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Review

Biochemistry and genetics of taste- and odor-producing cyanobacteria

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ABSTRACT

Cyanobacteria are one of the principal sources of volatile organic compounds (VOCs) which cause offensive taste and odor (T&O) in drinking and recreational water, fish, shellfish and other seafood. Although non-toxic to humans, these T&O compounds severely undermine public trust in these commodities, resulting in substantial costs in treatment, and lost revenue to drinking water, aquaculture, food and beverage and tourist/hospitality industries. Mitigation and control have been hindered by the complexity of the communities and processes which produce and modify T&O events, making it difficult to source-track the major producer(s) and the factors governing VOC production and fate. Over the past decade, however, advances in bioinformatics, enzymology, and applied detection technologies have greatly enhanced our understanding of the pathways, the enzymes and the genetic coding for some of the most problematic VOCs produced by cyanobacteria. This has led to the development of tools for rapid and sensitive detection and monitoring for the VOC production at source, and provided the basis for further diagnostics of endogenous and exogenous controls. This review provides an overview of current knowledge of the major cyanobacterial VOCs, the producers, the biochemistry and the genetics and highlight the current applications and further research needs in this area.

Contents

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1. Introduction

Cyanobacteria produce a vast array of secondary metabolites of major socio-economic importance. These include compounds which are of commercial value as food additives, pharmaceuticals and in other industrial applications, or at the other end of the spectrum, compounds which have negative effects, acting as toxins and/or adversely affecting water and food. This review focuses on a subset of the second group, volatile organic compounds (VOCs) which are major sources of offensive airborne odors along shorelines and recreational waters, and cause severe taste and odor (T&O) in drinking water, fish and shellfish. T&O compounds have no known toxicological effects towards humans and most organisms across the range of concentrations found in the environment (e.g. Watson, 2013; Burgos et al., 2014); nevertheless, they profoundly influence human behavior. Most people judge the safety and acceptability of food and drink by their aesthetics – taste, odor and color, and changes in these aesthetics, particularly if episodic, can elicit widespread public alarm and distrust in potable water supplies and impart major costs to the drinking water industry in treatment and customer relations (Dietrich and Burlingame, 2015; Dunlap et al., 2015). In extreme cases, T&O outbreaks can affect treatment plant operation and cause severe drinking water shortages - as seen, for example, in the 2007 Lake Taihu 'Wuxi crisis' where foul organosulfur-derived odors shut down the water supply to over 2 million residents for five days (Ma et al., 2013). T&O events also contribute to the escalating use of bottled water (with the associated environmental issues and cost to consumers) and are a serious problem for aquaculture industries, which suffer significant economic losses through consumer rejection of tainted fish and shellfish (Engle et al., 1995; Tucker, 2000; Howgate, 2004; Robin et al., 2006; Burr et al., 2012). More recently it has become apparent that, perhaps not surprisingly, the bioactivity of these metabolites extends far past their socio-economic impacts, functioning in a variety of chemical interactions in the aquatic food web as protectants, attractants, deterrents and toxins (Höckelmann et al., 2004; Watson et al., 2007; Jüttner et al., 2010).). Chemical ecology is a relatively new field in freshwater research which, to date, has been most focused on the semiochemical properties of cyanotoxins (e.g. Ibelings and Havens, 2008) but which also offers important insight into the functional roles of VOCs and the intra- and extracellular controls of their production.

The early detection of a T&O episode is fundamental to an effective management of waters used for drinking, recreation, aquaculture and other food and beverage industries. Currently, a largely reactive approach is used by most of the drinking water industry, focused on 'repair' i.e. the treatment of impaired raw water. Few utilities have the resources or tools for more proactive source water monitoring and management, which has been further confounded by the lack of effective diagnostic tools and the apparent unpredictability of T&O events. To meet this need, a growing body of research has been aimed at developing more rapid, sensitive methods to identify and monitor T&O producers and reduce the need for expensive and time-consuming microscopy and chemical analyses. In particular, the last few decades have seen significant advances in bioinformatics, with the development of robust new methods to diagnose, monitor and eventually forecast major cyanobacterial odorants. This paper will review our current understanding of the most problematic cyanobacterial VOCs that cause T&O: their biological and chemical sources, the major biosynthetic pathways, the cellular and genetic controls and the environmental factors that trigger or modulate production.

2. Major olfactants

Many biologically active cyanobacterial metabolites have no identifiable organoleptic properties - for example, the array of peptides and alkaloids known as cyanotoxins, which have lethal or sub-acute health effects on humans and other organisms, but are odorless and tasteless. By virtue of their organoleptic properties, T&O-causing cyanobacterial metabolites are biologically active, but these VOCs have no known adverse human health effects, although as noted earlier they may function as semiochemicals within food-webs. They include a wide variety of secondary metabolites, most of which are produced at trace levels and act as minor components to the overall organoleptic 'bouquet' - which in itself can be an important chemical cue to consumers such as humans, fish and invertebrates (e.g. McCleave and Jellyman, 2002; Höckelmann et al., 2004). The following review, focuses on the three major groups of VOCs produced by cyanobacteria that have arguably the most significant socio-economic effects, terpenoids, nor-carotenoids and sulfides. These compounds are not produced by all species or strains of cyanobacteria, and also are not unique to these taxa but produced by other microbiota such as actinomycetes and fungi, which has confounded many attempts at source-tracking (e.g. Bruchet, 1999). However, the recent development of new molecular tools has greatly advanced the capacity to identify and source track both the producers and the environmental drivers of these events, especially in the production of two of the most problematic VOCs, the tertiary alcohols geosmin and 2-methylisoborneol, laying the basis for the development and successful field application of molecular probes and formulation of new risk mitigation strategies.

2.1. Terpenoids: geosmin and 2-methylisoborneol (2-MIB)

The two secondary terpenoids geosmin ((4*S*,4a*S*,8a*R*)-4,8a-dimethyl-1,2,3,4,5,6,7,8-octahydronaphthalen-4a-ol) and 2-methylisoborneol (2-MIB; (1*R*-exo)-1,2,7,7-tetramethylbicyclo[2.2.1]heptan-2-ol) are perhaps the most ubiquitous and problematic biogenic odor compounds reported from freshwaters (e.g. Jüttner and Watson, 2007) and the focus of an ever-increasing body of research (Fig. 1). Both are highly potent, with a human odor threshold concentrations (OTCs) between 4 and 10 ng/L, and extremely stable, resisting natural degradation, boiling and conventional treatment processes. They are often described as 'earthy/muddy' although 2-MIB has a more 'moldy' odor, which at high concentrations takes on camphor-like overtones (Persson, 1979a,b). As lipophilic molecules, geosmin and 2-MIB are taken up rapidly through the gills and gut of fish and shellfish, causing muddy off-flavors which require prolonged depuration periods to remove. On the other hand geosmin is also responsible for the characteristic flavor in beets, and contributes to the desirable tastes in some cheeses, coffee, nuts, and vegetables (Maga, 1987; Reineccius, 1991; Lu et al., 2003). Geosmin and 2-MIB are chiral molecules, each with a (+), and a $\sim 10\times$ more potent $(-)$ enantiomer. Biological sources produce the $(-)$ enantiomers and thus tainted drinking water may elicit consumer complaints at concentrations below OTCs which are widely used by the drinking water industry (Krasner, 1988; Dietrich et al., 2004) and typically determined using commercially available racemic mixes. For example, the Metropolitan Water District of Southern California often receives customer complaints at geosmin and 2-MIB concentrations below 5 ng/L (Taylor et al., 2006). It is also likely that the bioactivity of these two enantiomers similarly differs, with implications for toxicity assays, many of which are based on commercial standards.

The severity and timing of geosmin, 2-MIB and other odor events are ultimately governed by a multidimensional scale of