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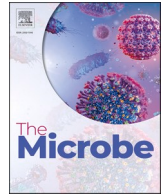
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Transgenic corn syrup enhances in vitro yeast ethanol production: Hidden cause of the US MASH epidemic?

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ABSTRACT

Over the last decade, the incidence of metabolic dysfunction-associated steatohepatitis (MASH) has increased, establishing it as a major health concern and the second most common cause of liver disease in the US. Recent studies have suggested a link between MASH and the endogenous production of alcohol in the digestive tract after consuming sugar. It is believed that bacteria such as *Klebsiella* and *Lactobacillus* play a key role in this fermentation process. More recently, the role of the gut mycobiota has also been suggested. In particular, MASH has recently been associated with yeast strains in the gut microbiota that produce high concentrations of alcohol. As the source of sugar varies by region — transgenic maize in the USA, sugar cane in Africa and beetroot in France — we hypothesised that consuming sweetened beverages alongside the gut mycobiota may contribute to MASH. Analysis of American and French Coca-Cola, as well as World-Cola from Mali, revealed significant differences in carbohydrate composition, including the presence of complex oligosaccharides in American Coca-Cola. Significantly higher ethanol production was observed when a *Candida albicans* yeast strain was cultured in American Coca-Cola than in the other two colas. These results suggest that consuming transgenic maize sweeteners may increase the risk of toxic endogenous alcohol production. This highlights the need for epidemiological studies to assess the link between these carbohydrates and the MASH epidemic in the US.

1. Introduction

There are several stages of liver damage in metabolic dysfunction-associated liver steatohepatitis (MASH). The first is steatosis, which in some cases can lead to fibrosis (Anstee et al., 2011), then to cirrhosis (Caldwell et al., 1999; Edmison and McCullough, 2007; Ertle et al., 2011), and finally to liver cancer (Bugianesi et al., 2002; White et al., 2012). Currently, MASH is a major liver problem, being the second most common cause of liver disease in patients awaiting liver transplantation in the United States (Cholankeril et al., 2017; Wong et al., 2015). In the last decade, the prevalence of MASH has increased by almost 100 % (Hamid et al., 2022). Recently, several studies have shown that MASH is probably related to the endogenous production of alcohol in the

digestive tract after the ingestion of sugar (Kaji et al., 1976; Logan and Jones, 2000; Tseng et al., 2023). Some authors have shown that *Klebsiella* bacteria are responsible for this fermentation (Xue et al., 2023); others have highlighted the role of *Lactobacillus* bacteria (Tsai et al., 2020; Vallianou et al., 2021) and confirmed the presence of alcohol in the hepatic portal vein of MASH patients sampled during bariatric surgery (Meijnikman et al., 2022). Another team also showed that alcohol in stool or blood samples from MASH patients was associated with specific *Klebsiella pneumoniae* strains (Yuan et al., 2019). Fungal colonisation of the human gastrointestinal tract is common, particularly with *Candida* spp., and half of the human population in the US is colonised with at least one *Candida* spp (Chevalier et al., 2018). Our team has shown that the presence of alcohol in stool samples from MASH

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patients is associated with *Candida* yeast colonisation (Mbaye et al., 2022). Others have shown that alcohol in stool or blood samples from MASH patients is associated with specific *Klebsiella pneumoniae* strains (Bernhardt, 1965) or *Saccharomyces cerevisiae* yeast (Demir et al., 2022). It has long been known that MASH is associated with sugar consumption (Tseng et al., 2023). In addition, the use of antibiotics prior to the onset of MASH can undoubtedly explain the change in the digestive ecosystem that favours the proliferation and spread of yeasts (d'Enfert et al., 2020). Struck by the significance of the MASH epidemic in the United States, we hypothesised that it might be related to the consumption of sweetened products, since the composition of sweet soft drinks, especially colas, varies from country to country. In the USA, colas are sweetened with sugar extract from transgenic maize, (Christophe Rondot, 2012; Tom Philpott, 2023) whereas in Africa the sugar comes from sugar cane (Rogier Mathieu, 2024; Oxfam-France, 2023) and in France (Coca Cola European Partners) from beetroot (Anonymous). The aim of this study was to evaluate the in vitro ethanol production of yeasts incubated in colas produced in the USA, Africa or France.

2. Materials and methods

2.1. Cola samples

We analysed a total of three different sugared colas produced by the Coca-Cola Company in the USA and in France. In Mali, World-Cola is produced by the Castel Group, which is present in 14 countries in sub-Saharan Africa. Coca-Cola original taste and World-Cola was purchased in local stores in France or Mali. Classic American Coca-Cola was purchased from the My American Market online store (21 August 2023). It is worth noting that the source of the sugar used to sweeten colas varies depending on where they are produced. Transgenic maize is used in the USA, sugar beet in France and sugar cane in Mali.

2.2. Analysis of the carbohydrate composition of colas

The carbohydrate content of colas was studied by ultra-high performance liquid chromatography-mass spectrometry (UHPLC-MS) according to an application note from Waters Corporation (Shelton, USA), with modifications (Fountain et al., 2009). Mono-, di- and oligosaccharides were separated by hydrophilic interaction liquid chromatography (HILIC) using a BEH amide column (2.1 × 50 mm, Waters) installed in an iClass UHPLC system (Waters), which in turn was connected to a Vion IMS mass spectrometer (Waters). To study the composition of free carbohydrate structures, samples were diluted in water only, whereas to study the monosaccharide composition of complex carbohydrates, samples were first evaporated and hydrolysed with trifluoroacetic acid (4 h, 100 %); the acid was then evaporated and the resulting samples dissolved in water. All samples were injected directly into the amide column and the compounds were separated according to the following solvent composition gradient (A: 80:20 % acetonitrile/water with 0.1 % NH₄OH; B: 30:70 % acetonitrile/water with 0.1 % NH₄OH): linear increase of B from 0 % to 60 % between 0 and 6 min. The carbohydrates were then ionised in negative mode using an electrospray ion source and the resulting ions were monitored using an accurate mass screening method including ion mobility separation and MSe data acquisition (HDMSe). Data processing was performed using UNIFI software (version 8.1.4).

2.3. Quantification of ethanol after inoculation with the *C. albicans* strain CSURL 0240

Inoculum and fermentation conditions: *C. albicans* strain CSURL 0240. This yeast was inoculated in triplicate at a cell density of 3 McFarland into 1 mL of each cola sample in the flask vial tube. The inoculated flasks were incubated at 28 °C for 48 h. Ethanol was quantified at 24, 36 and 48 h of incubation by headspace gas

chromatography-mass spectrometry (HS-GC/MS) as previously described (Magdy Wasfy et al., 2023). Briefly, the samples and ethanol standards (20–1800 mM) were all spiked with isopropanol as an internal standard. They were then heated to 60 °C to evaporate the alcohol molecules. The pressurised headspace gases were transferred to the gas chromatography system consisting of a Turbomatrix HS110 sampler connected to a Clarus 690 chromatograph and an SQ8 T single quadrupole mass spectrometer (Perkin Elmer, Waltham, MA, USA). The analytes were separated on an Elite BAC-2 column (Perkin Elmer). Ethanol and isopropanol were selectively detected and automated quantification was performed using Turbomass 6.1 software (Perkin Elmer). The influence of both the origin of the colas and the incubation time on the ethanol concentration was tested by two-way ANOVA using the statistical software SAS Stat (ver. 9.4). A *P* value less than 0.05 was considered statistically significant.

3. Results

3.1. The carbohydrate composition of colas

As illustrated in Fig. 1, UHPLC-MS detected a unique disaccharide, identified as sucrose, in both Malian World-Cola and French Coca-Cola. In contrast, sugars with a high degree of polymerisation were present in American Coca-Cola. The structures of the sugars from transgenic maize are drastically different from those of sugar cane or sugar beet, as the analysis revealed several oligosaccharides with up to 8 polymerised sugar branches (hexoses), and another disaccharide of unknown composition.

3.2. Quantification of ethanol production by *C. albicans* strain CSURL 0240

The concentrations of ethanol produced by *C. albicans* in colas of different origins are shown in Fig. 2. Both incubation time and cola substrate ($P < 10^{-4}$ each) had a statistically significant effect on the measured ethanol concentration. As shown in Fig. 2, yeast fermentation of carbohydrates produced a significantly higher ethanol concentration in American Coca-Cola than in the other colas after 36 h of incubation. Ethanol production was similar in French and Malian colas (Fig. 2).

4. Discussion

In this exploratory study, we highlighted the highly different carbohydrate composition between the colas from the USA compared to those from France or Europe. It should be noted that the coca samples selected were unbiased and representative of locally consumed beverages. The variety of oligosaccharides with a degree of polymerization ranging from 3 to 8 in the American *Coca-Cola* contrasted with the presence of unique shorter disaccharide structure in the other colas. In a previous work, we have shown a very high production of ethanol by the yeasts *Pichia kudriavzevii*, *C. glabrata* and *C. albicans* (Mbaye et al., 2022). Here, we point out the association of a high degree of polymerisation of the carbohydrates with a significantly higher yeast alcohol production. Indeed, the ethanol production of *C. albicans* CSURL 0240 in American Coca-Cola reached up to 49.7 g/L at 48 h, which is equivalent to drinking 1 L of beer at 6 % alcohol. People who have yeast in their gut microbiota and drink soda or eat any food sweetened with corn syrup derived from transgenic maize are therefore likely to have an increased risk of toxic endogenous alcohol production. Experimental studies investigating how oligosaccharides derived from transgenic maize specifically modulate *Candida albicans* metabolism in vivo would be of interest. Further epidemiological studies are needed to assess the influence of consuming carbohydrates derived from transgenic maize on MASH epidemics in the United States. We believe that if this hypothesis is confirmed, there is likely to be a major public health problem associated with the massive consumption of glucose and fructose oligosaccharide

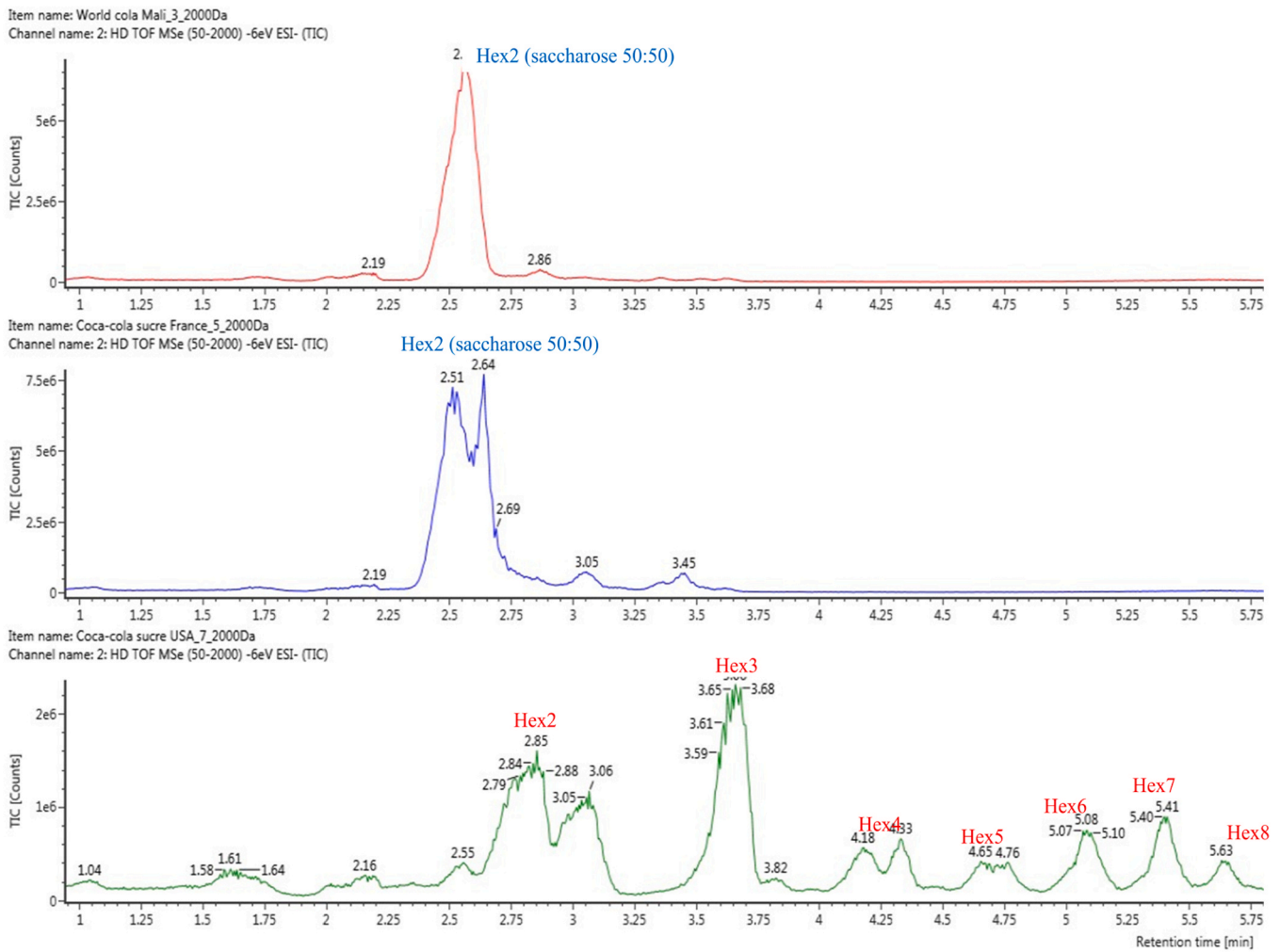


Fig. 1. Ultra-high performance liquid chromatography-mass spectrometry carbohydrate analysis showing the high degree of polymerisation of free sugars present in American Coca-Cola, in contrast to the unique presence of saccharose in colas from France or Mali. A: Coca-Cola from Mali; B: Coca-Cola from France; C: Coca-Cola from the USA.

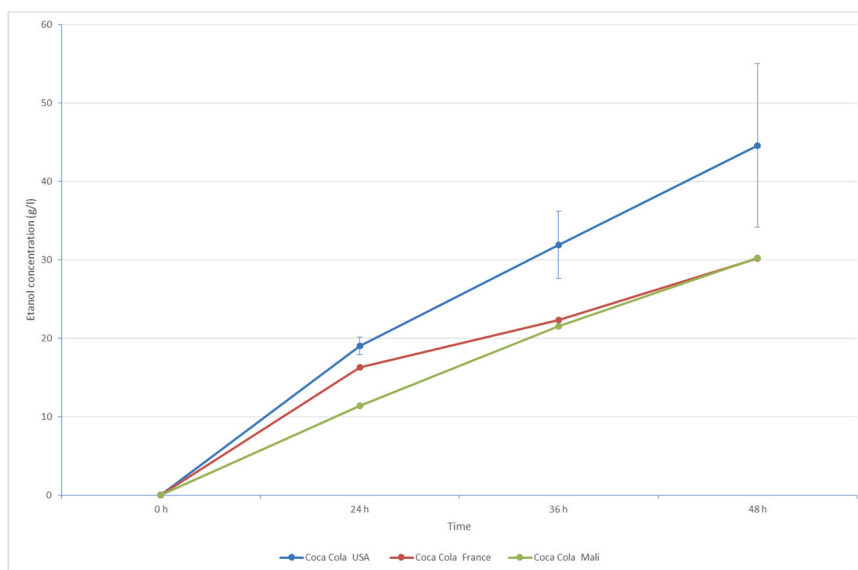


Fig. 2. Overtime in vitro ethanol production by *Candida albicans* CSURL 0240 in colas from the USA, France, or Mali. The yeast fermentation of carbohydrates produced a significantly higher ethanol concentration in American Coca-Cola than in the other colas (ANOVA, $p < 10^{-4}$).

combinations.

CRedit authorship contribution statement

Sibiri Sissoko: Writing – original draft, Investigation, Formal analysis. **Amaël Fadlane:** Writing – review & editing, Supervision, Resources. **Nicholas Armstrong:** Writing – review & editing, Validation, Supervision, Methodology, Investigation. **Stéphane Ranque:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Didier Raoult:** Writing – review & editing, Supervision, Resources, Project administration, Conceptualization. **Mahamadou Thera:** Writing – review & editing, Supervision, Conceptualization. **René Gerolami:** Writing – review & editing, Conceptualization. **Maryam Tidjani Alou:** Writing – review & editing, Visualization, Validation, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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