CAPÍTULO 4

PRODUCTION OF VOLATILE ORGANIC COMPOUNDS BY YEASTS IN BIOREFINERIES: ECOLOGICAL, ENVIRONMENTAL, AND BIOTECHNOLOGICAL OUTLOOKS

DOI: https://doi.org/10.56041/9786599841804-4

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ABSTRACT

Among the seventeen sustainable development goals (SDGs) of the United Nations 2030 Agenda, at least ten rely on better usage and valuation of wastes since this attitude leads to economic and sustainable development, water-food-energy security, and environmental protection. Considering the worldwide amount of daily produced agroindustrial residues and the employment of enzymes and/or microbial cells in transformation processes, biorefineries represent a growing economic sector with high potential to meet Agenda 2030's SGDs. Indeed, by employing lignocellulosic materials as feedstocks and microorganisms as catalysts, second-generation (2G) biorefineries stand out as a productive environment able to provide several high-added value compounds. This is the case for volatile organic compounds (VOCs), including ethanol, produced by yeasts from lignocellulosic hydrolysates. This chapter reviews the ecological yeast-insect-angiosperm relationship that is the reason behind most of the VOCs generated in natural environments. From then on, the chapter advances to biotechnological and sustainable traits of using lignocellulosic wastes in yeast fermentation processes aiming to produce these high-added value compounds.

Keywords: agroindustrial wastes, fermentation, flowers, insects, pollination, VOCs.

1. INTRODUCTION

Volatile Organic Compounds (VOCs) are solids or liquids composed of carbon that enters the gas phase easily under atmospheric pressure and room temperature. They have low molecular weight and low to moderate water solubility, of natural or synthetic origin, thus having various compounds that include acids, alcohols, aldehydes, esters, ketones, terpenes, heterocyclics, and aromatics. Regarding those of natural origin, such volatile compounds can be produced by different living beings, from bacteria to more complex organisms such as animals (Morath et al., 2012; Zhi-Lin et al., 2012).

In this sense, VOCs produced by fungi have many applications in several human activities; however, about 300 VOCs already identified come from the metabolism of only 100 species of fungi tested (Buzzini et al., 2003; Caileux et al., 1992). Of these applications, it should be highlighted their use in the food industry to increase the complexity of odors, even serving as indicators of expiration in grain stocks, in the jellies industry, and in bakery products (Arslan et al., 2018; Nieminen et al., 2008). For the biotechnology industry, they can be useful in the production of biofuels (known as mycodiesel) and in the production of biopesticides, giving plant resistance to pests, to control pests in the postharvest of strawberries, tangerines, and cherry tomatoes (Medina-Romero et al., 2017; Oro et al., 2018; Parafati et al., 2017). Additionally, VOCs can even be used as an indicator of indoor air quality of buildings, as a parameter of the "sick building syndrome", through odors produced in humid environments that can affect human health (Araki et al., 2012; Sarkhosh et al., 2021).

In the kingdom Fungi, yeasts (unicellular fungi) have been present in various human activities for thousands of years, such as in producing alcohol beverages and bread, playing a great biotechnological role. Note that, since the Neolithic revolution, the yeast *Saccharomyces cerevisiae* has been the most used microorganism in bioprocesses (Alves Jr et al., 2022b; Basso et al., 2022). This long period of domestication in anthropized environments led to the selection of different lineages of this species, fully adapted to different productive sectors (Alterthum, 2020; Eliodório et al., 2019). Due to this ease of use and the knowledge about its handling, the use of wild and industrial yeasts emerged as a promising alternative for producing VOCs in the context of multi-product biorefineries — in whose environment it is possible to extract different products from the same substrate. In this sense, this chapter proposes to discuss the role of volatile compounds produced by yeasts in nature, the main compounds that have added value for production in biorefineries, and the possibilities of using residues as substrates for their production.

2. THE ROLES OF VOCs PRODUCED BY YEASTS IN NATURE

In their natural environment, yeasts produce VOCs for adaptive reasons. These volatile compounds produced have roles such as attracting or repelling other organisms, helping their reproduction, and facilitating communication in terrestrial environments (Hung et al., 2015). As they are microorganisms that do not live alone and thus are always coexisting with other living beings, one of the most recurrent examples in which these compounds act is the attraction of pollinating insects exerted by VOCs. Thus, by producing these odoriferous compounds, yeasts serve as mediators for the pollination of plant species (Figure 1). In this insect-attracting scenario, Becher et al. (2018) demonstrated that *Drosophila melanogaster* flies were attracted to compounds such as 2-phenyl-ethanol, 3-methyl-1-butanol, acetoin, ethanol, ethyl acetate, 2-methyl-1-butanol, 3-methyl-3-butenol, 2-phenylethyl acetate, and acetic acid, which are produced by yeasts of the genera *Candida*, *Pichia*, *Saccharomyces*, *Yarrowia,* and *Dekkera*.

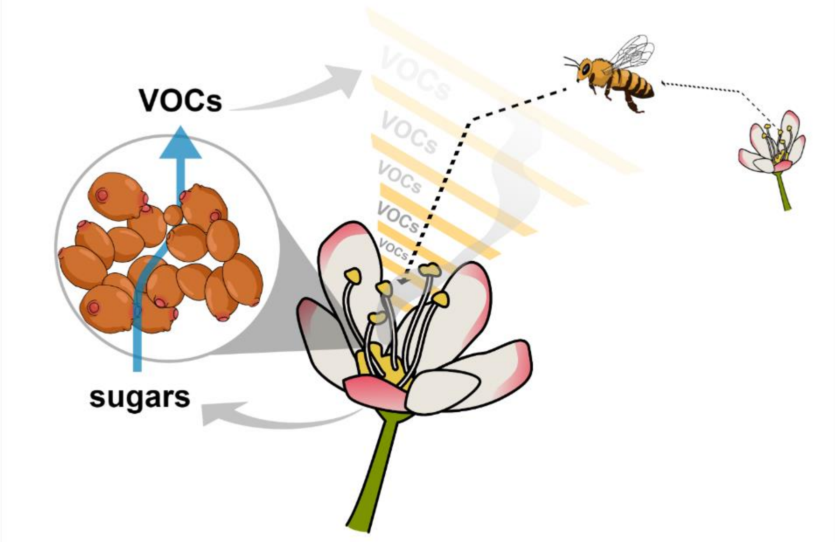

Figure 1. The production of volatile organic compounds (VOCs) by nectar-fermenting yeasts. Yeast cells inhabiting floral nectaries metabolize nectar sugars and produce volatile metabolites that attract nectarivorous insects pollinating angiosperm flowers.

In addition to emitting VOCs, yeasts influence the concentration of pollen and nectar in the flowers of angiosperm species, altering the profile of sugars available to pollinating species. De Vega et al. (2009), showed that the density of yeast species has a negative correlation between the factors of sugar content and nectar concentration, suggesting that this profile change occurs after pollination (after the presence of the pollinator), so that the plant be able to recover the energy spent in the production of this attraction.

For pollinating species, such as bees, Jacquemyn et al. (2021), argue that yeasts influence their behavior and aptitude, protecting them from pathogenic microorganisms, attracting them to flowers, and providing vitamin B. In this way, there is a benefit for the three parts included in this process: the plants reproduce sexually, insects feed, and yeasts ensure their survival by moving to new places (Mittelbach et al., 2016; Sobhy et al., 2018). In fact, this relationship is so fruitful that approximately 90% of all plant species benefit from animal-mediated pollination, which, in turn, is largely facilitated by floral nectar, where yeasts are found to metabolize sugars and, from them, produce VOCs (Jacquemyn et al., 2021; Roy et al., 2017).

Different yeast communities play important roles also for the development and health of angiosperms. In addition to assisting in pollination, yeasts of the genus *Saccharomyces* can produce indole acetic acid (IAA), which stimulates plant cell elongation, promotes root growth and development, and regulates plant growth (Liu et al., 2016; Petkova et al., 2022). In addition to these stimuli, microbial consortia of these fungi provide protection against pests, such as other fungi and insects, through the emission of terpenes, aldehydes, alcohols, and volatile hydrocarbons, such as those produced by species of the genera *Meyerozima*, *Candida*, *Wickerhamomyces*, and *Rhodortula*. It is worth noting that some compounds produced may be similar to those produced by the plant itself, such as β-citronellol and α-Terpineol. These substances, which can also inhibit the feeding of insect pest larvae, have already demonstrated effects on filamentous fungi such as *Penicillium digitatum*, *Pyricularia oryzae*, *Rhizoctonia solani*, *Fusarium moniliforme*, *Helminthosporium oryzae,* and *Curvularia luneta*, which cause plant and fruit deterioration (Agirman & Erten, 2020; Ljunggren et al., 2019; Yan et al., 2021).

3. PRODUCING VOCs IN MULTI-PRODUCT BIOREFINERIES

Of the wide range of VOCs produced by yeasts — ethanol, terpenes, and other compounds derived from fermentation processes that add flavors to foods — all come from processes arising from the consumption of sugars by these microorganisms (Figure 2). Ethanol is certainly the most well-known compound produced by yeast (Alves Jr et al., 2022b). In alcoholic fermentation, pyruvate, obtained from the glycolytic pathway, is decarboxylated by pyruvate decarboxylase to acetaldehyde, which is finally reduced to ethanol in the reaction catalyzed by the enzyme alcohol dehydrogenase. This alcohol has several applications in human activities, either as fuel (destination of the largest volume of its production) or as an additive in cleaning, food, and perfumery products. Furthermore, ethanol is also widely used in the pharmaceutical and solvent industries (Basile et al., 2018).

Although the yeast *S. cerevisiae* is the most widely used in alcoholic fermentation processes (Basso et al., 2022), regarding the production of ethanol from waste (second-generation ethanol or 2G ethanol), other wild microorganisms may be expected to take its place or to provide it with new genes (Barrilli et al., 2020; Tadioto et al., 2022). This is particuly due to the inability of *S. cerevisiae* to ferment xylose (the second-most abundant sugar in lignocellulosic-residues hydrolyzates), accumulating xylitol, which is secreted in the medium from the early interruption of the so-referred pentose metabolism. In fact, to be fermented to ethanol, xylose must be reduced to xylitol in a reaction catalyzed by xylose reductase (XR), which can then be oxidized to xylulose by xylitol dehydrogenase (XDH). Subsequently, xylulose must be phosphorylated and then forwarded to the pentose-phosphate pathway (PPP). However, the fermentative metabolism can already be interrupted between the first and second reactions, driven by XR and XDH. It turns out that, while XR can use NADPH or NADH as electron donors (the former being the preferred coenzyme for most yeasts), XDH depends on NAD⁺ as an electron acceptor (Figure 2). In this case, given the use of NADPH by XR, a redox imbalance occurs, generating an accumulation of xylitol at the expense of ethanol production (Alves Jr et al., 2022a; Estrada-Ávila et al., 2022; Stambuk et al., 2008). On the other hand, this by-product has high added value and can be applied as a sweetener in foods and the production of anticaries and cosmetics products (Peterson, 2013; Raj & Krishnan, 2020; Wu et al., 2018).

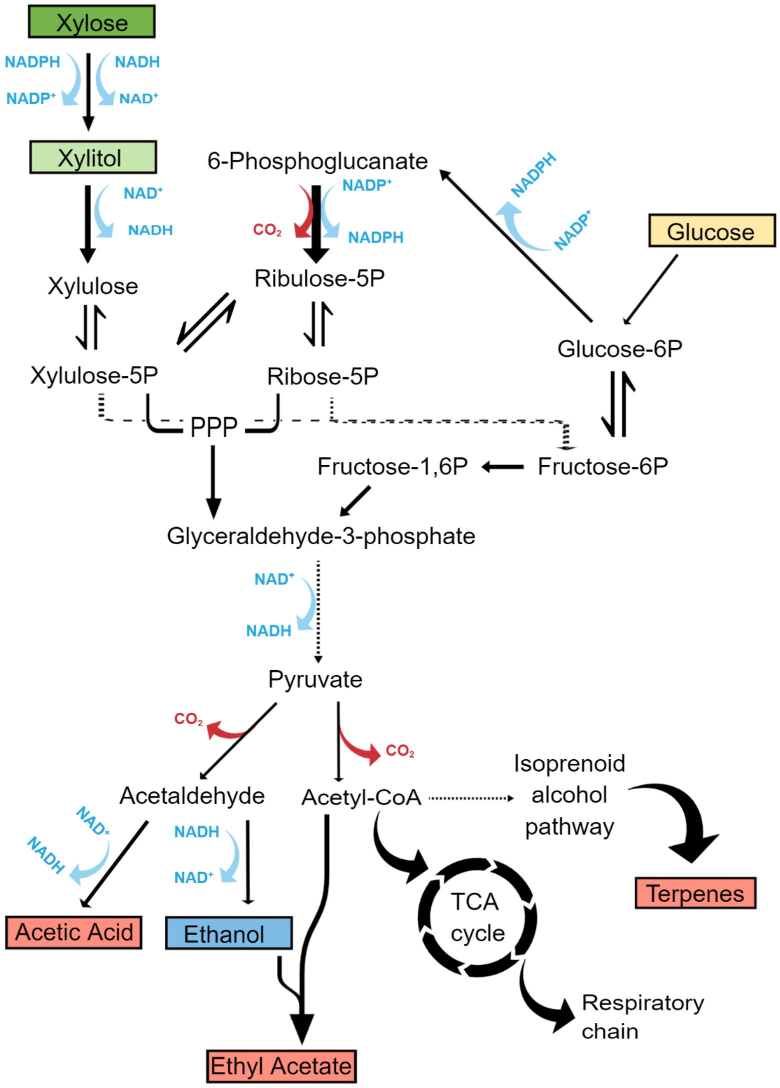

Figure 2. Xylose and glucose metabolism by yeast cells and examples of VOCs production. To be used as a carbon source, xylose must be converted into xylulose-5P, then into glyceraldehyde-3P or fructose-6P through the pentose-phosphate pathway (PPP). Both xylose and glucose can generate pyruvate, which can either follow alcoholic fermentation producing ethanol, the tricarboxylic acid (TCA) cycle through aerobic respiration, or be used to produce other VOCs such as acetic acid, ethyl acetate, and terpenes. Dashed arrows are omitting some reactions for simplification.

However, other VOCs do not find the same representation as ethanol in the literature. In contrast, these compounds tend to have higher added value, and they can be generated especially in multi-product biorefineries, taking advantage of the more efficient metabolic pathways of fermenting microorganisms to generate different products from each component of plant biomass. Among the VOCs related to pollinator attraction, acetaldehyde, acetic acid, ethyl acetate, ethyl butyrate, and isobutanol have already been reported (Crowley-Gall et al., 2021; Dzialo et al., 2017; Sobhy et al., 2019; Tylewicz et al., 2022), substances of interest to different industrial sectors that account for a global market of approximately US$ 15 billion[3,4,5,6,7].

Part of the VOCs produced by yeasts is derived from the breakage of glycosidic bonds that are established between the ß anomer of a monosaccharide and phenols or alkenes (Ohgami et al., 2015). This hydrolysis is promoted by ß-glucosidases, enzymes whose biotechnological versatility has been amplified recentely (Alves et al., 2018; Barrilli et al., 2020; Colomer et al., 2020; Kuo et al., 2018; Vervoort et al., 2016, 2018). In fact, it is worth noting that, in addition to their direct relationship with the production of VOCs, ß-glucosidases are also essential for the complete hydrolysis of cellulose, which is a fundamental part of the diet of herbivorous insects and is the main polymer of agroindustrial residues used as substrates in second-generation sectors (Alves Jr et al., 2019).

4. LIGNOCELLULOSIC WASTE AS SUBSTRATES IN BIOREFINERIES

To ethanol, other VOCs can be produced from carbohydrate-rich substrates (Table 1). However, in terms of sustainable production, it is desirable to use raw materials that does not compete with food production, do not require more planted areas, and have a positive life cycle, with a low water footprint and zero or almost zero greenhouse gas emissions (between production and consumption) (Lee et al., 2021).

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[3] https://www.statista.com/statistics/1245235/acetaldehyde-market-volume-worldwide/

[4] https://www.grandviewresearch.com/industry-analysis/acetic-acid-market#:~:text=The%20global%20acetic%20acid%20market,factor%20for%20the%20market%20growth.

[5] https://www.globenewswire.com/news-release/2022/02/22/2389567/0/en/Ethyl-Acetate-Market-to-Reach-USD-5-38-billion-by-2028-Global-Size-Estimation-Revenue-Stats-Applications-Analysis-Growth-Drivers-Business-Strategy-Key-Companies-and-Forecast-The-Br.html

[6] https://www.prnewswire.com/news-releases/global-butyric-acid-derivatives-market-to-reach-663-6-million-by-2026--301502537.html

[7] https://www.alliedmarketresearch.com/press-release/isobutanol-market.html

Table 1. Examples of VOCs production by yeasts in lignocellulosic hydrolysates.

Yeast	Feedstock	VOCs	Reference
Metschnikowia chrysoperlae WUT25	Hydrolyzed corn stover	2-phenylethanol (2-PE)	Mierzejewska et al. (2018)
Pichia fermentans WUT36	Hydrolized corn stover	2-phenylethanol (2-PE)	Mierzejewska et al. (2018)
Saccharomyces cerevisiae	Tobacco waste	2-phenylethanol (2-PE)	Wang et al. (2013)
Wickerhamomyces sp.	Hydrolyzed soybean residue	Ethanol	Vedovatto et al. (2021)
Kluyveromyces marxianus	*Opuntia ficus-indica*	Ethyl acetate Ethanol Acetic acid	Akanni et al. (2014)
Candida utilis	*Opuntia ficus-indica*	Acetic acid	Akanni et al. (2014)
Kluyveromyces marxianus	Corn stover Alfalfa Poplar	Ethyl acetate Ethanol	Hillman et al. (2021)
Rhodosporidium toruloides	Hydrolyzed corn stover	1.8-cineol	Zhuang et al. (2019)
Pichia kudriavzevii	Apple and grape pomaces	Acetic acid Ethanol	Steyn et al. (2021)
Saccharomyces cerevisiae	Apple and grape pomaces	Acetic acid Ethanol	Steyn et al. (2021)

In this sense, the most promising substrates are lignocellulosic residues, which can be used in second-generation biorefinery plants. Brazilian sugarcane and US corn production are classic examples of the importance of using agricultural residues, as both countries account for 80% of global ethanol production (RFA, 2021). Given this, it is noteworthy that, for each ton of sugarcane, it is possible to extract about 270–280 kg of bagasse and 140–165 kg of straw (wet basis) (de Oliveira et al., 2020). In the US, for each kg of dry corn grains harvested, there is 1 kg of residue (dry basis) (Graham et al., 2007). In 2021, 382 million tons of corn grain and 654 million tons of sugarcane were harvested, demonstrating the immense disposal of underutilized waste (CONAB, 2021; USDA, 2022).

Lignin constitutes the lignocellulosic residues with cellulose and hemicellulose, and the fractions of these constituents vary according to the type of plant biomass. Some studies that characterized plant biomass from waste showed fractions (%w/w) ranging from 7% to 22% lignin, 32% to 59% cellulose, and 14% to 27% hemicellulose (Jönsson & Martín, 2016; Kucharska et al., 2018). Thus, it is possible to consider around 60% of these residues as useful content for producing the high-added-value bioproducts presented in this chapter.

5. FINAL CONSIDERATIONS

Although 193 countries have ratified the United Nations 2030 Agenda and the same amount has committed to the Paris agreement, the planet is still far from what is expected to ensure development with environmental sustainability and control of greenhouse gas emissions. To achieve these two major goals, efforts that aim at the valuation and better use of solid waste (such as biotransformation processes) are needed. In this context, demand arises for biorefineries capable of converting agroindustrial wastes into different products, in addition to the well-studied biofuels — which, by the way, still face bottlenecks in terms of the economic viability of their production processes. Thus, multi-product plants, which propose to employ efficient metabolic routes and thus obtain a diversity of final products, emerge as a promissing prompting the use of lignocellulosic residues as raw material.

Some potential products are volatile organic compounds (VOCs) naturally produced by yeasts, and they have a higher added value than biofuels. The production of VOCs is species-dependent, and the literature has highlighted wild yeasts as the main producers, especially those associated with insects and flowers. In fact, it is partly up to these microorganisms to attract pollinating insects; in the floral nectary, yeasts metabolize sugars and other nutrients secreted by the plant, and produce volatile compounds that attract insects to the flowers.

On this account, second-generation biorefineries aiming for multi-product production may meet at least ten of the seventeen Agenda 2030's sustainable development goals (SDGs) by reducing (i) the need for dumping grounds; (ii) chemical and microbial contamination of soil, water, and air; (iii) the death of animals (currently recurrent, especially in the seas and oceans); (iv) deforestation; and, (v) the demand for extractive activities and non-renewable raw materials. Considering yeast's biotechnological potential and the high added value of several VOCs, top global authorities should be lead public policies aiming to boost the emergence of second-generation biorefineries worldwide. It is up to them.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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