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Prospecting the Potential of Agroresidues as Substrate for Microbial Flavor Production

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With the growing consumer demand for natural food products, including food flavors, efforts toward identifying biotechnological interventions for their production have increased tremendously. The present paper reviews the production of flavor compounds by microbial biosynthesis or biotransformation, and their enzymes involved in synthesis and conversion from progenitor substrates. More importantly, the use of abundant, inexpensive, and nutrient-rich lignocellulosic waste generated by the processing set-ups of agro-industries as a potential substrate for the microbial production of flavor compounds under solid-state fermentation is reviewed. The article provides insights regarding the development of an efficient and cost-effective process to produce important flavors from agroresidues. The biotechnological route will also help in safe and eco-friendly management of wastes generated from agriculture.

Keywords: flavors, microbial biotransformation, biosynthesis lignocellulose, solid-state fermentation, waste valorization

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INTRODUCTION

The sensation of flavor is stimulated by a complex matrix of volatile as well as non-volatile compounds with varying physicochemical properties. Throughout history, simple to complex flavor compounds have been extracted from plants. The subsequent elucidation of molecular structure of these compounds, has led to their synthetic production and, now almost all flavoring components are produced in this manner. However, with the growing shift of consumer preferences toward natural food products, flavors produced by chemical synthesis cannot be labeled as "natural." Furthermore, chemical production is not environment-friendly and lacks substrate sensitivity, resulting in the formation of undesirable racemic mixtures (Longo and Sanromán, 2006). Conversely, the process of extracting natural flavors from plants also has limitations. These include the high cost of enriching flavor compounds that are present at very low concentrations, the dependence on seasonal and climatic conditions, and ecological problems associated with extraction.

Alternatively, microbial transformation or bioconversion of suitable substrates is an environment-friendly and cost-effective alternative for the production of "natural flavors." This involves the use of (a) microbial cultures as an integral part of the food product and (b) microbes or their enzymes for bioconversion of appropriate substrates to the desired flavor compounds, followed by their extraction from the reaction medium/fermentate (**Figure 1**). In the latter case, solid-state fermentation (SSF), a process in which microbes are grown on a solid support in the absence of free-flowing water (Singhania et al., 2009), shows promise. Recently, SSF of food- and agroresidues has gained attention as a means for producing enzymes, flavors, colorants, and other

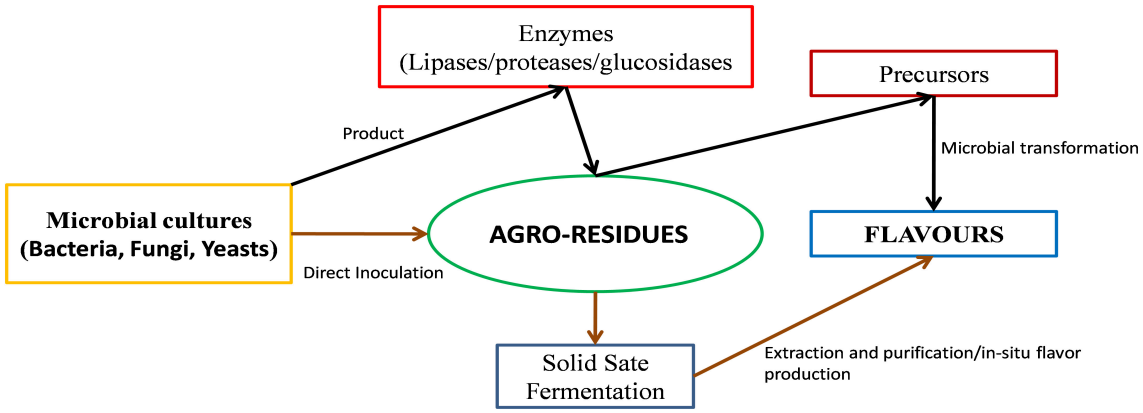

FIGURE 1 | Microbial production of bioflavors from agroresidues.

compounds relevant to the food industry. Compared with submerged fermentation, SSF offers numerous advantages, such as higher yields, lower energy requirements, and the efficient utilization and addition of value to waste (Cerda et al., 2019).

Food and agricultural wastes, rich in carbohydrates and other nutrients, are produced in large quantities and may serve as SSF substrates for the production of bulk chemicals and other compounds. These substrates also contain various bioactive metabolites, including flavor compounds, in different concentrations, and such compounds may be available by microbial fermentation or enzymatic catalysis. This review discusses the potential of microbial cultures and their enzymes to generate aroma and flavor compounds from agroresidues for use in the food industry.

AROMA COMPOUNDS

The organoleptic characteristics of a food product include its taste, flavor, and aroma. Among all these parameters, aroma is one of the most powerful characteristics that determine its acceptance and market success (Berger, 2009). Aroma and flavor compounds can be classified as acids, hydrocarbons, aldehydes, alcohols, ketones, esters, or lactones (Bicas et al., 2010). The classification of aroma compounds according to their chemical structures is depicted in **Figure 2**. Since time immemorial, microorganisms are employed for the production of flavors in many foods. Products like wine, beer, fermented vegetables and milk, soya, meat vinegar, and pickles are preserved, modified and flavored by means of microbes. As previously indicated, microbial strains can be used for production of flavor compounds, either as *in-situ* flavor production in the fermented food product or in appropriate substrates from which flavors can be extracted and subsequently used in different food items (Longo and Sanromán, 2006). The most important group of flavors used in the food industry, as well as their production from microorganisms is discussed below:

Lactones

Lactones are cyclic esters of gamma- and delta-hydroxy acids, which contribute a coconut-like, creamy, creamy, sweet, fruity, or nutty flavor. The biotechnological route for production of lactones during fermentation by various microorganisms is investigated by many researchers. For instance, Collin and Halim (1972) reported 6-pentyl-2-pyrone, which has a coconut aroma, to be the main volatile flavor component in cultures of *Trichoderma viride*. Some other fungi such as *Tyromyces sambuceus* and *Cladosporium suaveolens* also produce coconut flavor emanating lactones, namely, γ-decalactone and δ-dodecalactone from ricinoleic and linoleic acid, respectively (Kapfer et al., 1989; Allegrone et al., 1991). Yeasts such as *Candida tropicalis* and *Yarrownia lipolytica* can degrade ricinoleic acid to C16, C14, and C12 acids and also accumulate δ-decalactone, which exhibits fruity and oily aroma (Gatfield, 1999). While, Fadel et al. (2015) identified 6-pentyl-alpha-pyrone as responsible for the strong coconut aroma produced during solid-state fermentation of sugarcane bagasse by *T. viride* EMCC-107. Additionally, accumulation of delta-decalactone was obtained when the yeasts *Lindnera saturnus* CCMA 0243 and *Yarrownia lipolytica* CCMA 0242 were grown in residual castor oil (De Andrade et al., 2017). Recently, Marella et al. (2019) engineered oleaginous yeast *Yarrowia lipolytica* for hydroxylation of fatty acids and chain-shortening via β-oxidation to preferentially 12 or 10 carbons. The engineered strains were found to produce 4-fold higher concentrations of γ-dodecalactone from oleic acid and δ-decalactone from linoleic acid than the wild strain, thereby paving the way for the higher production of lactones by fermentation of available fatty feedstocks. The milky, buttery, and coconut-like flavors of these lactones produced by microbiological route is highly desirable in dairy products.

Fatty Acids

Triacylglycerides store fatty acids, which are released from acylglycerols by enzymatic oxidative degradation. The majority of the plant volatiles, including carboxylic acids, methylketones,

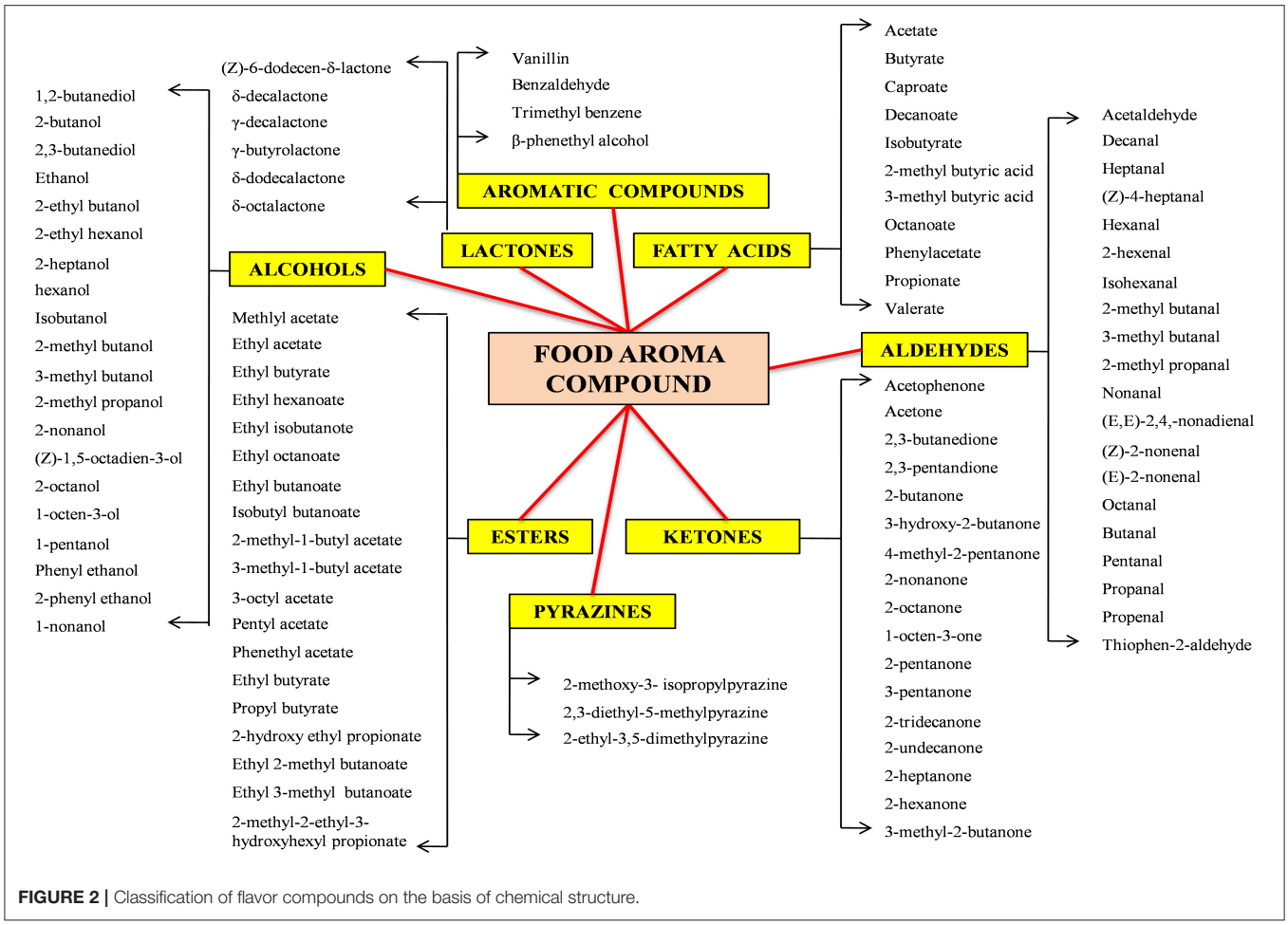

FIGURE 2 | Classification of flavor compounds on the basis of chemical structure.

esters, alcohols, and aldehydes, are derived from saturated and unsaturated fatty acids by alpha and beta-oxidation (Schwab et al., 2008). Dairy flavor fatty acids such as butyric acid and lactic acid can be produced by different lactic acid bacteria (Marshall, 1987). Madhavan Nampoothiri et al. (2010) have reviewed lactic acid production by various lactic acid bacterial (LAB) strains. Apart from LAB, lactic acid can also be produced by filamentous fungi, particularly *Rhizopus* sp. (Meussen et al., 2012). In a study by Meussen et al. (2012), *R. oryzae* was found to produce L-lactic acid, fumaric acid, and ethanol on different carbon sources with lactic acid being produced as the major product (Juturu and Wu, 2016). The dairy flavor of these fatty acids is desirable in many food and beverages.

Terpenes

Terpenes are volatile unsaturated hydrocarbons that impart characteristic odors to essential oils of plants (Janssens et al., 1992). Among all microorganisms, fungi are mainly responsible for the production of terpenes, a typical example being the genus *Ceratocystis* (Collin and Halim, 1972). The amount of terpenes formed by *Ceratocystis moniliformis* was found to be similar to that formed in plants (Lanza and Palmer, 1977). Zhao et al. (2010) observed a significant increase in terpene production in Norway spruce (*Picea abies*) after inoculation with *Ceratocystis polonica*. While, *Trametes odorata* and various species of the genus *Phellinus* also produce monoterpenes (Welsh et al., 1989). In a study by King and Dickinson (2000), three yeast species—*Saccharomyces cerevisiae, Torulospora delbrueckii,* and *Kluveromyces lactis*—were found to biotransformation monoterpene alcohols to terpenes, namely, citronellol, linalool, and nerol. Similarly, linalool and citranool produced by *Saccharomyces cerevisiae* (Carrau et al., 2005) were found to accumulate in wines. Chen et al. (2014) obtained terpenes and terpenoids from lychee wines fermented by *Kluvermyces lactis* strain KL71, with geraniol and citronellol having higher odor activity values (OAVs). In a recent study, the genome functional annotation for two *Ceratocystis* species identified pathways associated with the biosynthesis of various terpenes and volatile compounds (Molano et al., 2018). These terprenes are of considerable interest for application in the food flavor industry, especially linalool, nerol, geraniol, and citronellol due to their low sensory threshold.

Menthol is a terpene alcohol with a strong cooling, minty odor, and taste. It is extracted naturally from peppermint oil and produced synthetically by the hydrogenation of thymol. The compound is used in a variety of confectionaries

and cough syrups. *Bacillus subtilis, Absidiahyalospora, Geotrichumcandidum,* and two species of *Trichoderma* can catalyze the conversion of menthyl acetate, propionate, formate, and myristate to menthol and isomenthol (Moroe et al., 1970). Species from the genera *Rhodotorula*, *Trichoderma*, *Nocardia*, *Mycobacterium*, *Bacillus*, *Rhodococcus*, *Rhizopus*, *Candida*, *Hansenula*, *Streptomyces*, *Aerobacter*, *Arthrobacter*, *Pseudomonas*, *Gibberella*, and *Torulopsis* are also known to bioconvert appropriate substrates to menthol (Armstrong et al., 1989; Chatterjee, 2004; Chandran et al., 2011). Toogood et al. (2015) used an engineered *E. coli* strain expressing genes for "ene"-reductase and menthone dehydrogenases from *Mentha piperita* for one-pot enzymatic production of menthol and neomenthol from pulegone.

Esters

Esters are one of the most significant chemical groups that impart a fruity, candy flavor and are used in fruit-flavored dairy products (Longo and Sanromán, 2006). Volatile esters are responsible for fruity, candy, and perfume-like aroma character of the beer, wine, and sake. Among these volatile esters, isoamyl acetate, with its peculiar banana-like flavor, is the most significant acetate ester present in alcoholic beverages. The second important group comprises medium-chain fatty acid ethyl esters, which include ethyl hexanoate (aniseed aroma) and ethyl octanoate (sour apple aroma). Lactic acid bacteria and several yeasts are known to produce these fruity esters (Longo and Sanromán, 2006). Liu et al. (2004) reviewed the biosynthesis of fruity flavor esters in dairy products by lactic acid bacteria, yeasts, molds, propionibacteria, and *Pseudomonads*. Saerens et al. (2010) reviewed the production of volatile esters by *Saccharomyces cerevisiae*. Layton and Trinh (2016) reported that the fungi *Saccharomyces* sp., *Candida utilis*, and *Hansenula* sp. produce these esters in a glucose-based fermentation medium. While, Walsh et al. (2017) performed metagenomic sequencing of kefir milk over the course of 24 h fermentation and revealed that *Lactobacillus kefiranofaciens* was the dominant bacterial species during the early stages of fermentation, but *Leuconostoc mesentroides* became prevalent in later stages. The results thus illustrate that microbial succession pattern can be applied to optimize fermentation process and enhance particular flavor of fermented foods. On the other hand, van Mastrigt et al. (2018) demonstrated that retentostat cultivation is the preferred method to produce cheese flavors from *Lactococcus lactis* outside the cheese matrix by mimicking the slow growth of bacteria during cheese ripening. Ruiz Rodriguez et al. (2019) studied the diversity and functional properties of lactic acid bacteria isolated from wild fruits and flowers. The strains were found to produce fruity flavor esters and thus can be used in the manufacture of fermented fruit-based products.

Alcohols

Unsaturated alcohols give a characteristic aroma to food products. Many yeasts produce long-chain complex alcohols with distinctive organoleptic properties (Longo and Sanromán, 2006). Mallouchos et al. (2003) conducted batch fermentation of wine using *Saccharomyces cerevisiae* immobilized on delignified cellulosic material, resulting in the production of 2-phenylethanol, which produces a rose-like aroma, in the fermented wine. Thereby, providing an alternative microbial route for the production of this alcohol, which is usually extracted from rose petals or synthesized chemically. Stark et al. (2002) reported production of 2-phenylethanol from 2-phenylalanine by yeasts such as *Kluyveromyces marxianus, Saccharomyces cerevisiae, Hansenula anomala*. Interestingly, Kim et al. (2014) engineered *Kluyveromyces marxianus* to overexpress genes encoding phenylpyruvate decarboxylase (ARO10) and alcohol dehydrogenase (ADH2) from *Saccharomyces cerevisiae,* leading to the overproduction of 2-phenylethanol from glucose.

Ketones

The methyl ketones 2-heptaneone, 2-nonanone, and 2-undecanone are used to add fruity flavors to products. However, they are also produced during ripening of blue cheese by the action of microbial lipases (Engels et al., 1997). These lipases are mainly produced by *Agaricus bisporus, Aspergillus niger, Penicillium roqueforti*, and *Trichoderma viride* (Janssens et al., 1992).

Diacetyl is a vicinal diketone that imparts butter flavor and is thus used for simulating butter-like and other dairy flavors. It is produced by lactic acid bacteria and several other microorganisms in dairy foods (Longo and Sanromán, 2006). Interestingly, a high concentration of diacetyl (1.45 g/L) was produced in metabolically engineered *Enterobacter clocae*, whereas acetaldehyde and diacetyl were synthesized by the yeast *Candida tropicalis* strain D15 on a whey-based medium (Rosca et al., 2016).

Aldehydes

Vanillin (4-hydroxy-3-methoxybenzaladehyde) is an important flavor in the food industry. The extraction of vanillin from vanilla pods is labor-intensive and expensive. The chemical route is not preferred due to increasing consumer demand for natural vanillin (Kumar and Pruthi, 2014). As a result, many research groups have produced vanillin by microbial bioconversion of eugenol and isoeugenol, which are obtained from essential oils (Ashengroph et al., 2012; Tan et al., 2015). Interestingly, lignocellulosic agroresidue is a rich source of ferulic acid that acts as a precursor for vanillin production through microbial or enzymatic transformations (Kumar and Pruthi, 2014). However, the production of vanillin by this method requires the release of ferulic acid from the lignocellulosic waste by enzymatic or chemical treatment (Zamzuri and Abd-Aziz, 2013). The released ferulic acid can be further biotransformed to vanillin, vanillic acid, and protocatechuic acid by some bacteria and fungi. Consequently, the importance of ferulic acid as a precursor for vanillin production has been realized in the area of bioflavor production (Kumar and Pruthi, 2014). Biotransformation of ferulic acid to vanillin has been assessed using various microorganisms, including *Rhodococcus* ssp., *Actinomycetes* spp., *Corynebacterium glutamicum, Saccharomyces cerevisiae, Rhodotorula rubra, Debaryomyces hanseni, Halomonas elongata, Schizophyllum commune, Bacillus licheniformis, Bacillus coagulans, Bacillus subtilis, Pycnoporus cinnabarinus*

CGMCC1115, *Pseudomonas* sp. EF3, *Pseudomonas fluorescens, Pseudomonas putida, Escherichia coli* JM109/pBB1, *Aspergillus niger* CGMCC0774, *Lactic acid bacteria, Amycolatopsis* sp. HR167, *Streptomyces* sp. V-1, *Streptomyces setonii* ATCC39116, *Streptomyces sannanensis, Streptomyces halstedii* GE107678, and genetically engineered microbes (Chen et al., 2016). Ferulic acid esterase has been identified as one of the major microbial enzymes involved in the release of ferulic acid from natural substrates, which can be subsequently biotransformed into vanillin. A two-step bioconversion process has been implemented, wherein ferulic acid from sugarbeet pulp was converted to vanillic acid by *A. niger*, and then vanillic acid was reduced to vanillin by *Pycnoporous cinnabarinus* (Lesage-Meessen et al., 1996). Interestingly, high concentrations of vanillin were obtained from ferulic acid using lactic acid bacteria (Kaur et al., 2013) and *Streptomyces setonii* (Gunnarsson and Almqvist, 2006). However, since the process optimization is very difficult, the development of new recombinant strains able to produce vanillin is quite attractive. Narbad and Gasson (1997) demonstrated the transformation of ferulic acid to vanillin by *Pseudomonas fluorescens* involving a CoA ligase and side chain cleavage. In another work by Vaithanomsat and Apiwatanapiwat (2009), ferulic acid present in steam exploded hydrolysate of *Jatropha curcas* stem was successfully used as the substrate for one-step vanillin production by *Aspergillus niger* and *Pycnoporus cinnabarinus*. Torre et al. (2008) optimized the release of ferulic acid (1.17 g/L) from corn cobs using alkaline hydrolysis. In an interesting study by Tilay et al. (2008), various agricultural wastes, namely, maize bran, rice bran, wheat bran, wheat straw, sugar cane bagasse, pineapple peels, orange peels, and pomegranate peels were screened for the presence of esterified FA (EFA). Among the sources screened, maize bran was found to contain the highest amount of EFA. Pineapple peels, orange peels, and pomegranate peels were also found to contain traces of EFA. Several bacteria belonging to different genera are also able to use ferulic acid as their sole carbon source, thus producing vanillin, vanillic acid, and protocatechuic acid (Converti et al., 2010). Chen et al. (2016) also showed the potential of *Bacillus subtilis* B7-S to produce vanillin from ferulic acid.

Benzaldehyde is the second most important aldehyde after vanillin for producing cherry and fruity flavors. It can be extracted from apricots, but the process leads to the formation of undesirable hydroxycinnamic acid. Alternatively, microbial production of benzaldehyde from phenylalanine can be labeled as "natural," without the production of unwanted by-products. In this regard, the production of benzaldehyde in a medium supplemented with phenylalanine has been reported for cultures of *Pseudomonas putida* (Tsou et al., 1990), *Phanerochaete chrysosporium* (Jensen et al., 1994), *Polyporus tuberaster* (Kawabe et al., 1994), *Lactobacillus plantarum* (Groot, 1998), *Pycnoporus cinnabarinus* (Lomascolo et al., 1999), *Trametes suaveolens* (Lomascolo et al., 2001), and *Rhizopus oligosporus* (Norliza and Ibrahim, 2005).

Pyrazines

Pyrazines are nitrogen-containing heterocyclic compounds that impart roasted and nutty flavors. *Bacillus subtilis* was the first microorganism reported to produce pyrazines (Kosuge and Kamiya, 1962). *B. subtilis* IFO 3010 grown on soybeans supplemented with threonine and acetoin produced 2,5-dimethylpyrazine (2,5-DMP) and tetramethylpyrazine (TMP) (Besson et al., 1997). *Corynebacterium glutamicum* is also known to produce pyrazines from amino acids (Dickschat et al., 2010). Recently, Fadel and colleagues (Fadel et al., 2018) produced pyrazines with a nutty chocolate-like flavor by *C. glutamicum* grown on soyabean enriched with threonine and lysine. Pyrazines can also be produced in conventional cooking and roasting by Maillard reaction. However, due to change in the cooking techniques, for e.g., use of microwave ovens, pyrazines are not produced and thus causing need to supply natural pyrazines with roasty flavor as food additives.

MICROBIAL FERMENTATION OF AGRORESIDUES FOR THE PRODUCTION OF BIOFLAVORS

Agroresidues refers to lignocellulosic waste (LCW), comprising of lignin, cellulose and hemicellulose. LCW is the most abundant, renewable, and inexpensive source of organic compounds available. Furthermore, the bioconversion of LCW into useful products will help to safely dispose of this solid waste. As reviewed by Bicas et al. (2010) and Zamzuri and Abd-Aziz (2013), the high costs involved in microbial production of flavor compounds can potentially be overcome by using agri-waste as a substrate. Studies on the generation of flavor compounds from agro-waste are well-supported. In this regard, Christen et al. (1997) observed that the fungus *Ceratocystis frimbriata* produced a fruity aroma when grown on sugarcane bagasse supplemented with a synthetic medium containing glucose, and when the medium was supplemented with leucine or valine, banana flavor was produced. Thus, alteration of culture conditions also help in manipulating the aroma obtained from microbial fermentations of suitable substrates. Bramorski et al. (1998b) produced fruity aroma by growing a *C. fimbriata* strain on four agro-industrial wastes: cassava bagasse, apple pomace, amaranth, and soybean. The authors identified esters and alcohols as the major flavor components, while small amounts of acid, aldehyde, and ketones were also detected. The authors also found a clear correlation between the growth and production of volatile compounds, based on the observation that the maximum production of volatiles always occurred a few hours before or after the maximum respirometric activity (Bramorski et al., 1998b).

Food and agricultural wastes are produced in large amounts and are rich in carbohydrates as well as other nutrients and thus can be used efficiently as substrate for the production of bulk chemicals, flavors per se under solid-state fermentation conditions. In addition to the supply of nutrients to the microbial cells, solid substrate also provides an anchorage site for the cells (Yan et al., 2016). The work of various researchers that have used food and agroresidues for microbial production of flavor compounds is summarized in **Table 1**.

TABLE 1 | Microbial production of flavor compounds using different agroresidues.

Agri-waste	Microorganisms	Flavor compounds	Fermentation conditions (Temperature, incubation time, % inoculation)	References
Rice koji	*Aspergillus oryzae*	Volatile compounds	36°C, 26 h 10^5 cells/gds	Ito et al., 1990
Pre-gelatinzed rice	*Neurospora* sp.	Fruity aroma	30°C, 6 days, 1% v/w of cell suspension	Pastore et al., 1994
Miso	*Zygosaccharomyces rouxii*	HEMF(4-hydroxy-2-ethyl-5-methyl-3-furanone)	30°C, 14 days, 4×10^5 cells/gds	Sugawara et al., 1994
Soybean by- products	*Bacillus subtilis*	2,5-Dimethyl-pyrazine and tetramethylpyrazine	27°C, 14 days, 10^5-10^6 cells/gds	Besson et al., 1997
Cassava bagasse and soybean meal	*Rhizopus oryzae*	Acetaldehyde, 1-propanol, ethyl acetate, ethyl propionate, and 3-methyl butanol	30°C, 40 h, 1×10^7 spores/gds	Bramorski et al., 1998a
Cassava bagasse, apple pomace and soybean	*Ceratocystis fimbriate*	Fruity flavor	30°C, 15 h, 1×10^7 spores/gds	Bramorski et al., 1998b
Cassava bagasse, apple pomace	*Rhizopus oryzae*	Acetaldehyde, ethanol, 1-propanol, ethyl acetate, ethyl propionate	30°C, 24 h, 1×10^7 spores/gds	Christen et al., 2000
Coffee husk	*Ceratocystis fimbriata*	Ethanol, acetaldehyde, ethyl acetate, ethyl propionate and isoamyl acetate	30°C, 1×10^7 spores/gds	Soares et al., 2000
Cassava wastewater	*Geotrichum fragans*	aroma compounds (alcohols, esters and acids)	24°C, 24 h, 10% v/w	Damasceno et al., 2003
Cassava bagasse and giant palm bran	*Kluveromyces marxianus*	Fruity aroma	28°C, 24 h, 10^7 cells/gds	Medeiros et al., 2001
Soybean meal:rice husk	*Rhizopus oligisporus* USM R1	Benzalaldehyde	30°C, 4 days 10^5 spores/gds	Norliza and Ibrahim, 2005
Semi solid-maize	*Pediococcus pentosaceus* and *Lactobacillus acidophilus* (3:1)	Dairy flavor compounds	32°C, 120 h, LAB (2×10^6 CFU/gds, strain ratio 1:1 P/L)	Escamilla-Hurtado et al., 2005
Wheat bran	*E. coli* strain JM109(pBB1) expressing genes from *Pseudomonas flouroscens* BF13	Vanillin	37°C,11 h, 4 g wet weight/L of substrate	Barghini et al., 2007
Wheat bran	*E. coli* JM109 (pBBI) carrying a catabolic cassette for the conversion of ferulic acid into vanillin	Vanillin	37°C, 48 h, 2% (v/w)	Di Gioia et al., 2007
Rice bran oil	*A. niger* and *P. cinnabarinus*	Vanillin	30°C, 48 h, 4% v/v	Zheng et al., 2007
Wort	*Saccharomyces cerevisiae*	Ethyl ester	30°C, 2% (v/v)	Saerens et al., 2008
Citric pulp	*C. fimbriata*	Fruity flavor esters	30°C, 48 h 10^7 spores/g	Rossi et al., 2009
Rice husk, Groundnut shell	*Phanerochaete chrysosporium* NCIM *1197*	Vanillin	28°C, 72 h 1% (v/w)	Karode et al., 2013
Waste residue of rice bran oil	*P. chrysosporium* ATCC 24725	Vanillin	35°C, 48 h, 10^6 spores/ml	Motedayen et al., 2013
Rice bran	*Pediococcus acidilactici* P2	Vanillin	37°C, 24 h, 1% (v/w)	Kaur and Chakraborty, 2013
Wheat straw	*Clostridium tyrobutyricum*	Butyric acid	37°C, 120 h, 10% (v/w)	Baroi et al., 2015
Orange peels	*Saccharomyces cerevisiae*	Fruity esters (isoamyl acetate, ethyl decanoate, decanoate, Octanoate, and phenyl ethyl acetate)	25°C, 5 days, 10 cfu/gds	Mantzouridou et al., 2015
Sugarcane bagasse	*Trichoderma viride*	6-pentyl-α-pyrone (coconut aroma), δ-octalactone, γ-nonalactone, γ-undecalactone, γ-dodecalactone, and δ-dodecalactone	28°C, 5 days 2% (v/w)	Fadel et al., 2015
Rice straw	Mixed microbial cultures	Butyric acid	35°C,4th day, 5% (v/v) cellulolytic butyrate-producing mixed culture was derived from cattle manure, pig manure compost, corn field soil and rotten wood	Ai et al., 2016

(Continued)

TABLE 1 | Continued

Agri-waste	Microorganisms	Flavor compounds	Fermentation conditions (Temperature, incubation time, % inoculation)	References
Carboxylates from processing of lignocellulosic biomass	*E. coli* DL208 harnessing alcohol acyltransferase genes	Butyl and pentanoate esters	37°C, 24 h	Layton and Trinh, 2016
Wheat bran	*Streptomyces sannanensis*	Vanillin	28°C, 5 days, One pot reaction	Chattopadhyay et al., 2018

ENZYMES INVOLVED IN THE PRODUCTION OF FLAVOR COMPOUNDS FROM MICROORGANISMS

Microorganisms can be directly used for the production of flavor compounds by solid-state fermentation of suitable substrates followed by extraction of the desired flavors, as discussed above. On the other hand, microbial enzymes can also be used for the release of flavors or appropriate precursors from agroresidues, which are finally biotransformed into the desired flavor compounds. Many researchers have used various microbial enzymes for the production of flavor compounds or their precursors by fermentation of appropriate substrates as summarized in **Table 2.** The most commonly used enzymes related to the production of aroma compounds or their precursors are described below:

Lipolytic Enzymes

Lipases are prominent biocatalysts that catalyze the esterification of alcohols and carboxylic acids. They are some of the most important enzymes that produce flavoring esters (Rajendran et al., 2009). A number of lipases produced from microorganisms have been tested for their ability to promote ester synthesis in aqueous media, such as those from *Candida cylideracea, Pseudomonas fluorescens, Rhizomucor meihei, Mucor meihei, Aspergillus* sp.*, Candia rugosa* (Longo and Sanromán, 2006). Lipases can be successfully utilized for modification of skim milk (0.5% fat) into full-fat milk flavor by producing volatile flavor components (Zhang et al., 2016). In a study by Omar et al. (2016), lipases were used to hydrolyze anhydrous milk fat for the development of milk fat flavors due to the synthesis of volatile flavoring esters, acids, and ketones.

Interestingly, lipases can also resolve D, L-methylmenthol esters into pure L-menthol (Schreier, 2006). In this context, lipase from the fungus *Candida rugosa* exhibited high potential to resolve D,L–menthol in an organic solvent (Wang et al., 2002). Lipase from *Thermomyces lanuginosus* can perform high enantioselectivity for the kinetic resolution of (±)-menthol in organic solvent (De Yan et al., 2017).

Proteases

Proteases hydrolyze protein into peptides, which have significant organoleptic as well as biological activity (Longo and Sanromán, 2006). The enzymatic treatment favors pyrazine production through Maillard reaction as well as co-production of alcohols. Many *Lactobacillus* species are used as starter culture in the dairy industry for the degradation of milk casein into small peptides and free amino acids through the action of various proteolytic enzymes (Razzaq et al., 2019). Proteases also contribute significantly to the flavor characteristics of cheese by accelerating cheese ripening, modifying properties, and reducing the allergenicity of milk products (Damhus et al., 2013).

Esterases

Esterases are hydrolases that split esters into alcohols and acid in a chemical reaction with water. Free fatty acids liberated during the process of cheese ripening by the action of microbial esterases and lipases are responsible for the development of its characteristic flavor (Esteban-Torres et al., 2014). One of the most important examples of the application of esterases to flavor production is the use of carboxylesterases in the release of ferulic acid from plant cell walls. Ferulic acid serves as a precursor for the production of vanillin, avital flavor compound (Faulds et al., 1997). Feruloyl esterases have been isolated from a wide range of microorganisms, including *Aspergillus, Streptomyces, Lactobacillus,* and *Pseudomonas* (Topakas et al., 2007). Mathew and Abraham (2004) have reviewed the release of ferulic acid from different plant materials by the action of ferulic acid esterases. Recently, Uraji et al. (2018) elucidated the relationship between the structure and activity of ferulic acid esterase from *Streptomyces* sp. and observed that a catalytic triad (consisting of Ser-191, Asp-214, and His-268), typical for the serine esterase family, forms a loop-like structure (the R18 loop) that is responsible for the release of ferulic acid from biomass.

Glucosidases

Glucosidases are the enzymes involved in breaking down complex carbohydrates into their monomers. They catalyze the cleavage of individual glucosyl residues from various glycoconjugates, including alpha- or beta-linked polymers of glucose. These enzymes enhance the aroma of wines by liberating glycoside-linked terpenes and other flavor precursors (Longo and Sanromán, 2006). Beta-glucosidases are produced by many microorganisms, including species of *Trichoderma, Aspergillus, Bacillus,* and *Candida* (Kuhad et al., 1997). A very efficient beta-glucosidase from *Candida molischiana* releases a number of flavor compounds, namely, nerol, geraniol, linalool, 2-phenylethanol, and benzyl alcohol in Muscat wine and linalool, alpha- and gamma-terpinene, alpha-terpineol, 2-phenylethanol, and alpha-pinene from apricot fruit juice (Gueguen et al., 1996).

TABLE 2 | Microbial enzymes in flavor production.

Enzyme	Microorganism	Substrate	Flavor/precursor	References
Xylanase, ferulic acid esterase	*Trichoderma* sp., *A. niger*	Wheat bran	Ferulic acid	Faulds et al., 1997
Lipase	*Candida rugosa*	DL-menthol	Optically active menthol	Wang et al., 2002
Xylanase, ferulic acid esterase	*Trichoderma* sp., *Aspergillus* sp.	Oat hulls	Ferulic acid	Yu et al., 2002
Lipase	*R. oryzae* NRRL352	Vinyl butyrate in methanol and octanol in vinyl acetate	Methyl butyrate and octyl acetate	Garlapati and Banerjee, 2013
β-glucosidase	*Aureobasidium pullulans*	Wine	Monoterpenes	Baffi et al., 2013
Lipase	*E. coli* expressing heterologous lipase gene	Glyceryl tributyrin, Glyceryl trioctanoate, Glyceryl trioleate	Short chain flavor esters	Brault et al., 2014
Lipase	*L. plantarum*	Adipose tissue from chicken	Short chain fatty acid esters	Uppada et al., 2017
Feruloyl esterase	Corn bran	*Sterptomyces cinnamoneus*	Ferulic acid	Uraji et al., 2018
Ferulic acid esterase	Wheat arabinoxylan	*E. coli* expressing heterologous FAE genes	Ferulic acid	Holck et al., 2019

The role of yeast beta-glucosidase in improving the aroma of wines is due to the release of glycoside terpenes, as confirmed by Villena et al. (2007).

CONCLUSION

The processing of various agricultural commodities produces a huge amount of waste biomass that needs to be recycled. Microbial fermentation of this lignocellulosic biomass not only contributes to its eco-friendly disposal but also its valorization in the form of flavor products, which can find immense applications in the food industry. This review has illustrated the various facets of microbial synthesis of aroma compounds, with a focus on the use of lignocellulosic agro-waste as a substrate in SSF. Substrates from the agro-industry often have low costs, and closeness to the food industry, in general, leads to more easily obtained consumer acceptance of bioflavors as compared to synthetic flavors of petrochemical origin. The survey of literature highlights that the production of flavor compounds through a microbial route offers several advantages when compared with chemical synthesis or extraction from plant sources. Furthermore, the use of lignocellulosic agro-waste through SSF for the production of aroma compounds by microorganisms makes the process cost-effective as well as environment-friendly.

LIMITATIONS AND FUTURE IMPLICATIONS

In any fermentation process, product recovery is often a crucial step. This is especially true for aroma compounds because their volatility and low solubility often make recovery challenging during downstream processing, Presently, several methods for flavor extraction from the fermentate have been used viz. absorption on resins, extraction in two-phase systems, membrane permeation, and pervaporation (a combination of membrane permeation and evaporation). However, all of these methods make the process cost-intensive and also result in low productivities. Therefore, cost-effective technologies for the extraction of flavor compounds are the subject of growing research interest to make the process of microbial production of flavor compounds feasible at a larger scale. Another challenge is the fact that many flavor compounds or their added precursors are inhibitory or toxic to the producer strains. In this respect, slow continuous feeding of low precursor levels (fed-batch fermentation), cell protection via immobilization or *in-situ* flavor extraction membranes and solvents are the main fermentation technologies, which could help to circumvent these limitations. Alternatively, a careful choice of production strains is also essential, since tolerance to the product may vary widely between same species. Similarly, process conditions must be chosen to maintain high physiological as well as the catalytic activity of the microbe. Furthermore, strain adaptation—or genetic engineering—may be used to increase the tolerance to the product. The continuous development of genetic engineering and systems biology tools, in combination with improved process design, will enable more bioflavors to be produced in this manner in the future.

Besides, the ultimate purpose of an industrially produced flavor compound is to induce a sensory effect, most often in humans. However, when volatile compounds are analyzed using GC coupled to any headspace-sampling or other sample preparation techniques, it is not sure whether detected compounds are contributing to odor or flavor. Moreover, the quantity of volatiles in the original sample is not directly related to the intensity of the smell. One solution is to divide the GC eluent before the instrumental detector and steer it partly to the human nose (GC–olfactometry) or using specific methods to identify the key odorants is aroma extract dilution analysis (AEDA).

It is thus clear that interdisciplinary cooperation between microbiologists, mycologists, biochemists, organic chemists, and bioprocess engineers is a prerequisite to develop interesting flavors in laboratory leading to an industrial process for bioflavor production.

AUTHOR CONTRIBUTIONS

AS written the main text of the mini review by searching and analyzing the literature. PS has searched the literature and helped in making table and figure. JS has written a part of the manuscript. SS has guided the authors in writing the review and also written a part of it. LN has given guidance as well as motivation in review writing along with her knowledge and expertise in the field.

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