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Microbial valorization of waste cooking oils for valuable compounds production – a review

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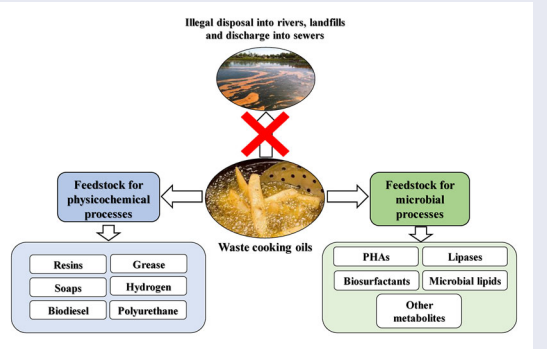
ABSTRACT



Waste cooking oils (WCO) are vegetable oils discarded after food frying and great amounts are produced worldwide. Its management is a challenge, due to the environmental risk of illegally disposal into rivers and landfills. The main approaches for WCO valorization included their incorporation as component of animal feed and biodiesel manufacturing. Yet, the development of new feasible approaches is attractive from an economic and ecological standpoint. Due to their composition in triglycerides, untreated WCO can be used as feedstock for microbial growth (several species are able to use them as carbon source) and production of added-value compounds. In this way, microbial valorization of WCO is a sustainable biotechnological approach to upgrade a waste into a renewable feedstock for bio-based industry, favoring the circular economy concept. The objective of this review is to highlight the potential use of WCO in bioprocesses as an alternative to other physicochemical treatments. Firstly, an introduction to WCO problematic is presented, describing most common applications used currently. Then, an extensive review on the use of WCO by microorganisms is shown, focusing on bacterial and fungi species and its exploitation for bioprocesses development to produce metabolites of industrial interest, such as biopolymers, biosurfactants, lipases and microbial lipids.

KEYWORDS Added-value compounds; microbial conversion; waste cooking oils

1. Waste cooking oils: General overview

Waste cooking oils (WCO) are generated from vegetable oils (coconut, sunflower, soybean, palm tree, cottonseed, rapeseed, olive, etc.) employed to fry foods in household and HORECA (Hotels, Restaurants and Catering) segments and are no longer suitable for human consumption. Specifically, in HORECA sector, fast food restaurants (particularly those of chicken and

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hamburger) are the principal generators of WCO (Rincón, Cadavid, & Orjuela, 2019). During the frying process, which occurs at high temperatures (160 °C–200 °C), vegetable oils (composed by triacylglycerols, TAGs) undergo many physical and chemical modifications and toxic compounds are formed through oxidation reactions, hydrolysis and polymerization of TAGs (Tsoutsos, Tournaki, Paraíba, & Kaminaris, 2016). After an open air frying process, cooking oils structure is modified by oxidation reaction and hydroperoxide is produced, which may be further oxidized into toxic products, namely 4-hydroxy-2-alkenals (Panadare & Rathod, 2015). The water molecules of food may attack the ester linkage of TAGs, producing free fatty acids (FFA), glycerol, diacylglycerols (DAG) and monoacylglycerols (MAG). These hydrolysis reactions occur more easily in vegetable oils with short-chain and unsaturated fatty acids because these compounds are more soluble in water than long-chain and saturated fatty acids (Gillatt, 2001). The hydrolysis products exhibit higher reactivity and predisposition for oxidation reactions than the TAGs of vegetable oils, and FFA contribute to the formation of smoke, undesirable smells and off-flavors, which hamper the further utilization of WCO (Frega, Mozzon, & Lercker, 1999). The polymerization of TAGs leads to the formation of non-polar dimers and other oligomers and the extension of this reaction depends on the fatty acid composition of vegetable oil, frying temperature and frying's number (Tompkins & Perkins, 2000; Tsoutsos et al., 2016). The oxidation of oils rich in oleic acid produces high amount of unsaturated aldehydes, such as 2-decenal and 2-undecenal, but lower quantities of saturated ones (nonanal and octanal) and hydrocarbons. On the other hand, the oxidation of linoleic acid generates 2,4-decadienal, 2,4-nonadienal, 2,4-octadienal, 2-heptenal, 2-octenal, hexanal, 2,4-heptadienal, 2,4-hexadienal, butenal, propanal and 2-propenal (also known as acrolein) (Chang, Wu, Zhang, Jin, & Wang, 2019; Yang et al., 2017; Zhang et al., 2018). All of these compounds generated from cooking oils degradation have harmful effects to human health and are recognized as having mutagenic, carcinogenic, neurotoxic and hepatoxic effects, among others (Tsoutsos et al., 2016).

Several parameters are employed to evaluate the extension of chemical reactions and the degradation of repeated frying oils, such as saponification index (measures the average molecular mass of fatty acids), acid value (quantifies the percentage of FFA), iodine value (measures the degree of oil unsaturation), peroxide value (indicator of initial oxidation), p-anisidine value (measures the oil oxidation), total oxidation value (estimates the oxidative deterioration of oil lipids), 2-thiobarbituric acid value (estimates the oxidation of polyunsaturated fatty acids) and total polar compounds (measures the thermo-oxidative degradation of frying oil). In food industry, the maximum value of each parameter allowed until the discard of deep frying

oil depends on the type of food being fried (Nayak, Dash, Rayaguru, & Krishnan, 2016).

Physical parameters of vegetables oils, such as color, viscosity, density and surface tension are also affected by deep-frying processes. Some of physical changes could be rapidly evaluated by visual inspection and are indicators of WCO quality. The increase of cooking oil darkness is attributed to the development of pigments during fatty acids oxidation, Maillard reactions and oxidation of phenolic compounds of vegetable oils (Nor, Mohamed, Idris, & Ismail, 2008; Sulieman, El-Makhzangy, & Ramadan, 2006). The viscosity of WCO increases with the number of frying cycles due to non-polar dimers and high molecular weight polymeric compounds produced during the polymerization of TAGs (Tarmizi, Niranjan, & Gordon, 2013).

Despite the undesired substances produced during food frying, which may have an adverse impact on the environment and human health, this cooking process is increasingly popular (Hanisah, Kumar, & Tajul, 2013) since deep frying enhances the sensorial properties (unique fried flavor, golden brown color and crispy texture). As the use of vegetable oils on food frying should not be prolonged, an accumulation of WCO is inevitable (Nayak et al., 2016). The information about the amount of WCO produced worldwide is very scarce and difficult to find, mainly because the production of cooking oils changes drastically among regions and countries. It is estimated that approximately 0.9 million tons of WCO are produced per year in European Union. In highly populated countries, large waste amounts are produced: China – 5.6 million tons, United States of America – 1.2 million tons, India – 1.1 million tons, Japan – 570 thousand tons, Germany – 493 thousand tons, Republic of Korea – 411 thousand tons, Spain – 300 thousand tons and Canada – 148 thousand tons (Teixeira, Nogueira, & Nunes, 2018).

The final disposal of WCO is a heavy burden due its high volume, and the incorrect discharge into sewers or drains cause blockages and odor or vermin problems. WCO have compounds that linger in the environment for many years, increase the organic load on water sources and form a thin layer over water surface that reduces the dissolved oxygen concentration required for subaquatic species, changing the ecosystem (Guerrero, Guerrero-Romero, & Sierra, 2011). These lipids-rich wastes can hamper the wastewater treatment due to the adsorption of long chain fatty acids (LCFA) onto the biomass (which causes sludge flotation and mass transfer problems), foam formation (resulting from the accumulation of non-degraded LCFA), and inhibition of anaerobic microbial communities (as a result of an increase of LCFA) (Alves et al., 2009; Appels et al., 2011).

To reduce the negative impacts on ecosystems, it becomes urgent the management, recycling and valorization of WCO. In order to avoid the

illegal practice of discharge WCO through public sewerage system, many developed countries have set policies that penalize this action. Particularly in European Union, the Directive 2008/98/EC of the European Parliament establishes the legal regime of WCO management produced in industrial, HORECA and domestic sectors (https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32008L0098&from=EN). This Directive aims to standardize, implement and inspect the selective collection circuits and the proper transport and treatment of WCO by licensed operators. However, many countries have no specific legislation for WCO and the management practices adopted are not identified, particularly in highly populated and underdeveloped countries. The recycling and reutilization of WCO can minimize environmental and technological impacts while contribute to an economic efficiency, according to the circular economy concept. Traditionally, WCO were used as a component of animal feed. However, in 2002, this application was strictly prohibited in European Union to avoid the transfer of carcinogenic compounds to human body through food chain (Lam et al., 2016). The transformation of WCO into biodiesel dominates the reutilization of these oily wastes because, among biofuels, biodiesel produced from WCO has the lowest greenhouse gas emissions (Wallace, Gibbons, O'Dwyer, & Curran, 2017), which led to the implementation of public strategies worldwide and to the increase of subsidies for production (tax breaks or exemptions or favorable price) (Rincón et al., 2019). However, the processing costs is still high and the conditions used in frying methods, as well the fried material (vegetables, meat, fish), cause physical and chemical changes in WCO that affect the biodiesel production. The high content of free fatty acids and water (which difficult the separation of esters from glycerol and form soap) and the presence of dimeric and polymeric acids and glycerides in WCO (which increase its viscosity) might interfere in the transesterification reactions and affect the final quality of biodiesel. Additionally, the amount of WCO available for biodiesel production cannot fulfill the increasing demand of this renewable fuel in near future and only 1.5 % of EU28 diesel consumption could be replaced by biodiesel obtained from WCO (Wallace et al., 2017).

Although the main biorefinery concept around WCO are focused on biodiesel, other valorization options have been exploited, including its use as raw material for the production of soaps, resins, polymers, grease lubricants and polyurethane (Abdulbari & Zuhan, 2018; Félix, Araújo, Pires & Sousa, 2017; Fernandes, Kirwan, Lehane, & Coles, 2017; Feng et al, 2018; Maotsela, Danha & Muzenda, 2019; Salleh, Tahir, & Mohamed, 2018; Sipaut et al, 2012; Suzuki, Botelho, Oliveira, & Franca, 2018; Zheng et al, 2018). WCO can also be used as a source for energy production, such as biohydrogen, pyrolytic oil, electricity (by direct combustion), hydrocarbons (by gasification

and liquefaction) or blend to solid fuels (Chen & Wang, 2019; Nanda et al, 2019; Panadare & Rathod, 2015; Rincón et al., 2019; Rodrigues et al., 2018; Teixeira et al., 2018; Xiong et al, 2019; Xu et al, 2019).

Some of these processes are environmentally unfriendly, thus more eco-efficient solutions should be pursuit, like biotechnological approaches that use microorganisms for the conversion of WCO.

2. WCO as feedstock for microbial processes

Carbon and nitrogen sources of culture media, particularly for industrial purposes, should satisfy as much as possible the following parameters: (a) come from cheap substrates, (b) be economically available throughout the year, (c) be easily disinfected, (d) enable maximum yield of biomass and product formation, (e) be compatible with different cultivation modes (batch, fed-batch or continuous), (f) do not generate any harmful wastes and in higher quantity than initial residue and (g) be easy to manipulate at all stages of cultivation (production, extraction, purification and waste treatment). Currently, WCO have potential to be a low-cost and abundant substrate for microbial growth and metabolites production, fulfilling the above criteria.

The design of strategies involving microorganisms to simultaneously degrade oily wastes and obtain high added-value products was developed by several researchers (Batista, Rufino, Luna, Souza, & Sarubbo, 2010; Benesova, Kucera, Marova, & Obruca, 2017; Csutak, Corbu, & Vassu, 2017; Helal, Abdelhady, Abou-Taleb, Hassan, & Amer, 2017; Kamilah, Al-Gheethi, Yang, & Sudesh, 2018; Kanna, 2018; Lopes, Miranda, Alves, Pereira, & Belo, 2019; Niu, Wu, Wang, & Chen, 2019; Pernicova, Enev, Marova, & Obruca, 2019; Santos, Teixeira, Converti, Porto, & Sarubbo, 2019). The utilization of WCO directly as feedstock for microbial processes is a great opportunity to reduce the production costs of valuable compounds and also to increase the economic value of these wastes, since they are considered dangerous to the environment and have high energy demanding degradation processes (El Bialy, Gomaa, & Azab, 2011). Some species of yeast, fungi and bacteria have the ability to use WCO as carbon and energy source and convert them into added-value metabolites. In this review, the use of WCO as feedstock for microbial processes will be discussed, and recent data illustrating the diversity of microbial species and metabolites produced from WCO will be presented.

2.1. Microbial species

Several bacterial species were proposed by various researchers for conversion of WCO into added-value products. While sugars are directly

Table 1. Examples of bacterial species used for WCO bioconversion and respective compounds produced.

Bacterium	Compounds	WCO ($g \cdot L^{-1}$)	Reference
Alcaligenes sp.	Biodemulsifier	40	Liu et al. (2011)
Bacillus cereus	Biosurfactants and PHA	20	Durval et al. (2019); Tufail et al. (2017)
	Lipase	80	Awad, Mostafa, Danial, Abdelwahed, and Awad (2015)
Bacillus pumilus	Biosurfactants	50	Oliveira and Garcia-Cruz (2013)
Bacillus stratosphericus		10	Hentati et al. (2019)
Bacillus subtilis	Biosurfactants	50	Vedaraman and Venkatesh (2011)
	PHA	20	Tufail et al. (2017)
Brevibacterium halotolerance	PHA	20	
Burkholderia thailandensis	Biosurfactants and PHA	40	Kourmentza et al. (2018)
Citrobacter freundii	Biosurfactants	20	Ibrahim (2018)
Co-culture of *Bacillus spp.* and *Pseudomonas putida*	Microbial lipids	8.5	Tzirita et al. (2018)
Cupriavidus necator	Lipase and PHA	12.5	Rao et al. (2010); Kamilah et al. (2018)
		20	Benesova et al. (2017)
			Cruz et al. (2016)
			Martino et al. (2014)
			Kamilah et al. (2018)
			Rao et al. (2010)
			Verlinden et al. (2011)
Enterobacter cloacae	Lipase	10	Iboyo, Asitok, Ekpenyong, and Antai (2017)
Klebsiella pneumoniae	PHA	20	Tufail et al. (2017)
Marinobacter hydrocarbonoclasticus	PHA	20	Zenati et al. (2018)
Ochrobactrum anthropi			Ibrahim (2018)
***Paracoccus* sp.**	PHA	10	Kumar and Kim (2019)
Pseudomonas aeruginosa	Biosurfactants	10	Ekpenyong, Antai, and Asitok (2016)
		15	Luo et al. (2013)
		20	Chen et al. (2018)
			George and Jayachandran (2013)
		30	Zhang, Xu, Zhu, Lundaa, and Scherr (2012)
		35	Venkatesh &Vedaraman (2012)
		50	Ozdal et al. (2017)
			Wadekar et al. (2012)
	PHA	20	Tufail et al. (2017)
Pseudomonas cepacia	Biosurfactants	20	Silva et al. (2017)
Pseudomonas citronellolis	PHA	20	Cruz et al. (2016)
Pseudomonas chlororaphis		10	Sharma et al. (2017)
Pseudomonas mendocina		20	Lukasiewicz et al. (2018)
Pseudomonas oleovorans			Cruz et al. (2016)
Pseudomonas putida			Pernicova et al. (2019)
Pseudomonas resinovorans		8.5	Follonier et al. (2014)
		20	Cruz et al. (2016)
Pseudomonas SWP-4	Biosurfactants	40	Lan et al. (2015)
Propionibacterium freudenreichii	Volatile fatty acids and vitamin B12	40	Hajfarajollah et al. (2015)
Stenotrophomonas rhizoposid	PHA	20	Tufail et al. (2017)
Streptomyces sp.	Biosurfactants	10	Santos et al. (2019)
Virgibacillus salarius		20	Elazzazy, Abdelmoneim, and Almaghrabi (2015)

metabolized by bacterial cells, an enzymatic hydrolysis is required when WCO is the carbon source. The first step involves the hydrolysis of triglycerides by extracellular lipase, releasing to the culture medium glycerol and fatty acids such as stearic, palmitic, oleic and linoleic acids, depending on WCO source. These fatty acids are transported across the cell membrane

Table 2. Examples of yeasts and filamentous fungi species used for WCO bioconversion and respective compounds produced.

Species	Compound	WCO ($g \cdot L^{-1}$)	Reference
*Ashbya gossypii**	Riboflavin	40	Wei et al. (2013)
Aspergillus niger	Lipase	15	Papanikolaou et al. (2011)
		25	Kempka et al. (2017)
	Microbial lipids	15	Papanikolaou et al. (2011)
Aspergillus sp.	Lipase, microbial lipids and oxalic acid	15	
Blakeslea trispora	Carotenes	50	Nanou and Roukas (2016)
Candida bombicola	Biosurfactants	50**	Pinto et al. (2018)
Candida lipolytica		20**	Kanna (2018)
Candida tropicalis	Biosurfactants	10	Csutak et al. (2017)
		20	Batista et al. (2010)
		25**	Almeida et al. (2017) Junior et al. (2018)
		100**	Rubio-Ribeaux et al. (2017)
	Microbial lipids	10	Csutak et al. (2017)
Candida utilis	Biosurfactants	60**	Campos et al. (2014)
Cryptococcus curvatus	Microbial lipids	20	Patel and Matsakas (2018)
Cunninghamella echinulata	Biosurfactants	5	Andrade et al. (2018)
		20	Souza et al. 2018
Mocur circinelloides		80	Zadeh et al. (2017)
Penicillium expansum	Citric acid, lipase and microbial lipids	15	Papanikolaou et al. (2011)
Pichia jadinii	Biosurfactants	100	Dzięgielewska and Adamczak (2013)
Pseudozyma aphidis		95	Niu et al. (2019)
Rhizopus oryzae	Lipase	10	Helal et al. (2017)
Rhodotorula glutinis		30	Taskin et al. (2016)
Wickerhamomyces anomalus	Microbial lipids	5**	Arous et al. (2017)
	PHA	50**	Ojha and Das (2018)
Yarrowia lipolytica	Citric acid	80	Liu et al. (2015)
	Lipase	10	Nunes et al. (2014) Lopes et al. (2019)
		30**	Domínguez et al. (2010)
		40	Liu et al. (2015)
	Microbial lipids	5**	El Bialy, Gomaa, and Azab (2011)
		8.5	Tzirita et al. (2018)
		30	Katre et al. (2012); Lopes et al. (2019)
		140	Liu et al. (2015)
*Yarrowia lipolytica**	Erythritol and lipase	30	Xiaoyan et al. (2017)
	Microbial lipids	100	Katre et al. (2017)

*Mutant strains; **WCO were used as co-substrate or inductor.

and metabolized via β-oxidation pathway to acetyl-CoA (Rao, Sridhar, & Sehgal, 2010; Ruggieri, Artola, Gea, & Sánchez, 2008; Serikovna, Serikovich, Sakenovna, Murzakhmetovich, & Khamitovich, 2013). Table 1 lists several bacterial species used for compounds production by biotechnological conversion of WCO. Concentrations of around $40\,g \cdot L^{-1}$ WCO in the medium were possible to be degraded by batch cultures of several species, such as *Propionibacterium freudenreichii*, *Burkholderia thailandensis*, *Alcaligenes* and some *Pseudomonas spp*. Moreover, biosurfactants and lipases are common products produced by oils degrading bacteria, since these extracellular products have important roles in the accessibility of the fatty acids to the bacterial cells.

Some filamentous fungi and yeast species were also reported as capable of growing on oily substrates, since these microorganisms are able to (a) synthetize biosurfactants for lipids solubilization, (b) modify the cell surface to enable the adhesion of lipids and (c) secrete extracellular lipases that hydrolyze the triglycerides into glycerol and fatty acids. Particularly in yeasts, fatty acids droplets bind onto the protrusions formed in the cell surface and enter into the cytosol. Here, fatty acids degradation is finalized through the β-oxidation pathway in the peroxisomes, by the interaction between the glyoxylate cycle (peroxisome) and citrate cycle (mitochondrion) or stored in lipid bodies as TAGs and steryl esters (SE). Lipids accumulated intracellularly in lipid bodies could be also mobilized by intracellular lipases, encoded by the *TGL* genes, to the peroxisome to carry out the β-oxidation (Beopoulos, Chardot, & Nicaud, 2009; Fickers et al., 2005).

Some yeasts and fungi species were studied to explore their ability to use WCO as feedstock for the production of added-value compounds, such as lipases, carotenes, citric acid, erythritol or for the accumulation of microbial lipids (Table 2).

2.2. Added-value compounds produced from WCO

2.2.1. Polyhydroxyalkanoates (PHAs)

Polyhydroxyalkanoates (PHAs), an environmental friendly alternative to synthetic polymers, stand out as one of the main metabolites obtained by microbial conversion of WCO, particularly by bacterial species. These biodegradable biopolymers, which are accumulated in the form of intracellular granules, have a wide range of applications in many fields like cosmetics, pharmacology, tissue engineering, food industry (packaging, molding and coating), agriculture and denitrification in water and wastewater treatment (Kourmentza et al., 2018; Lukasiewicz et al., 2018; Muhammadi, Afzal, & Hameed, 2015). It is expected that PHAs market grows to an estimated € 84.4 million by 2021 (Kourmentza et al., 2018), but the commercial scale production of PHAs is still hindered by the cost of substrate (mainly carbon source), which contributed up to half of the overall production cost (Song, Jeon, Choi, Yoon, & Park, 2008). Thus, the use of cheap substrates and waste materials like WCO, is an alternative way to address the cost issue of bacterial bioplastics production. In fact, this oily waste is the most studied food waste at laboratory scale owing to their composition in fatty acids that can act as precursors for different types of PHAs (Cruz et al., 2016; Rodriguez-Perez, Serrano, Pantión, Alonso-Fariñas, 2018). Moreover, PHAs yields obtained by bacterial species from oily substrates ($0.6\,g{\cdot}g^{-1}$ – $0.8\,g{\cdot}g^{-1}$) is considerably higher than those obtained from sugars ($0.3\,g{\cdot}g^{-1}$ – $0.4\,g{\cdot}g^{-1}$) (Chee et al., 2010).

Several bacterial species are capable to accumulate PHAs intracellularly from WCO (Table 1), including *Pseudomonas* sp., *Cupriavidus necator*, *Klebsiella pneumonia*, *Bacillus* sp., *Burkholderia thailandensis*, among others (Benesova et al., 2017; Kamilah et al., 2018; Kourmentza et al., 2018; Lukasiewicz et al., 2018; Tufail et al., 2017). However, some naturally PHA-storing bacteria are not able of hydrolyzing triglycerides to release free fatty acids, due to the lack of an effective lipolytic activity. In these cases, a prior hydrolysis of WCO must be performed by exogenous commercial lipases or by chemical reactions, like saponification (alkaline hydrolysis), being those hydrolysis methods common to the ones applied to natural pure oils (Ashby & Solaiman, 2008). In the literature, few papers address the use of WCO for accumulation of PHAs by yeasts or fungi. Ojha and Das (2018) studied the production of PHAs by the yeast *Wickerhamomyces anomalus*, concluding that the addition of small amounts of waste frying palm oil as co-carbon substrate of sugarcane molasses enhances the PHA production.

A wide range of WCO concentrations ($10\,g{\cdot}L^{-1}$ – $40\,g{\cdot}L^{-1}$) is used for PHA production, depending on bacterial species. Similarly, a considerable variation in PHA production ($0.1\,g{\cdot}L^{-1}$ – $25\,g{\cdot}L^{-1}$) is reported. Besides bacterial species, these discrepancies could be ascribed to culture conditions, since several operational and nutritional factors affect PHAs production from WCO. The amount of nitrogen in WCO-based media was proven to be a factor affecting bacteria growth and biopolymers production, though the reports found in the literature are not consensual. The addition of higher nitrogen concentration (Martino et al., 2014; Verlinden et al., 2011) or a complex nitrogen source (alkali-hydrolyzed feathers) instead of inorganic nitrogen (Benesova et al., 2017) improves the *Cupriavidus necator* growth and polyhydroxybutyrate (PHB) productivity. Furthermore, a higher PHA yield obtained from WCO than from untreated pure oil was reported for *Cupriavidus necator*, *Pseudomonas chlororaphis* and *Paracoccus* sp. cultures (Kumar & Kim, 2019; Sharma et al., 2017; Verlinden et al., 2011), possibly because there is more nitrogen in heated oil, since thermal degradation products can contain readily available nitrogen (Verlinden et al., 2011). The presence of food residues (residual proteins, fats and carbohydrates), short-chain compounds and peroxides generated during frying process could also be metabolized and may also contribute to increase bacterial growth and consequently total PHAs production (Verlinden et al., 2011). By contrast, Song et al. (2008) verified that PHA production was higher when *Pseudomonas* sp. strain DR2 grew on pure corn oil-based medium with limitation of nitrogen and phosphate than on WCO as carbon source. In fact, some authors reported higher storage yields on stationary phase of growth due to the nitrogen starvation, and in other works the cultivation was carried out under nitrogen limitation (Cruz, Sarraguça, Freitas, Lopes, & Reis, 2015; Follonier

et al., 2014; Kamilah et al., 2018; Obruca, Marova, Snajdar, Mravcova, & Svoboda, 2010; Rao et al., 2010; Sharma et al., 2017).

Oxygen transfer from gas phase to the culture medium was also found as a parameter affecting PHA production by *Pseudomonas putida* KT2440 growing on WCO. High PHA levels was obtained increasing the volumetric oxygen transfer coefficient, probably because the metabolization of WCO occurs through the β-oxidation pathway, which is a highly oxygen-demanding metabolic route (Acuña, Aravena-Carrasco, Gutierrez-Urrutia, Duchens, & Poblete-Castro, 2019).

Different operation modes were used in attempt to increase PHAs production from WCO, such as fed-batch (Obruca et al., 2010) and 2-step fermentation with hydrolyzed pomace as growth substrate and WCO as PHA precursor (Follonier et al., 2014). The content of PHA accumulated by *Pseudomonas fluorescens* S48 increased by scaling up the working volume from 2 L to 10 L. Moreover, the highest value of polymer production was obtained in high-cell density fed-batch cultures, followed by two-stage batch and one-stage batch cultures (Gamal et al., 2013).

Genetic manipulations were also used to increase the accumulation of PHAs by bacteria cells from WCO. By knocking out the *tctA* gene of *Pseudomonas putida* KT2440, which encodes an enzyme of the tripartite carboxylate transport system, an improvement of intracellular level of *mcl*-PHA was attained (Acuña et al., 2019). Mutants of *Cupriavidus necator* H16, obtained by random chemical mutagenesis, exhibited a significantly enhancement of NADPH/$NADP^+$ ratio and, as a side effect, the PHB accumulation was improved due to the increase of activity of PHB biosynthetic pathway (Obruca, Snajdar, Svoboda, & Marova, 2013).

It was demonstrated that PHAs produced from WCO has high quality and with a molecular weight and thermal and chemical properties similar to those produced from pure oils or glucose (Kamilah et al., 2018; Sharma et al., 2017; Verlinden et al., 2011). Yet, the origin and composition of WCO may affect PHAs yields, since the amount of saturated bonds and free fatty acids (which are converted to acetyl-CoA by β-oxidation cycles) seem to be crucial factors for biopolymers production. The presence of high content of readily available free fatty acids in WCO, produced due to frying process, enhanced PHB production by *C. necator* cells. Additionally, it was suggested that saturated fatty acids (namely palmitic acid) are more easily transformed into acetyl-CoA than unsaturated fatty acids, leading to a build-up of more energy-rich PHB (Kamilah et al., 2018; Verlinden et al., 2011).

2.2.2. Biosurfactants

Biosurfactants are amphiphilic molecules with hydrophobic and hydrophilic portions that reduces the surface (air-water) and interfacial (water-oil)

tensions between fluids of different polarities, enhancing the solubility, bioavailability and biodegradation of hydrophobic substrates (Almeida et al., 2018). Based on their chemical structure, biosurfactants are classified as lipopeptides, glycolipids, phospholipids, neutral lipids, and polymeric compounds (Liu et al., 2015). These surface-active compounds have aroused interest in recent years due to their environmental advantages over synthetic surfactants (Singh, Patil, & Rale, 2019). The global market for biosurfactants was predicted to reach USD 2.6 – 5.5 billion by 2023, growing at an annual rate of 5.6 % from 2017 to 2023 (Singh et al., 2019). Regardless of the large market demand, biosurfactants production is still not competitive compared to its synthetic counterparts. The high production costs and low yields still hamper the industrial production of biosurfactants (Marchant & Banat, 2012). Hence, exploring the use of cheap waste materials for biosurfactants production is an effective cost-cutting strategy, since the use of low-cost renewable substrates may decrease 10 % to 30 % of the total production costs (Zenati et al., 2018).

Biosurfactants production from WCO is strongly associated with the opportunistic pathogen *Pseudomonas aeruginosa* (Chen et al., 2018; Wadekar et al., 2012), but other bacterial species are known to produce surface-active agents, like *Bacillus* sp. (Durval et al., 2019; Hentati et al., 2019; Vedaraman & Venkatesh, 2011) and *Streptomyces* sp. (Santos et al., 2019), among others (Table 1). Regarding yeast strains, *Candida* species, particularly *Candida tropicalis* (Almeida et al., 2017; Batista et al., 2010; Junior et al., 2018; Rubio-Ribeaux et al., 2017), are the most studied for biosurfactants production from WCO, but other species (Andrade et al., 2018; Camargo et al., 2018; Niu et al., 2019) were studied (Table 2). Unlike to bacteria cultures, in biosurfactants production by yeast, normally WCO are used as co-substrate or inductor and not as the only carbon source (Almeida et al., 2017; Campos et al., 2014; Junior et al., 2018; Kanna, 2018; Pinto et al., 2018; Rubio-Ribeaux et al., 2017). Usually, the synthesis of biosurfactants requires a hydrophilic and hydrophobic carbon source in the culture medium (Campos et al., 2014) and, probably, this need is more pronounced for yeast species.

A wide range of WCO concentrations ($9\,g{\cdot}L^{-1}$ – $100\,g{\cdot}L^{-1}$) and biosurfactants production ($0.6\,g{\cdot}L^{-1}$ – $67\,g{\cdot}L^{-1}$) are reported by several authors, depending on microbial species and culture conditions. The concentration of WCO demonstrated to be statistically significant in the production of biosurfactants by the bacteria *Cunninghamella echinulata* (Souza et al., 2018), *Pseudomonas aeruginosa* (George & Jayachandran, 2013; Ozdal et al., 2017; Venkatesh &Vedaraman, 2012), *Pseudomonas* SWP-4 (Lan et al., 2015) and *Anoxybacillus* sp. (Khairuddin, Mulok, Khalil, Omar, & Saleh, 2016) and by the yeasts *Candida tropicalis* (Almeida et al., 2017) and

Pseudozyma aphidis (Niu et al., 2019). By contrast, Oliveira and Garcia-Cruz (2013) does not observed a direct relation between WCO concentration and biosurfactant production by *Bacillus pumilus*. Moreover, there are works reporting that biosurfactant production was higher with waste oils from frying process than with pure coconut oil (George & Jayachandran, 2013), olive oil (Csutak, Corbu, Stoica, & Vassu, 2018) and soybean oil (Niu et al., 2019), probably due to higher free fatty acids content in waste oil.

Nitrogen concentration and carbon nitrogen ratio (C/N) are other parameters reported as two of the most critical factors affecting the biosurfactant production by microbial species. It is suggested by several authors that a low C/N ratio might cause cell lysis and affect the accumulation of biosurfactants, whereas excess C/N ratio may stimulate microbial growth, cause metabolic disturbance and limit biosurfactants synthesis (Chen et al., 2018; Lan et al., 2015). It is reported in the literature that, in WCO-based media, nitrogen-limiting or low C/N ratio conditions are the most suitable for biosurfactant production by *Anoxybacillus* sp. (Khairuddin et al., 2016), *Virgibacillus salaries* (Elazzazy et al., 2015), *Pseudomonas* SWP-4 (Lan et al., 2015), *Pseudomonas aeruginosa* (Chen et al., 2018; Luo et al., 2013; Ozdal et al., 2017; Venkatesh &Vedaraman, 2012), *Mocur circinelloides* (Zadeh et al., 2017) and *Candida tropicalis* (Almeida et al., 2017; Batista et al., 2010). However, for the production of biosurfactants by *Cunninghamella echinulate* from WCO, considerable amounts of corn steep liquor (8 %, v/v) were used as nitrogen source (Souza et al., 2018). Besides nitrogen concentration or C/N ratio, also the nitrogen source (organic or inorganic) plays an essential role in the biosurfactant production by microorganisms in WCO-based media. Some authors reported that higher biosurfactant yields are obtained with inorganic nitrogen instead of complex organic sources (peptone, yeast extract, tryptone) (Elazzazy et al., 2015; Xia et al., 2012). Studies conducted by Xia et al. (2012) demonstrated that $NaNO_3$ was more effective than urea and ammonia for biosurfactant production by *Pseudomonas aeruginosa* WJ-1. Lan et al. (2015) observed that nitrate nitrogen ($NaNO_3$) was more efficient than amino nitrogen (yeast extract) for rhamnolipids production by *Pseudomonas* SWP-4. In *Virgibacillus salaries* cultures, the biosurfactant production was favored by urea and $NaNO_3$ and the use of ammonium salts in the form of ammonium nitrate and ammonium chloride led to a decrease on biosurfactant production (Elazzazy et al., 2015). By contrast, biosurfactant production by *Candida utilis* was enhanced by the addition of ammonium nitrate and sulfate and using urea or corn steep liquor a remarkable decrease on biosurfactant synthesis was observed (Campos et al., 2014). Among several organic nitrogen sources tested, rhamnolipids production by *Pseudomonas*

aeruginosa OG1 was higher with chicken feather peptone and the use of yeast extract resulted in the lowest yield (Ozdal et al., 2017).

Other operational and nutritional factors, such as temperature (Elazzazy et al., 2015; Khairuddin et al., 2016; Luo et al., 2013; Santos et al., 2019; Venkatesh & Vedaraman, 2012), stirring speed (Campos et al., 2014; Durval et al., 2019; Santos et al., 2019), aeration (Santos et al., 2019), medium volume (Niu et al., 2019), incubation time (Campos et al., 2014; Durval et al., 2019; George & Jayachandran, 2013), pH (Chen et al., 2018; Elazzazy et al., 2015; George & Jayachandran, 2013; Khairuddin et al., 2016; Niu et al., 2019; Santos et al., 2019; Venkatesh & Vedaraman, 2012), salinity (Khairuddin et al., 2016), inoculum ratio (Almeida et al., 2017; Campos et al., 2014; Lan et al., 2015; Niu et al., 2019) or mineral elements (Batista et al., 2010; Lan et al., 2015; Luo et al., 2013) are mentioned as affecting biosurfactants production by microorganisms from WCO. However, it seems that their influence is more dependent on the microbial species than on the fact that WCO are used as carbon source.

The mode of operation, as well the working volume, can affect biosurfactants production from WCO. The results of Luo et al. (2013) show that rhamnolipids production by *Pseudomonas aeruginosa* ATCC 9027 was enhanced by feeding WCO in two batches with an interval of 72 h. The production of sophorolipids using *Starmerella bombicola* increased from 24.7 $g{\cdot}L^{-1}$ to 55.6 $g{\cdot}L^{-1}$ by changing the mode operation from batch to fed-batch (Maddikeri, Gogate, & Pandit, 2015). Moreover, the authors concluded that yeast cultivation assisted with ultrasound led to an overall increase in the sophorolipids yield, attributing this result to cavitational effects that increase the cell permeability and improve WCO intake and metabolism of yeast cells. The production of biosurfactants by *Pseudomonas cepacia* from WCO was improved from 8 $g{\cdot}L^{-1}$ (Silva et al., 2017) to 40.5 $g{\cdot}L^{-1}$ (Silva et al., 2018), varying the scale from 500-mL Erlenmeyer flasks to a semi-industrial 50-L bioreactor. The biosurfactant yield obtained in *Candida tropicalis* cultures had an improvement of 40 %, 53 % and 75 % when produced in 2-L, 3-L and 50-L stirred tank bioreactors, respectively, comparatively to results attained in flasks experiments (Almeida et al., 2017; Junior et al., 2018).

During the frying process, oils undergo degradation reactions leading to the formation of peroxides, hydroperoxides, aldehydes and ketones. These by-products may affect the overall metabolism of the oils as carbon source for microbial growth and metabolites production. A pretreatment of WCO with activated earth to remove these components and reduce the peroxide value was tested, and higher rhamnolipids (Wadekar et al., 2012) and sophorolipids (Maddikeri et al., 2015) production was obtained.

2.2.3. Lipases

Lipases are exploited for several applications, namely in food and detergent industries, wastewater treatment, leather processing and, recently, in the field of bioenergy for biodiesel production (Darvishi et al., 2017; Salihu & Alam, 2015). It is estimated that lipase market will reach € 533 million by 2020 (https://www.marketsandmarkets.com/PressReleases/lipase.asp), but the industrial production of microbial lipase is still hindered by the costs of cultivation media. Several microorganisms secrete extracellular lipases to hydrolyze triglycerides of vegetable oils into free fatty acids, using them as carbon source. Yet, few works were published regarding lipase production from WCO. Particularly for bacterial species, only 4 works were published in the last 10 years regarding the use of WCO for lipase synthesis. This fact is surprising, since it was already mentioned that, in cultures of *Cupriavidus necator*, waste frying palm oil is a better inductor of lipase than fresh palm oil (Kamilah et al., 2018). Similarly, the use of waste frying oils was proven to be better than pure sunflower and olive oil for lipase synthesis by *Enterobacter cloacae* (Iboyo et al., 2017), *Yarrowia lipolytica* (Lopes et al., 2019; Xiaoyan et al., 2017) and *Rhizopus oryzae* (Helal et al., 2017). These results are of particular importance, since they confirm the potential of a non-edible oil waste (WCO) to replace expensive edible oils (namely olive oil) for industrial lipase production, reducing the global costs. Moreover, pure vegetable oils are broadly used for food purposes, being its availability for microbial production of lipase lesser than WCO. However, Nunes et al. (2014) observed a significantly higher production of extracellular lipase using olive oil as carbon source than using waste frying soybean oil. In some cases, WCO are added to submerged (Domínguez et al., 2010) or solid state (Kempka et al., 2017) fermentations only as a supplementary carbon source and lipase inductor.

The sources of food (fish, meat, potatoes, vegetables) affect the oxidative reactions that occur in oils during the frying process, originating waste oils with different iodine and peroxide values. For instance, chicken-frying oil has a peroxide value (11.53 meq/kg) much higher than fish-frying oil (2.07 meq/kg) (Kamilah et al., 2018). This difference may explain that in cultures of *Rhizopus oryzae*, lipase obtained using fish-frying oil as carbon source were significantly higher than that attained with chicken-frying oil (Helal et al., 2017). However, the stimulation of lipase production is associated not only to the free fatty acids content and degree of unsaturation of WCO but also to the frying oil concentration. In WCO-based medium, oil concentration had a significant effect on lipase production by *Bacillus cereus* and, increasing this parameter, higher extracellular lipase activity was obtained (Awad et al., 2015). Lipase production by free cells of *Rhodotorula glutinis* was significantly influenced by WCO concentration and a 2.4-fold

improvement was attained by increasing the oil concentration from $10\,g{\cdot}L^{-1}$ to $40\,g{\cdot}L^{-1}$ (Taskin et al., 2016). Xiaoyan et al. (2017) also reported that lipase production by *Yarrowia lipolytica* M53 was statistically affected by WCO concentration, whose increase from $10\,g{\cdot}L^{-1}$ to $50\,g{\cdot}L^{-1}$ led to a 3.5-fold improvement on lipase synthesis. By contrast, Liu et al. (2015) found that an increase of frying oil concentration from $40\,g{\cdot}L^{-1}$ to $140\,g{\cdot}L^{-1}$ reduced considerably lipase production by *Yarrowia lipolytica* SWJ-1b. Helal et al. (2017) and Lopes et al. (2019) found that WCO concentration ($10\,g{\cdot}L^{-1}$ - $50\,g{\cdot}L^{-1}$) had no significant effect on lipase production by *Rhizopus oryzae* and *Yarrowia lipolytica* W29, respectively, and the lower amount of WCO ($10\,g{\cdot}L^{-1}$) was sufficient to obtain the maximum lipase activity. Probably, the increase of oil concentration leads to a decrease of oxygen transfer rate to the culture medium, reducing the growth rate and the metabolites production (Xiaoyan et al., 2017). Moreover, the accumulation of high amounts of free fatty acids may inhibit the lipase production (Tamilarasan & Kumar, 2011).

Nitrogen sources and carbon/nitrogen ratio are referred by some authors as being essential for cell growth and consequently for lipase production using WCO as carbon source. Generally, organic nitrogen sources are preferred over inorganic sources, probably because inorganic nitrogen is quickly consumed and usually cause repression of enzyme induction, while organic sources can provide amino acids and cell growth factors needed for cellular metabolism and lipase synthesis (Böhm & Boos, 2004). In WCO media, the utmost yield of lipase was observed using organic nitrogen sources, such as yeast extract, peptone, beef extract, corn steep liquor or urea (Awad et al., 2015; Helal et al., 2017; Xiaoyan et al., 2017). Among inorganic nitrogen sources, ammonium oxalate has been mentioned as the most adequate for lipase production by *Yarrowia lipolytica* M53 (Xiaoyan et al., 2017) and *Rhizopus oryzae* (Helal et al., 2017). It was reported that peptone and yeast extract concentrations had no significant effect on lipase production by *Rhizopus oryzae* in WCO medium, whereas a high $(NH_4)_2SO_4$ concentration and an adequate C/N ratio were crucial for maximum lipase synthesis by *Yarrowia lipolytica* M53 (Xiaoyan et al., 2017) and *Yarrowia lipolytica* SWJ-1b (Liu et al., 2015), respectively. Moreover, when WCO are used as carbon source, lipase is essential to hydrolyze oily substrate, and high initial nitrogen concentration is needed to increase the synthesis of extracellular lipase at the beginning of process (Calvey, Su, Willis, McGee, & Jeffries, 2016).

It was reported that some physicochemical factors such as pH, temperature, incubation time, inoculum size and agitation may affect lipase production by microbial cells in WCO media in identical manner that from pure oily substrates. Lipase production by *Rhizopus oryzae* was not statistically

affected by initial medium pH (Helal et al., 2017). However, this parameter had a significant impact on lipase production by *Yarrowia lipolytica* W29 (Lopes et al., 2019) and by *Rhodotorula glutinis* HL25 (Taskin et al., 2016). Temperature, time of incubation and inoculum size were proved as parameters with great influence on lipase production by *Rhizopus oryzae* (Helal et al., 2017) and *Rhodotorula glutinis* HL25 (Taskin et al., 2016).

The addition of surfactants or emulsifiers to WCO-based medium can result in a significant increase of lipase production (Awad et al., 2015; Taskin et al., 2016), but the effect depends on agent type and concentration used. While triton X-100 affected positively the lipase production by *Bacillus cereus*, Tween 80 had a negative contribution (Awad et al., 2015). Taskin et al. (2016) also observed that, though both surfactants increased lipase production, triton X-100 was better for lipase synthesis by *Rhodotorula glutinis*. The positive effect of surfactants could be assigned to the increase of membrane permeability, but higher concentrations reduce lipase activity probably due to the loss of cell viability caused by excessive increase in membrane permeability and toxicity. By contrast, Lopes et al. (2019) found that arabic gum had no significant effect on lipase production by *Yarrowia lipolytica* and higher lipase was obtained in cultures without emulsifier.

The upscaling of process from flask to bioreactor experiments resulted in an improvement of enzyme production in WCO media (Domínguez et al., 2010; Lopes et al., 2019). This fact may be due to the faster oil consumption observed, which could be related to: (a) the formation of small sized air bubbles, dispersed in the cultivation medium, increases transfer area for oxygen mass transfer ; (b) the reduction on the thickness of the liquid layer on the gas/liquid interface, due to the turbulence caused by efficient agitation, decreases the resistance to oxygen mass transfer; and (c) the contact between microbial cells and oily substrate is improved by an efficient agitation, facilitating its consumption (Domínguez et al., 2010). Lopes et al. (2019) reported a 23-fold improvement in lipolytic activity upscaling the process from flask to bioreactor experiments. Moreover, the authors also studied the effect of oxygen transfer and concluded that highly aerated cultures had a negative impact on lipase production by *Yarrowia lipolytica* W29, probably due to oxidative stress resulted from high oxygen dissolved concentration. Domínguez et al. (2010) observed that the mode of operation affects lipase production from WCO, reporting that in fed-batch *Yarrowia lipolytica* CECT 1240 cultures, a 5-fold improvement on lipase activity was attained comparatively to batch flask experiments. By contrast, lipase production by *Yarrowia lipolytica* M53 from WCO was not enhanced by upscaling the process to a 5-L bioreactor (Xiaoyan et al., 2017).

2.2.4. Microbial lipids

Oils derived from microorganisms, commonly called microbial lipids, microbial oils or single cell oils (SCO) are mainly composed by triacylglycerols and neutral lipids accumulated in the cytosol in a structure denominated lipid body. These lipids can be a potential source for food supplements or replacement of essential fatty acids (some microbial species produce polyunsaturated fatty acids, such as those belonging to the omega-3 and omega-6 series) and as feedstock for biodiesel production (in some cases, their composition is similar to common vegetable oils) (Béligon, Christophe, Fontanille, & Larroche, 2016; Carsanba, Papanikolaou, & Erten, 2018). Though there is an upsurge interest in microbial lipids accumulation, its large-scale production is still hampered by the high cost of fermentation and oil extraction. Thus, the use of low-value or negative cost byproducts and/or crude wastes as substrate for microbial lipids production can decrease the overall process costs.

Among the works describing the use of WCO as substrate for intracellular lipids accumulation, only one was performed with bacterial species. The consortium of *Bacillus* spp. and *Pseudomonas putida* demonstrated the ability to degrade waste cooking olive oil, accumulating lipids intracellularly during the exponential growth phase. When bacterial consortium reached the stationary phase, lipids previously accumulated were re-consumed. The composition of these microbial lipids were dependent on growth phase, being only composed by unsaturated fatty acids (oleic and linoleic acids) during exponential phase and mainly composed by saturated fatty acids (stearic and palmitic acid) during the late growth phase (Tzirita et al., 2018).

In oleaginous yeasts, the accumulation of intracellular lipids from WCO (hydrophobic substrate) is a primary anabolic process and growth coupled mechanism (*ex novo* synthesis). This lipid synthesis is no more than the bio-modification, by oleaginous microorganisms, of oils used as substrate, which fatty acid composition greatly affects the process of lipids production. In *ex novo* synthesis, microbial lipids composition is regulated by the incorporation rate of fatty acids of substrate and the enzymatic system that control the intracellular modifications of the incorporated fatty acids (Donot, Fontana, Baccou, Strub, & Schorr-Galindo, 2014; Papanikolaou & Aggelis, 2010; Papanikolaou & Aggelis, 2011a).

The oleaginous yeast *Yarrowia lipolytica* is considered an outstanding biolipids producer and was used as a unicellular model microorganism for fatty acids metabolism and the *ex novo* lipids synthesis. In fact, this species was the most studied for the accumulation of intracellular lipids from WCO (Table 2). When *Y. lipolytica* grows in WCO, a large battery of extracellular lipases is secreted to hydrolyze the oily substrate, producing

free fatty acids and glycerol. FFA are rapidly incorporated into the cell and, in the cytosol, are activated by fatty acyl-CoA synthetase (FAA1) to produce acyl-CoA (Figure 1). This oleaginous yeast accumulates lipids in the form of TAGs (85 %) and steryl esters (8 %) in specialized compartments known as lipid bodies. Through the Kennedy pathway, acyl-CoA is converted to diacylglycerol (DAG), which is transformed into TAGs by *DAG1* and *DAG2* genes. Steryl esters are formed from acyl-CoA, and sterol esterification is due to the expression of *ARE1* gene. The reactions to form TAGs and steryl esters occur between the endoplasmic reticulum and lipid bodies surface, where the responsible enzymes are located (Ledesma-Amaro & Nicaud, 2016).

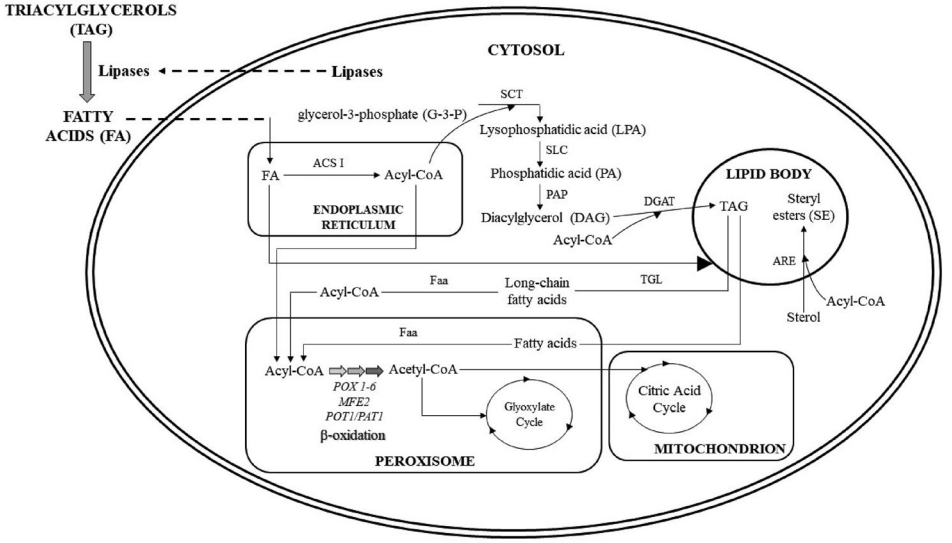

Figure 1. Overview of metabolic pathways involved in lipids assimilation and degradation in yeasts. Model created from the available data for the oleaginous yeast Yarrowia lipolytica. Abbreviations were used for the following enzymes: ACS (fatty acyl-CoA synthetase), ARE (acyl-CoA:cholesterol acyltransferase), DGAT (acyl-CoA:diacylglycerol acyltransferase), Faa (fatty acyl-CoA synthetase), PAP (phosphatidate phosphatase), SCT (glycerol-3-phosphate acyltransferase), SLC (acyl glycerol-3-phosphate acyltransferase) and TGL (triacylglycerol synthetase); and for genes which encode the following enzymatic activities: POX (acyl-CoA oxidase); MFE (multifunctional enzyme); POT (thiolase). The remaining metabolic intermediates are described in the figure.

Some approaches, including metabolic engineering for manipulation of genes involved in the lipid biosynthesis pathway, were attempted to increase lipid content in *Y. lipolytica* (Abghari & Chen, 2017; Beopoulos et al. 2012). A random mutagenesis combining the chemical *N*-methyl-*N*′-nitro-*N*-nitrosoguanidine and a treatment with cerulenin was successfully applied to the wild type *Y. lipolytica* NCIM 3589, and three mutant strains with improved lipid synthesis from WCO were selected (Katre et al., 2017).

The effect of WCO concentration on *ex novo* lipid synthesis was studied for some *Y. lipolytica* strains and the optimum concentration was dependent on yeast strain. While no substrate inhibition of WCO on lipid content up to 100 $g \cdot L^{-1}$ (Katre et al., 2012) and 140 $g \cdot L^{-1}$ (Liu et al., 2015) was observed for *Y. lipolytica* 3589 and SWJ-1b, respectively, the maximal accumulation of lipids by W29 (Lopes et al., 2019) and 3472 (Katre et al., 2012) strains were attained with 30 $g \cdot L^{-1}$ of WCO. In cultures of *Cryptococcus curvatus*, the increase of WCO concentration from 20 $g \cdot L^{-1}$ to 100 $g \cdot L^{-1}$ had a negative effect on lipids biosynthesis (Patel & Matsakas, 2018). This effect could be attributed to different factors: (a) high oil concentration affects the oxygen transfer from the gas phase to the liquid medium and the access of yeast cells to substrate, inhibiting cell growth and lipid yield (Tamilarasan & Kumar, 2011); and (b) as WCO concentration increases, considerable amounts of nitrogen will also be available in the culture medium, owing to the release of nitrogen from food into the oil during the frying process. In general, the onset of the oleaginous phase in yeasts are triggered by excessive amounts of carbon source and low concentration of nitrogen (Bellou, Triantaphyllidou, Mizerakis, & Aggelis, 2016). In nitrogen-limited cultures, nicotinamide adenine dinucleotide isocitrate dehydrogenase (NAD-IDH) vanishes from mitochondria of oleaginous yeasts, which results in repression of tricarboxylic cycle (TCA) and modification the metabolic pathway - synthesis of proteins are interrupted and lipids are accumulated (Pan et al., 2009). In fact, the lipid content of *Wickerhamomyces anomalus* (Arous et al., 2017) and *Y. lipolytica* (El Bialy et al., 2011) significantly decreased in media supplemented with WCO containing high nitrogen concentration (waste oils from potato, meat, chicken and fish frying process). Moreover, the maximum synthesis of lipids by *Y. lipolytica* was reached when WCO of frying vegetables (low nitrogen amount) was added to culture medium (El Bialy et al., 2011). Contrariwise, Liu et al. (2015) observed that the addition of $(NH_4)_2SO_4$ from 0 $g \cdot L^{-1}$ to 0.4 $g \cdot L^{-1}$ led to an increase of *Y. lipolytica* SWJ-1b lipid content, but these concentrations are still relatively low. Besides the concentration, lipogenic ability is also dependent on the type of the nitrogen source (inorganic or complex organic sources), since the release of NH^{4+} affects the C/N ratio in the cytoplasm (Bellou et al., 2016).

The supplementation of WCO-based medium with other nutrients and emulsifiers or surfactants was also attempted in order to increase the lipids accumulation by microbial species. The addition of magnesium and phosphate to *Y. lipolytica* cultures gave rise to an improvement of lipid content (Liu et al., 2015). To enhance the solubility of WCO and its bioavailability to microbial cells, several authors add to the medium chemical surfactants or emulsifiers, such as Tween 80 (Arous et al., 2017; El Bialy et al., 2011;

Papanikolaou et al., 2011; Tzirita et al., 2018) or arabic gum (Lopes et al., 2019). However, Patel and Matsakas (2018) found an alternative approach to improve the accessibility of *Cryptococcus curvatus* cells to the WCO, avoiding the use of chemical compounds. The ultra-sonication of WCO medium reduced the size of lipid droplets, improving their miscibility and forming a stable oil in water emulsion, which resulted in easy assimilation and higher lipids accumulation by *Cryptococcus curvatus* cells.

Several authors recognize that oxygen has an important role on microbial lipids biosynthesis from oils and fats. Since a water-immiscible substrate is used, oils can coat the gas-liquid interface with a layer of oil, reducing the oxygen mass transfer to the culture medium. While some authors suggest that the *ex novo* lipids accumulation is boosted by high dissolved oxygen concentration due to the upregulation of ATP-citrate lyase and malic enzymes (involved in lipid biosynthesis), other states that this condition drives the cellular metabolism toward the synthesis of lipid-free biomass (Bellou, Makri, Triantaphyllidou, Papanikolaou, & Aggelis, 2014; Rakicka, Lazar, Dulermo, Fickers, & Nicaud, 2015). Particularly with WCO as sole carbon source, the accumulation of lipids by *Y. lipolytica* cells was negatively affected by increasing the oxygen transfer rate, and the highest lipids synthesis was attained when dissolved oxygen in the medium remained nearly to zero almost all cultivation (Lopes et al., 2019).

In WCO-based medium, the lipogenic phase can be followed by a lipid turnover phase (Lopes et al., 2019; Papanikolaou et al., 2011; Tzirita et al., 2018), even when considerable amounts of oily waste remained unconsumed in the culture medium (Papanikolaou et al., 2011). In this case, the lipids accumulated by cells are subjected to degradation since the cells can not cover their metabolic activities from the oil that is still in the medium, or lipids already accumulated are inhibiting the uptake of extracellular fatty acids (Aggelis, Papadiotis, & Komaitis, 1997). In conditions of carbon starvation, intracellular lipids mobilization occurs because previously stored TAGs can be used as precursors for the biosynthesis of other cellular components. The hydrolysis of TAGs is catalyzed by intracellular lipases, releasing cellular fatty acids that are catabolized through β-oxidation process and the subsequently acetyl-CoA produced will be catabolized via the Krebs cycle or used for anabolic reactions via the glyoxylic acid bypass (Athenaki et al., 2017; Dourou, Mizerakis, Papanikolaou, & Aggelis, 2017; Papanikolaou & Aggelis, 2011b).

Lipids accumulated by microbial cells may have a similar or different fatty acid composition comparatively to initial oily substrate, originating compositional changes and leading to the production of specialty lipids with high added-value. Moreover, the lipids synthesis is microbial species and fatty substrate specific, meaning that different oily wastes will promote

the accumulation of TAGs with specific composition depending on the microorganism. Using waste cooking olive oil (oleic acid 72 %, palmitic acid 16 %, linoleic acid 7 % and stearic acid 2 %) as substrate, cells of *Penicillium expansum* accumulated lipids more unsaturated (91 %) than the initial oil waste (79 %) and rich in oleic acid (76 %), followed by linoleic (15 %) and palmitic (7 %) acids. By contrast, intracellular lipids of *Aspergillus* sp. were more saturated (31 %) than WCO (18 %) and a decrease of oleic acid (62 %) and an increase of stearic acid (19 %) were obtained comparatively to initial substrate (Papanikolaou et al., 2011). A bio-modification of waste cooking olive oil was also observed in co-cultures of *Bacillus* sp. and *Pseudomonas putida*, in which microbial lipids were much more unsaturated (99 %) than the initial substrate (85 %) (Tzirita et al., 2018). The profile of lipids accumulated by *Cryptococcus curvatus* had lower saturated (SFA) and polyunsaturated fatty acids (PUFA) content, whereas the monounsaturated fatty acid (MUFA) content increased comparatively to the feedstock WCO (rapeseed oil, rich in oleic acid). Moreover, the yeast was able to synthesize docosadienoic acid that did not exist in the initial substrate (Patel & Matsakas, 2018). Independently of WCO origin (potato, meat or fish frying oil), *Wickerhamomyces anomalus* lipids were rich in oleic acid (49 % - 52 %), followed by linoleic (18 % - 19 %) and palmitic acids (17 % - 19 %), even though the initial oily wastes showed lower amounts of oleic acid (26 % - 34 %) and higher concentration of linoleic acid (37 % - 49 %). These results suggest the predisposition of this yeast to use polyunsaturated fatty acids for growth and maintenance and to accumulate the monounsaturated ones (Arous et al., 2017). *Yarrowia lipolytica* was employed as a model oleaginous yeast for the *ex novo* lipid synthesis, since is recognized its ability to upgrade the composition of low value fatty substrates. Lipids accumulated by yeast cells growing in waste oil from frying vegetables were 28 % more unsaturated than the substrate, whereas the profile obtained using waste oil from frying fish shown lipids 36 % more saturated (El Bialy et al., 2011). *Yarrowia lipolytica* 3472 growing in WCO accumulated lipids with a high amount of MUFA (72 %), reasonable concentration of SFA (28 %) and negligible content of PUFA, in contrast to the profile of oily substrate which had equal amounts (41 %) of SFA and MUFA and low concentration of PUFA (10 %). By contrast, intracellular lipids of *Y. lipolytica* 3590 shown a considerable increase of SFA (77 %) and PUFA (21 %) and decrease of MUFA (1 %) comparatively to WCO used for yeast cultivation (Katre et al., 2012). The profile of lipids accumulated by a mutant strain of *Y. lipolytica* was similar to that of wild type and an increase of SFA and decrease of MUFA contents were attained comparatively to WCO feedstock (Katre et al., 2017). *Yarrowia lipolytica* W29 demonstrated the ability to increase its cellular oleic and palmitic acids comparatively to initial oily waste. Furthermore,

these intracellular lipids shown higher content of SFA and MUFA and lower amount of PUFA than WCO (Lopes et al., 2019).

2.2.5. Other compounds

The metabolites described above are the most studied in lab-scale experiments using WCO as substrate, but the bioconversion of frying oils to other important compounds was also reported. In a waste frying sunflower oil-based medium, *Propionibacterium freudenreichii* was able to produce simultaneously vitamin B_{12}, propionic acid and acetic acid. Besides WCO concentration, also dimethylbenzimidazolyl, cobalt chloride, ferrous sulfate and calcium chloride was identified as factors having significant effect on vitamin B_{12} production (Hajfarajollah, Mokhtarani, Mortaheb, & Afaghi, 2015).

The use of WCO as substrate to produce biodemulsifiers is an economical option to decrease production costs and to expand its application in the oilfield. *Alcaligenes* sp. S-XJ-1 was able to synthesize a biodemulsifier using WCO as sole carbon source, and it was observed that the increase of initial pH of culture medium led to an enhancement of biodemulsifier yield. Additionally, fed-batch cultivation of *Alcaligenes* sp. using WCO as supplementary carbon source proved to be a feasible method to increase biodemulsifier production (Liu et al., 2011).

Carotenes, important antioxidant agents with application in food, pharmaceutical and medical areas, is successfully produced from vegetable oils and pure fatty acids (Nanou & Roukas, 2011; Nanou, Roukas, & Papadakis, 2012). However, the cost of virgin vegetable oils is still high, increasing the manufacturing costs of carotenes. Nanou and Roukas (2016) found that WCO is a promising substrate for carotenes production by *Blakeslea trispora*. The highest yield ($2\,g{\cdot}L^{-1}$) was obtained using WCO as sole carbon source supplemented with corn steep liquor and butylated hydroxytoluene, and in this condition the carotenes produced consisted of β-carotene (74.2 %), γ-carotene (23.2 %) and lycopene (2.6 %). Upscaling the process to a 1.4-L bubble column reactor did not favored the production of carotenes and lower amount was attained comparatively to flask experiments (Nanou, Roukas, Papadakis, & Kotzekidou, 2017).

The bioconversion of WCO into riboflavin (precursor of FAD and FMN and widely used in pharmaceutical, food enrichment and feed supplements) by an UV mutant of *Ashbya gossypii* was described by Wei et al. (2013). The authors concluded that WCO concentration had no significant effect on riboflavin production, and small differences in yield were obtained varying the WCO concentration from $30\,g{\cdot}L^{-1}$ to $50\,g{\cdot}L^{-1}$. By contrast, initial medium pH was found as a crucial parameter to maximize the riboflavin production and pH values above 6.5 led to a considerable decrease of

productivity. Moreover, when pH was controlled in the range of 6.5 – 6.8 the riboflavin concentration increased from 4.8 $g \cdot L^{-1}$ to 6.8 $g \cdot L^{-1}$.

The ability of *Y. lipolytica* M53 to produce the sweetener erythritol from WCO was reported by Xiaoyan et al. (2017), demonstrating that frying oils are even more favorable than pure vegetable oils. The WCO concentration and C/N ratio were factors with significant effect on erythritol production, and ammonium oxalate, corn steep liquor and ammonium sulfate were the best nitrogen sources. A slight improvement on erythritol concentration was obtained upscaling the production from flask (20.5 $g \cdot L^{-1}$) to 3-L bioreactor (22.1 $g \cdot L^{-1}$) experiments.

The bioconversion of WCO to organic acids, namely oxalic acid by *Aspergillus* sp. (Papanikolaou et al., 2011) and citric acid by *Penicillium expansum* (Papanikolaou et al., 2011) and *Yarrowia lipolytica* (Liu et al., 2015) was successfully studied. Particularly for citric acid, which is widely used in food and beverage industry with a market demand continuously growing, the use of a low-cost carbon source will contribute to the reduction of its price. To attain the maximum citric acid production by *Y. lipolytica* from WCO, extra nitrogen and magnesium were needed, which meant that frying oil used in this study was rich in carbon but poor in nitrogen. By contrast, the addition of magnesium and vitamin B1 had a negative effect on citric acid production. Moreover, WCO concentrations above 80 $g \cdot L^{-1}$ decrease the citric acid synthesis, probably because excessive oil may hamper the access of cells to oxygen (Liu et al., 2015).

3. Final remarks and future perspectives

Waste cooking oils are generated in great quantities and their management is a huge challenge. Traditional approaches for WCO valorization such as bioenergy production have some disadvantages. Valorization of WCO based on microorganisms to achieve added-value products, such as biosurfactants, enzymes, bioplastics and microbial lipids, could be a promising biotechnological approach with great market potential. In spite of some impurities present in WCO, TAGs, glycerides and fatty acids are the major constituents of these oily wastes, which makes them a suitable carbon source for microbial growth and metabolites production. Moreover, WCO are an abundant and low cost substrate, and the main suppliers are usually located within urban areas where collection points and transformation can be easily accomplished (Rincón et al., 2019). The incorporation of WCO in the media formulation for the production of added-value compounds by microorganisms might improve its production economics. Thus, it is expected that the Research & Development (R&D) activities on this field increase, since the microbial valorization of WCO may contribute to the development of a circular economy model around added-value compounds production in urban biorefineries.

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