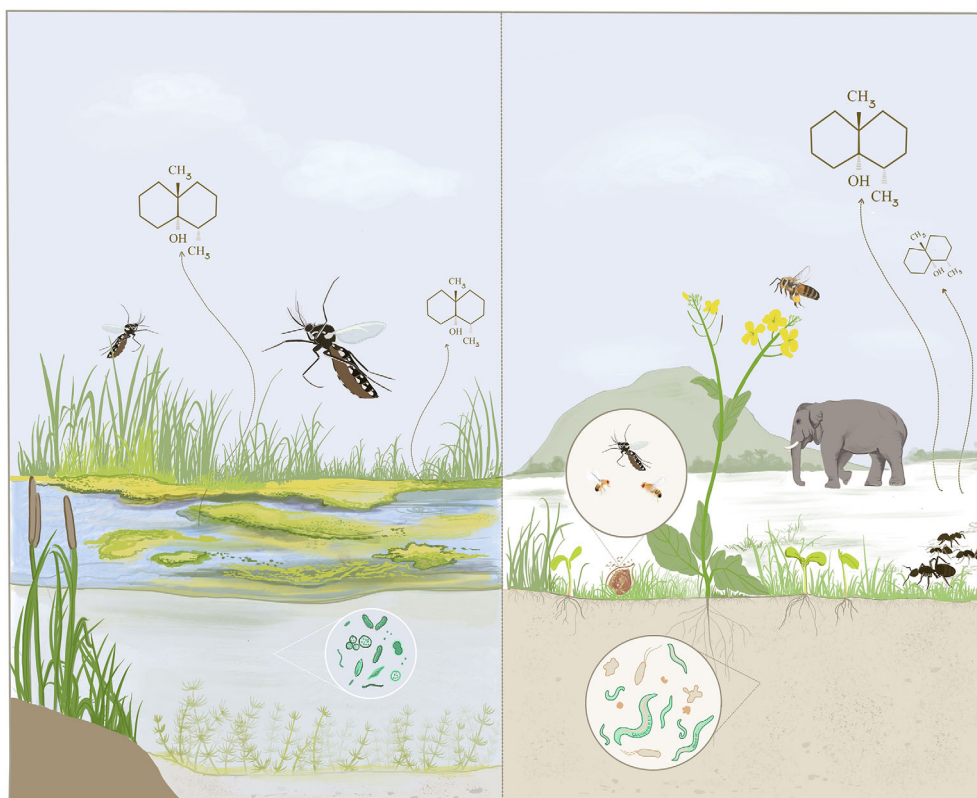


FIGURE 1 Ecological role of geosmin in aquatic (Left) and terrestrial (Right) environment. (Left) The main geosmin producers in aquatic environments are cyanobacteria and Actinobacteria. Geosmin acts as a repellent or attractant. It can have algicidal activity. (Right) In terrestrial environments, geosmin acts as an important info-chemical repellent or attractant. For example, geosmin repels fruit flies as well as predators (nematodes and protists). Geosmin is an attractant for honeybees, ants, mosquitoes and springtails. Geosmin can act as a regulator of seed germination and can be used as a cue by elephants for water source location.

hypothesised that the geosmin in beet was of microbial origin, recent studies suggest that geosmin is produced by beet itself (Freidig & Goldman, 2014; Hanson et al., 2021).

Surprisingly little is known about the biological role of geosmin in ecological interactions. The biological role of geosmin in all ecosystems ranges from its function as a signal to being a toxin and depends on its concentration. It should be noted that in studies reporting toxic effects of geosmin the concentrations far exceed those typically encountered in the environment (Dionigi et al., 1993; Nakajima et al., 1996). Thus, the environmental background is an important factor when considering ecological roles, since accumulated geosmin concentrations and, as a result, actions are different at microscale (rhizosphere, biofilms, cyanobacterial scums) and macroscale (open water, air) levels.

In nature, geosmin is often produced together with 2-methylisoborneol (2-MIB), and it is likely that there is interplay between the two compounds, with overlapping or complementary biological roles in specific concentrations and ratios. Future studies should aim at studying the two compounds simultaneously, which could help to offset gaps in our knowledge about geosmin. Still, while nearly all streptomycetes produce geosmin, only about a third produce 2-MIB (Martín-Sánchez

et al., 2019), strongly suggesting an independent function, and in particular that geosmin play a more critical role in the *Streptomyces* life cycle than 2-MIB. To better understand the role of geosmin in natural environments, it is also important to understand the regulation of geosmin biosynthesis. Indeed, geosmin production is controlled by transcription factors that regulate sporulation, which suggests that geosmin may promote spore dispersal. Studying ecological interactions, such as microbe-microbe and microbe-plant interactions, should help us to better understand the natural role of geosmin.

It is currently unknown if microbes can degrade geosmin or may serve as a ‘public good’ that can be used by different members of the community. Such a conserved molecule deserves more research attention to reveal the biological role of geosmin for the organisms producing it as well as to reveal receptors in (micro)organisms sensing it.

AUTHOR CONTRIBUTIONS

Paolina Garbeva: Conceptualization (equal). **Mariana Avalos:** Writing – original draft (equal). **Dana Ulanova:** Writing – original draft (equal). **Gilles van Wezel:** Writing – review and editing (equal). **Jeroen Dickschat:** Writing – original draft (equal).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

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