




Review

Agro-Industrial Residues Used as Substrates for the Production of Bioaroma Compounds with Basidiomycetes: A Comprehensive Review

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Abstract: Flavoring compounds are substances that directly influence the acceptance or rejection of a product. They are considered as essential components in the industrial sector due to their wide range of applications in different areas, such as food, cosmetics and pharmaceuticals. With the growing demand and concern of consumers for the acquisition of flavors from natural products, alternatives for the sustainable and low-cost production of such compounds becomes mandatory. Among these alternatives, biotechnological processes involving fungi are considered ecologically suitable and sustainable, as they tend to use conditions that are less harmful to the environment. The application of filamentous fungi such as basidiomycetes in biotechnological processes has been very promising, although it depends on the strain and growing conditions for obtaining bioaromas. The present review aims to compile reports on the potential of several basidiomycete fungi in the production of bioaromas using biotechnological methods. This review also includes the availability of nutrients and covers the new perspectives created with the application of agro-industrial residues as alternative cultivation substrates for these microorganisms. Thus, this is expected to consequently alleviate environmental pollution problems and enable the production of promising volatile compounds in a natural and sustainable way.

Keywords: aroma; volatile compounds; natural; microorganisms; biotransformation; waste valorization



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1. Introduction

Volatile compounds are important substances for the perception of a product's taste and aroma, which are the main sensory attributes that influence its acceptance or rejection by consumers. Thus, aromas have become essential components for the industrial sector with applications in the areas of pharmaceuticals, cosmetics and especially in the food area, representing more than a quarter of the world market for food additives, with an estimated projected value of about USD 19.72 billion up to 2026 [1].

Volatile aroma compounds can be produced by direct extraction from natural sources, chemical synthesis and biotechnological pathways. The natural extraction process has limitations such as seasonality, low yield of the compounds and high production costs, all contributing as the main limiting factors in the market [2,3]. The chemical synthesis of the compounds, on the other hand, has been dominating the artificial flavors segment, due to its low cost. However, chemical synthesis has complex process conditions and can produce

compounds with sensory alterations different from the desired aroma and which are not labeled as “natural”, which could directly reflect on their acceptability by consumers who are looking for healthy and natural products [2,3].

Aroma compounds with a “natural” designation can be obtained through biotechnological processes as bioflavors. The biotechnological method could be desirable for overcoming the problems associated with other production methods, and it could meet the intense consumer demand for healthy eating, stimulated by the consumption of natural, functional and high-quality products [3,4]. The processes involving fungi, yeasts and bacteria are considered ecologically suitable and sustainable, as they tend to use conditions that are less harmful to the environment. They do not use toxic catalysts and could present solutions to the problems associated with waste management. In addition to these factors, biotechnological processes have advantages such as production with higher yields of aromatic compounds compared to those obtained by extraction from natural sources such as fruits and/or other vegetables. Thus, the use of agro-industrial residues as raw materials for substrates in the fermentation processes has been found to contribute ecological and economic sustainability, as the use of these materials reduces the large volume of residues discarded into the environment, besides serving as low-cost raw materials [3,5,6].

Several studies have been developed on the production of aromas through biotechnological processes using various residues and agro-industrial by-products as substrates. Various microorganisms have been tested and found to possess the potential of generating aromatic compounds, such as terpenes, esters, aldehydes and alcohols [7–10].

Basidiomycete fungi, often referred to as ‘higher fungi’, have the potential to synthesize a variety of aroma compounds similar to vanilla, cherry, apple, citrus fruits and others, depending on the strain and the growing conditions [11–13]. Using specific substrates and different reactions such as oxidation, hydrolytic reduction, dehydration, formation of new carbon–carbon bonds and various degradation reactions, the fungi produce several natural flavors and aromas [14]. Thus, the objective of the present work is to compile a report on the potential of basidiomycete fungi for the production of bioaromas by fermentation in a culture medium consisting of agro-industrial residues.

2. Aryl Compounds

Filamentous fungi, particularly white-rot basidiomycetes, are notable for their efficiency in the biotransformation of aryl substrates, producing compounds with valuable commercial applications such as vanillin and benzaldehyde, among others. Some of these microorganisms are detailed in Table 1, with an emphasis on basidiomycete species involved in the production of aroma compounds. Vanillin, an aryl compound with a pleasant aroma found in vanilla pods, is extensively used as a flavoring additive in the food, cosmetic and pharmaceutical industries [15]. Traditionally, vanillin has been predominantly produced through chemical synthesis, due to its lower cost compared to natural extraction methods. However, consumer demand for natural flavors and the high price of natural vanillin obtained from vanilla pods have stimulated research into the natural production of vanillin from lignocellulosic biomass [16]. In these processes, microorganisms are employed in the bioconversion of vanillic acid to vanillin, with filamentous fungi, especially white-rot basidiomycetes, being widely recognized for their efficiency in metabolizing ferulic acid into vanillic acid and vanillin [17].

Ferulic acid is the most abundant hydroxycinnamic acid found in plant cell walls. The compound was recently found to be produced from the degradation of lignin by white-rot fungi [18,19]. Thus, several researchers have efficiently used them as precursors for the bioconversion process into vanillic acid and subsequently to vanillin [18,19]. Investigations into the potential of two strains of white-rot fungi, namely, *Trametes hirsute* and *Phanerochaete chrysosporium*, in the degradation of ferulic acid have been reported earlier [18]. The research group found that the fungi *T. hirsute* completely degraded 350 mg/L ferulic acid in 20 h, while *P. chrysosporium* degraded ferulic acid into vanillin or vanillic acid (250 mg /L) in 28 h during the process of bioconversion [18]. Similarly,

Ghosh et al. [20] reported the degradation of ferulic acid using the white-rot basidiomycete *Schizophyllum commune* via cleavage of the propionic chain and found vanillic acid to be the main product, along with oxidation of vanillin as an intermediate product in the culture medium studied [20].

Table 1. Basidiomycetes used in the production of aroma compounds.

Basidiomycetes	Compounds	Yield	Substrates	References
<i>Pycnoporus cinnabarinus</i>	Vanillin	8 mmol/L	Vanillic acid	[21]
<i>Phanerochaete chrysosporium</i>	Vanillin	503 mg/L	Vanillic acid	[22]
<i>Pycnoporus cinnabarinus</i>	Vanillin	1575 mg/L	Vanillic acid	[17]
<i>Pycnoporus cinnabarinus</i>	Vanillin	64 mg/L	Ferulic acid	[23]
<i>Pycnoporus cinnabarinus</i>	Vanillin	1.15 µmol/L	[5-2H]-labeled ferulic acid	[24]
<i>Pycnoporus cinnabarinus</i>	Vanillin	12.3 mg/L	[5-2H]-labeled ferulic acid	[24]
<i>Pycnoporus cinnabarinus</i>	Vanillin	560 mg/L	Vanillic acid	[25]
<i>Pycnoporus cinnabarinus</i>	Vanillin	237 mg/L	Vanillic acid	[26]
<i>Pycnoporus cinnabarinus</i>	Vanillin	760 mg/L	Vanillic acid	[19]
<i>Phanerochaete chrysosporium</i>	Vanillin	6.61 mg/L	Ferulic acid	[18]
<i>Pycnoporus cinnabarinus</i>	Vanillin	126 mg/L	Ferulic acid	[16]
<i>Polyporus tuberaster</i>	Benzaldehyde	7.89 mM	L-phenylalanine	[27]
<i>Ischnoderma benzoinum</i>	Benzaldehyde	114 mg/L	L-phenylalanine	[28]
<i>Bjerkandera adusta</i>	Benzaldehyde	1.56 g/kg	L-phenylalanine	[29]
<i>Bjerkandera adusta</i>	Benzaldehyde	587 mg/L	L-phenylalanine	[30]
<i>Bjerkandera adusta</i>	Benzaldehyde	71 mg/L	L-phenylalanine	[31]
<i>Bjerkandera adusta</i>	Benzaldehyde	404 mg/L	L-phenylalanine	[32]
<i>Pleurotus florida</i>	Benzaldehyde	20–220 µg/L	-	[33]
<i>Ischnoderma resinatum</i>	Benzaldehyde	12.0 mg/kg	D-Glucose; D-fructose	[34]
<i>Pycnoporus cinnabarinus</i>	Benzaldehyde	790 mg/L	L-phenylalanine	[35]
<i>Trametes suaveolens</i>	Benzaldehyde	710 mg/L	L-phenylalanine	[36]
<i>Tricholoma matsutake</i>	Benzaldehyde	3.25 nM	-	[37]
<i>Tricholoma matsutake</i>	Benzaldehyde	13.7 µM	L-phenylalanine	[37]
<i>Polyporus tuberaster</i>	Benzyl alcohol	11.93 mM	L-phenylalanine	[27]
<i>Bjerkandera adusta</i>	Benzyl alcohol	3.75 g/kg	L-phenylalanine	[29]
<i>Ischnoderma benzoinum</i>	Benzyl alcohol	500 mg/L	L-phenylalanine	[30]
<i>Bjerkandera adusta</i>	Benzyl alcohol	484 mg/L	L-phenylalanine	[31]
<i>Bjerkandera adusta</i>	Benzyl alcohol	338 mg/L	L-phenylalanine	[32]
<i>Pleurotus ostreatus</i>	4-Methoxybenzaldehyde	2610 µM	L-tyrosine	[38]
<i>Pleurotus florida</i>	4-Methoxybenzaldehyde	130–1450 µg/L	-	[33]
<i>Ischnoderma resinatum</i>	4-Methoxybenzaldehyde	104.9 mg/kg	-	[11]
<i>Ischnoderma resinatum</i>	4-Methoxybenzaldehyde	239.6 mg/kg	D-Glucose; D-fructose	[34]
<i>Volvariella volvacea</i>	4-Vinyl guaiacol	637.8 mg/L	Ferulic acid	[39]
<i>Schizophyllum commune</i>	4-Vinyl guaiacol	0.04 mmol/L	Ferulic acid	[40]
<i>Ischnoderma resinatum</i>	3,4-Dimethoxybenzaldehyde	27.8 mg/kg	D-Glucose; D-fructose	[34]
<i>Pycnoporus cinnabarinus</i>	p-Hydroxybenzaldehyde	155 mg/L	Phospholipids/p-coumaric acid	[41]
<i>Schizophyllum commune</i>	p-Hydroxybenzaldehyde	0.16 mM	-	[42]
<i>Pycnoporus cinnabarinus</i>	Methylanthranilate	18.7 mg/L	-	[43]
<i>Pleurotus sapidus</i>	(+)-Nootkatone	280 mg/L	(+)-Valencene	[44]
<i>Fumalia trogii</i>	(+)-Nootkatone	1100 mg/L	(+)-Valencene	[45]
<i>Pleurotus sapidus</i>	(+)-Nootkatone + β-nootkatol	284 mg/L	(+)-Valencene	[46]
<i>Pleurotus sapidus</i>	(E)-verbenol	152.2 mg/L	α-Pineno	[47]
<i>Tyromyces floriformis</i>	α-Ylangene	>40 mg/L	-	[48]
<i>Pleurotus sapidus</i>	Carveol	9.8 mg/L	R-(+)-limonene	[49]
<i>Pleurotus sapidus</i>	Carveol	59 mg/L	Limonene	[50]
<i>Pleurotus sapidus</i>	Carvone	39 mg/L	Limonene	[50]
<i>Trametes elegans</i>	cis-Verbenol	2.9 mg/g	α-Pinene	[51]
<i>Pleurotus sapidus</i>	α-Nootkatol	62 mg/L	(+)-Valencene	[44]
<i>Pleurotus sapidus</i>	β-Nootkatol	14 mg/L	(+)-Valencene	[44]
<i>Pleurotus ostreatus</i>	Perillene	80.3 mg/L	α-(Z)-acardiol	[52]
<i>Pleurotus ostreatus</i>	Perillene	5 mg/L	β-Myrcene	[53]
<i>Pleurotus ostreatus</i>	Perillene	3.8 mg/L	α-(Z)-acardiol	[52]
<i>Pleurotus ostreatus</i>	Perillene	24.0 mg/L	α,α-Acarylactol	[52]
<i>Pleurotus sapidus</i>	Perillene	32.8 mg/L	β-Myrcene	[54]
<i>Pleurotus sapidus</i>	Rosefurane	13.3 mg/L	β-Myrcene	[54]
<i>Pleurotus sapidus</i>	Verbenone	149.3 mg/L	α-Pinene	[47]
<i>Rhodotorula aurantiaca</i>	γ-Decalactone	6.5 g/L	Ricinoleic acid	[55]
<i>Rhodotorula aurantiaca</i>	γ-Decalactone	6.6 g/L	Ricinoleic acid	[56]
<i>Sporidiobolus salmonicolor</i>	γ-Decalactone	12 mg/L	Ricinoleic acid	[57]

Table 1. Cont.

Basidiomycetes	Compounds	Yield	Substrates	References
<i>Sporidiobolus ruinenii</i>	γ -Decalactone	40 mg/L	Ricinoleic acid	[57]
<i>Sporidiobolus ruinenii</i>	γ -Decalactone	200 mg/L	Ricinoleic acid	[58]
<i>Tyromyces sambuceus</i>	γ -Decalactone	880 mg/L	-	[59]
<i>Piptoporus soloniensis</i>	γ -Decalactone	14 mg/L	Ricinoleic acid	[60]
<i>Piptoporus soloniensis</i>	γ -Decalactone	16mg/L	12-hydroxystearic acid	[60]
<i>Sporidiobolus salmonicolor</i>	γ -Decalactone	135 mg/L	-	[61]
<i>Sporidiobolus salmonicolor</i>	γ -Decalactone	131.8 mg/L	Ricinoleic acid	[62]
<i>Sporobolomyces odorus</i>	γ -Decalactone	54.6 mg/L	Castor oil	[63]
<i>Sporobolomyces odorus</i>	γ -Decalactone	71.8 mg/L	Ricinoleic acid	[64]
<i>Tyromyces sambuceus</i>	γ -Decalactone	120 mg/L	Castor oil	[65]
<i>Sporidiobolus johnsonii</i>	γ -Decalactone	>200 mg/L	Ricinoleic acid	[66]
<i>Sporidiobolus ruinenii</i>	γ -Decalactone	>200 mg/L	Ricinoleic acid	[66]
<i>Sporidiobolus salmonicolor</i>	γ -Decalactone	1.6 mg/L	-	[67]
<i>Rhodotorula aurantiaca</i>	γ -Decalactone	6.5 g/L	4-hydroxydecanoic acid	[55]
<i>Sporobolomyces odorus</i>	γ -Dodecanolactone	1.1 ppm	Oleic acid	[68]
<i>Sporobolomyces odorus</i>	(R)- γ -decanolactone	10.8 ppm	Oleic acid	[68]
<i>Sporobolomyces odorus</i>	(Z)-6- γ -dodecenolactone	28.7 ppm	Oleic acid	[68]
<i>Sporidiobolus salmonicolor</i>	(Z)-6- γ -dodecenolactone	11 mg/L	-	[67]
<i>Trichosporon asahii</i>	β -ionone	327.6 μ M; 63 mg/L	Lutein	[69]
<i>Trichosporon asahii</i>	β -ionone	60 mg/L	Lutein	[70]
<i>Marasmius scorodoni</i>	β -ionone	0.6 mg/L	β -carotene	[71]
<i>Nidula niveo-tomentosa</i>	4-(4-hydroxyphenyl)-butan-2-one	3.2 mg/L	-	[72]
<i>Nidula niveo-tomentosa</i>	4-(4-hydroxyphenyl)-butan-2-one	160 mg/L	L-phenylalanine	[72]
<i>Nidula niveo-tomentosa</i>	4-(4-hydroxyphenyl)-butan-2-one	8.7 mg/L	L-phenylalanine	[73]

Falconnier et al. [23] studied the white-rot fungus *Pycnoporus cinnabarinus* in the metabolism of ferulic acid, wherein they reported that a concentration of 64mg/L of vanillin was produced after 6 days of fermentation. They also observed that the biotransformation process also resulted in the production of 2-methoxyhydroquinone and the alcohols coniferyl and vanillyl, in addition to the release of laccase in the growth medium [23]. Tilay et al. [16] also reported the use of *P. cinnabarinus* in the biotransformation of ferulic acid to vanillin using glucose as a carbon source and corn steep liquor and ammonium chloride as a source of organic and inorganic nitrogen, respectively, producing 126 mg/L of vanillin during fermentation [16].

A combination of two filamentous fungi was applied in a study to increase the production of vanillin from ferulic acid in a two-step bioconversion process; in the first step, the *Aspergillus niger* strain was used to transform ferulic acid into vanillic acid, and in the second step, a high-density culture of *P. cinnabarinus* was employed to transform vanillic acid into vanillin [19]. Similar fermentation media have been found to produce 920 mg/L of vanillic acid from ferulic acid with *A. niger* at a molar yield of 88%, and, in the second step, vanillin (237 mg/L) from vanillic acid with *P. cinnabarinus* at a molar yield of 22%. The research team found that the yield was not found to be higher due to the vanillic acid oxidative system that produced methoxyhydroquinone in the fermentation medium, which decreased the concentration of vanillin [26]. In order to avoid the oxidative process with the production of compounds that interferes with the yield of vanillin production, Lesage-Meessen et al. [25] studied the addition of cellobiose and maltose disaccharides in the biotransformation of vanillic acid into vanillin by two strains of *P. cinnabarinus* MUCL39532 and MUCL38467, and they observed that the application of maltose as a carbon source for the microorganism favored the increase in the hydroxyquinone–methoxy content formed from vanillic acid. On the contrary, the supply of cellobiose to the culture of *P. cinnabarinus* MUCL39532 and *P. cinnabarinus* MUCL38467 produced 510 mg/L and 560 mg/L of vanillin at a molar yield of 50.2% and 51.7%, respectively. Their study indicated that cellobiose inhibited vanillic acid decarboxylation, thereby preventing the formation of methoxyhydroquinone during fermentation [23]. Correspondingly, the use of glucose-phospholipid as a carbon source for the biotransformation of ferulic acid into vanillin with *P. cinnabarinus* was studied by Oddou et al. [19]. The research group found that, when the glucose-phospholipid medium was applied in a bioreactor (2 L) and during

a period of 15 days, the production of vanillin was found to be 760 mg/L, at a molar yield of 61% (4 mmol/L), with the formation of by-products such as methoxyhydroquinone and vanillic alcohol [19].

As an approach to avoid the transformation of vanillin into undesirable products such as vanillic alcohol, alternatives were investigated, namely, the use of adsorbents to trap the vanillin before its biotransformation into vanillic alcohol [17]. Stentelaire et al. [22] observed that, when XAD-2 resin was applied to the culture medium of *P. chrysosporium*, the fungal strain efficiently and selectively adsorbed vanillin and prevented the transformation into vanillyl alcohol [17]. Such an application becomes very important, as the process could counteract the production of methoxyhydroquinone at higher concentrations and subsequently could increase vanillin production. Another study reported the production of vanillin from vanillic acid employing *P. cinnabarinus* using a laboratory-level bioreactor in a condition of reduced dissolved oxygen concentration. The vanillin production was found to be 1260 mg/L, along with the formation of significant amounts of methoxyhydroquinone. The experimental conditions employed by the research group also revealed the fact that vanillin becomes toxic for the growth of *P. cinnabarinus* on agar medium when it reaches concentrations above 1000 mg/L. Thus, the application of selective XAD-2 resin reduced the toxicity to the fungus and the amount of methoxyhydroquinone in the medium, thereby enabling an increase in the production of vanillin at concentrations of 1575 mg/L [17].

Benzaldehyde is the second most important aryl compound after vanillin as a flavoring agent in the food and aroma industries owing to its apricot, cherry and almond notes. Natural benzaldehyde was obtained in two ways: (i) extraction from apricots (however, during the production process, the unwanted compound hydroxycinnamic acid was also found to be formed), and (ii) biotechnological production using microorganisms, without any formation of unwanted intermediates and products [74]. So far, several basidiomycetes such as *Poria subacida* and *Dichomitus squalens* [75], *Ischnoderma resinatum* [11,34], *Sarcodontia setosa* and *Hericiium erinaceus* [76] have been found to be capable of producing benzaldehydes. Furthermore, the production of benzaldehyde by biotransformation of the phenylalanine supplement in the culture medium has also been reported for cultures of *Bjerkandera adusta* [32], *P. cinnabarinus* [35], *Trametes suaveolens* [77], *Stropharia rugosoannulata* [78] and *Tricholoma matsutake* [37].

Earlier investigations into the odor characteristics of several edible mushrooms grown in liquid culture have been reported for the production of benzaldehyde as the major compound in cultures. For instance, the basidiomycete *Polyporus tuberaster*, when supplemented in the culture medium with *L*-phenylalanine, enabled higher yields of benzaldehyde [27,79]. Furthermore, when *B. adusta* was cultivated in a liquid medium enriched with *L*-phenylalanine and phospholipids, it yielded high concentrations of benzaldehyde (404 mg/L) [32]. In addition, when *B. adusta* was cultivated on a solid medium using wheat bran, it oxidized benzyl alcohol to benzaldehyde due to the activity of aryl alcohol oxidase, thereby increasing the production of benzaldehyde in a shorter period of time compared to fermentation in a liquid medium [29]. However, the presence of high concentrations of benzaldehyde in the culture medium was also found to be toxic to fungal metabolism, and it inhibited the growth of the microorganism. As an approach to counteract this effect, the use of HP20 resin, a copolymer of styrene-divinylbenzene, in the culture medium selectively adsorbed and immobilized benzaldehyde and allowed the microorganism to grow in the culture medium [35,77]. Similarly, when *T. suaveolens* cultures were cultivated in the presence and absence of HP20 resin, it was found that the addition of resin favored the biotransformation of *L*-phenylalanine directly to benzaldehyde and trapped the transformation of benzyl alcohol, thereby resulting in an increase in benzaldehyde production from 33 (absence of resin) to 710 mg/L (presence of resin) [77]. In other research, remarkable amounts (587 mg/L) of benzaldehyde production were found in cultures of *B. adusta* when grown in a liquid medium supplemented with *L*-phenylalanine and benzyl alcohol, wherein the cells were immobilized on polyurethane foam cubes, than were found in the non-immobilized cells [30]. Lomoascolo et al. [35] also reported that, when the fungus

P. cinnabarinus was cultured and supplemented with *L*-phenylalanine and HP20 resin, the benzaldehyde production was found to increase eight-fold, i.e., from 100 mg/L to 790 mg/L in the culture medium.

Wickramasinghe and Munafo in the years 2019 and 2020 investigated the biotechnological production of benzyl derivatives from the basidiomycete *Ischnoderma resinorum* [11,34,80]. The same research team, with other coworkers, elucidated the biosynthetic pathway of benzyl derivatives and vanillin production from *I. resinorum* by employing isotope incubation studies. The findings of the study demonstrated that both benzyl alcohol and benzoic acid converted into benzaldehyde (12 mg/kg); hydroxylation and subsequent methylation at the 4-C position converted benzaldehyde into 4-methoxybenzaldehyde (vanillin, 239.6 mg/kg). After being hydroxylated and methylated at the 3-C position, 4-methoxybenzaldehyde was transformed to 3,4-dimethoxybenzaldehyde (169 mg/kg) using different *I. resinorum* isolates. The mechanism of this biosynthetic pathway also paved the way to understand the production of vanillin from vanillic acid [38]. Submerged cultures of *Pleurotus florida* supplemented with *L*-phenylalanine also produced notable amounts of benzaldehyde (1560 µg/L) and 4-methoxybenzaldehyde (1634 µg/L) after 30 days of fermentation [33]. Further, the supplementation of the culture medium with *L*-tyrosine was found to produce greater amounts of 4-methoxybenzaldehyde by the basidiomycetes *P. ostreatus* and *B. adusta* [38,81].

Basidiomycetes have been demonstrated to produce several other aromatic compounds, including methylanthranilate (18.7 mg/L), possessing a grape odor note, produced in liquid cultures of *P. cinnabarinus* at a low nitrogen concentration and with maltose as a carbon source [43]. The white-rot fungus *Bjerkandera* sp. produced chlorinated compounds such as veratraldehyde (100 µM) and 3-chloro-anisaldehyde (50 µM) by de novo synthesis [82–84]. *S. commune* and *P. cinnabarinus* were able to transform *p*-coumaric acids into *p*-hydroxybenzaldehyde (155 mg/L), a compound with a natural vanilla flavor in the presence of phospholipids [42]. Furthermore, *S. commune* showed the potential to convert ferulic acid into 4-vinyl guaiacol by decarboxylation, oxidizing it to vanillin and vanillic acid, while *Volvariella volvacea* produced 4-vinyl guaiacol from ferulic acid at maximum concentrations ranging from 88.2 mg/L to 637.8 mg/L [39,40,85].

3. Terpenes

The class of terpenes and their derivatives are formed in several plants and fruits as a defense mechanism to protect themselves from predators and parasites [86]. They are generally considered as strong odorous compounds and are widely used as fragrances and flavors in consumer products, especially food and drink products. Terpenes are hydrocarbons structurally formed by the condensation of isoprene molecules (C₅H₈) and are classified as monoterpenes, sesquiterpenes, diterpenes, triterpenes and tetraterpenes. However, under modifications and the presence of oxygen atoms in their structure, they are called terpenoids, such as norisoprenoids, etc. Their characteristic aroma differentiates food as aroma-pleasant or off-flavor [86–88]. In foods, the characteristic aroma notes such as citrus, fruity and floral flavors serve as important quality parameters in determining the quality of food products. Among terpenes, limonene, which is commonly found in citrus fruits, has been applied as a substrate for biotechnological transformations. Several microorganisms, including basidiomycetes, are capable of transforming this terpene into other monoterpenoids such as carvone, carveol, peryl alcohol, α -terpineol and linalool oxide (Table 1). They are value-added compounds that are used as flavors and fragrances in the food, beverage and pharmaceutical industries [8,49,50,87,88].

Submerged cultures of *P. sapidus* have been found to transform limonene by allylic oxidation into carvone and *cis/trans*-carveol as main products, the latter being produced in a *cis* and *trans* ratio of about 2:3. These products were in higher concentrations in the aqueous culture medium, and the cultivation of pre-cultures upon continuous addition of limonene increased the concentration of the products to 59 mg/L of carveol and 39 mg/L of carvone after 12 days of transformation [50]. Furthermore, the cat-

alytic potential of basidiomycetes *P. sapidus* in biotransforming limonene to carvone, which selectively dehydrogenated *trans*-(-)-carveol into *R*-(-)-carvone enantiopure, has also been reported [49]. *P. sapidus* was also applied in the conversion of sesquiterpene, (+)-valencene to (+)-nootkatone, characterized with a grapefruit flavor even at a low odor threshold of about 1 µg/L in water [89]. The conversion was observed to be carried out through its enzyme valencene dioxygenase (ValOx) and through hydroperoxides derived from valencene, such as 6(*R*)-isopropenyl-4(*R*),4a(*S*)-dimethyl-2,3,4,4a,5,6,7,8-octahydro-naphthalen-4(*S*)-yl-hydroperoxide and 6(*R*)-isopropenyl-4(*R*),4a(*S*)-dimethyl-2,3,4,4a,5,6,7,8-octahydro-naphthalen-2(*R*)-yl-hydroperoxide, which were rapidly converted to enones [44,90]. The selective and efficient allylic oxidation of (+)-valencene to (+)-nootkatone sesquiterpene was also achieved with the use of the basidiomycete, *P. sapidus* in its lyophilized form. After 16 h of incubation with the rehydrated lyophilized *P. sapidus* with (+)-valencene, the biotransformation resulted in producing 280 mg/L of (+)-nootkatone, in addition to 62 mg/L of α -nootkatol and 14 mg/L of β -nootkatol in the culture medium [44,46]. The edible basidiomycete *P. sapidus* possessed the ability to convert sesquiterpene (+)-valencene to the valuable grapefruit aroma (+)-nootkatone when using linoleic acid as a substrate. This fungal strain presented a high specificity for linoleic acid, and the enzyme produced was classified as lipoxygenase type 1. The conversion of linoleic acid mainly into (*S*)-13-hydroperoxy-9-(*Z*) and 11E-octadecadienoic acid (94%) was identified to be the first lipoxygenase from a terpenic hydrocarbon as substrate [91].

Other species of basidiomycetes also showed potential for bioconversion of the precursor (+)-valencene to (+)-nootkatone. A laccase obtained from the basidiomycete *Funalia trogii*, combined with a peroxidase, completely converted the (+)-valencene to (+)-nootkatone to a maximum concentration of 1100 mg/L after 24 h [45]. Studies of crosses between *P. sapidus* and *P. florida* monokaryotes show an improved biotransformation of (+)-valencene to (+)-nootkatone, indicating that a classical genetic approach resulted in altered and partially improved terpene transforming capacity (more than 60%), in addition to the lipoxygenase activity of the strains [92]. Thus, sesquiterpene (+)-nootkatone obtained via biotechnological processes proves to be a viable alternative, since its isolation from natural plant sources has low yields and chemical synthesis involves carcinogenic or hazardous compounds [93].

Submerged, lyophilized cultured cells and microsomal fractions of the basidiomycete *P. sapidus* have also been found to possess the potential to enzymatically convert α -pinene to verbenols and verbenone, which can be interpreted as an oxidation catalyzed by cytochrome P450 monooxygenase of α -pinene. About 20 mg of (*E*)-verbenol and up to 4 mg of verbenone were found in the culture liquid after 48 h. The mycelium concentrates and the freeze-dried mycelium of *P. sapidus* responded to the presence of α -pinene with a significant increase in the concentration of (*E*)-verbenol (39.3 mg/L and 155.6 mg/L, respectively) and verbenone (9.8 mg/L and 61.9 mg/L, respectively). The research group also observed a significant increase in verbenone concentration (149.3 mg/L), along with recombination of the supernatant and microsomal pellet (microsomal fraction). Based on the identification of new products and intermediates, the reaction mechanism was elucidated and two enzymes, a regiospecific α -pinene dioxygenase and a stereoselective (*Z*)-verbenol dehydrogenase, were described for the first time in their study as being responsible for the biotechnological formation of verbenone [47].

Several other odorous compounds were produced using different basidiomycetes, illustrating the relevance of the microorganism in the production of bioaromas. The α -ylangene compound with a fruity aroma was biosynthesized using *Tyromyces floriformis* when cultivated along with *Cerrana unicolor* in submerged cultures. The addition of acetyl donors increased the concentration of the compound to more than 40 mg/L; however, they observed that some polysaccharides such as chitin, starch and agarose had blocking effects on α -ylangene during synthesis [48]. Submerged cultures of *P. ostreatus* converting β -myrcene to perillene, a rare furanoid monoterpene with a citrus and floral flavor, along with the production of α -(*Z*)-acaridiol and 1,4-butanediol derivative generated through

a base catalyzed epoxide opening, being a suitable precursor of perylene, have been reported [52,53,94]. The enzymatic synthesis of β -myrcene furanoterpenoids and related monoterpenes was also observed using an enzyme fraction solubilized from mycelium lyophilizates from various *Pleurotus* species. The study showed the biotechnological potential for the formation of compounds such as perylene and rosofuran, which were found in concentrations of 32.8 mg/L and 13.3 mg/L, respectively [54].

Volatile aroma compounds were also produced through the degradation of carotenoids by basidiomycetes. Two extracellular peroxidases capable of degrading carotenoids were isolated from culture supernatants of the basidiomycete *Marasmius scorodoni* (garlic mushroom) and produced norisoprenoid flavor compounds [71]. Volatile products derived from carotenoids were detected in submerged cultures of *Ischnoderma benzoinum*, *M. scorodoni* and *Tirametes versicolor*; wherein the generation of β -ionone was proved to be the main metabolite which resulted from β -carotene degradation [95].

4. Lactones and Ketones

Lactones are substances widely used in the flavoring and food processing industries due to their pleasant and highly fruity aroma. Among lactones, γ -decalactone carries a peach aroma and its production from microorganisms by biotechnology has represented a very valuable alternative recently. Basidiomycetes are found to be capable of converting fatty acids into lactones, and γ -decalactone, one of the most studied lactones, can be obtained with several species of basidiomycetes as listed in Table 1.

γ -Decalactone is a fruity aroma compound resulting from the β -oxidation of fatty acids by microorganisms such as *Sporobolomyces odorus*, *Sporidiobolus salmonicolor* and *Sporidiobolus ruinenii*, and it was one of the first to be studied for the production of lactones. The addition of [9,10-2H₂] oleic acid to cultures of *S. odorus* led to the formation of (R)- γ -decalactone and the enantiomers (Z)-6- γ -dodecenolactone and γ -dodecanolactone, showing that oleic acid could be a genuine precursor of this aromatic compound, through the enantioselective (R)-12-hydroxylation of oleic acid followed by its β -oxidation [68]. The incubation of racemic ethyl [2,2-2H₂]-(*E*)-3,4-epoxydecanoate and the corresponding acid with *S. odorus* cells led to the formation of γ -decalactone, and the results indicated that (*E*)-3,4-epoxydecanoic acid formed from (*E*)-3-decenoyl-CoA, an intermediate in the β -oxidation of linoleic acid, is also considered a genuine precursor in γ -decalactone biosynthesis [96].

The addition of ricinoleic acid (0.06%) to the medium at the beginning of the cultivation of *S. odorus* resulted in a maximum yield of approximately 135.4 mg/L of γ -decalactone after 9 days of cultivation [64]. Similar results were also found when castor oil (3%) was added after 24 h of cultivation (8.62 mg/L) [97]. Using jar fermenters, *S. odorus* grew rapidly and entered the stationary growth phase after approximately 72 h of cultivation, reaching a maximum γ -decalactone yield of 54.6 mg/L after 120 h of cultivation; and culture-fed *S. odorus* with additions of castor oil hydrolyzate on the 3rd, 4th and 5th day resulted in a maximum yield of 208 mg/L of γ -decalactone after 7 days of cultivation [63].

S. salmonicolor is an aroma-producing yeast that imparts a peachy smell to culture media and produces lactones such as γ -octalactone, γ -nonalactone, γ -dodecalactone, (Z6)- γ -dodecenolactone and γ -decalactone [67]. Studies with this species have reported varying amounts of γ -decalactone: 1.6 mg/L, 12 mg/L, when 4.1 g/L of ricinoleic acid methyl ester was added to the medium; 131.8 mg/L after 5 days of fermentation with cells immobilized with calcium alginate, compared to a maximum of 107.5 mg/L for free cells; and 135 mg/L after 5 days of fermentation with cells immobilized with calcium alginate [57,61,62,67].

During the bioconversion of ricinoleic acid to γ -decalactone under controlled pH conditions, *S. salmonicolor* produced only the lactone form, while the strains of *S. ruinenii* were able to produce the lactone form and a precursor 4-hydroxydecanoic acid which is less toxic for microorganisms than lactone [98]. Dufossé et al. [57] obtained 12 mg/L of γ -decalactone by bioconversion of ricinoleic acid methyl ester with *S. salmonicolor*, *S. ruinenii* strains, producing 40 mg/L. When applied in a 7 L bioreactor, the production of γ -decalactone, after 4 successive cultivations, was 5.5 g/L every 10 days, and this increase

was due to the open formation of γ -decalactone (4-hydroxy-decaoic acid) in the culture medium [57]. *S. ruinenii*, as well as *S. johnsonii*, was able to produce amounts above 200 mg/L of γ -decalactone when using dithiothreitol (DTT) as a reducing agent and ricinoleic acid as the substrate [66]. In addition to these species, other basidiomycetes were also able to biosynthesize γ -decalactone using castor oil, such as *Tyromyces sambuceu*, *Rhodotorula aurantiaca* and *Piptoporus soloniensis*. *R. aurantiaca* had mean concentrations of 6.5 g/L of γ -decalactone [55,56,59,99], and γ -decalactone yields with *P. soloniensis* were obtained at concentrations ranging from 7.9 mg/L to 16 mg/L when cultivated without fatty acid addition [60].

In addition to lactones, some basidiomycetes were also capable of biosynthesizing aroma ketones such as 4-(4-hydroxyphenyl)-butan-2-one, being of great industrial interest due to its raspberry aroma. This ketone is found in several genera of plants; however, its isolation from these natural sources is low-yielding and economically expensive, which implies the importance of studies on its production via biotechnology. The basidiomycete *Nidula niveo-tomentosa* has been reported to be a potent producer of this ketone. Reported results showed that the supplementation of the culture medium of *Nidula niveo-tomentosa* with *L*-phenylalanine for submerged cultures provided an increase in the production of 4-(4-hydroxyphenyl)-butan-2-one, with concentrations varying from 3.2 mg/L to 160 mg/L [69,72,99]. The basidiomycete *Trichosporon asahii*, on the other hand, bioconverted lutein into the ketone β -ionone, with a characteristic violet aroma, at an average concentration of 60 mg/L [70,100].

5. Fermentation with Basidiomycetes Using Agro-Industrial Residues as Substrates for Production of Bioaromas

The aroma compounds produced with basidiomycetes through fermentation in a synthetic medium have been reviewed as cited before. However, agro-industrial residues have become an important alternative for the production of aromatic compounds by biological means. The biotechnological conversion of low-cost agro-industrial by-products contributes to the preservation of the environment and makes the aroma synthesis process economically sustainable [15,101]. The potential of basidiomycetes for the generation of aroma compounds by novel or biotransformation synthesis, using residues obtained after agro-industrial processing as substrates, are discussed henceforth. Table 2 lists various aroma compounds which are produced using different agro-industrial residues.

An agro-industrial residue, namely coconut fiber, was used for ferulic acid extraction, through chemical pre-treatment with alkaline hydrolysis, acidification and liquid–liquid extraction methods. The ferulic acid obtained (1.2 g/50 g) was used as a substrate for biotransformation into vanillic acid with *Aspergillus niger*, and then vanillic acid was fermented with the basidiomycete *Phanerochaete chrysosporio* to produce vanillin. The amount of vanillic acid produced on the third day of incubation was 0.773 g/L, while the optimum yield of vanillin on the sixth day of incubation was 0.628 g/L. The chemical extraction of ferulic acid from coconut fiber resulted in bioconversion into vanillin, thus becoming an alternative substrate for aroma production [102]. In another study, green coconut residue (shell) was processed in two different ways, sun drying and mechanical pressing, and later used for the production of vanillin through the bioconversion of ferulic acid by solid-state fermentation with the basidiomycete *Phanerochaete chrysosporium*. The composition of the culture medium was optimized, which improved the production of vanillin from 44.4 μ g/g to 52.5 μ g/g in 24 h of fermentation, wherein the mechanically pressed coconut was used as the substrate for the production of vanillin [103].

Table 2. Basidiomycetes used in the production of aroma compounds from different agro-industrial residues.

Basidiomycetes	Compounds	Productivity	Precursor	Substrates	References
<i>Phanerochaete chrysosporium</i>	Vanillin	0.628 g/L	Ferulic acid	Coconut fiber	[102]
<i>Phanerochaete chrysosporium</i>	Vanillin	131 mg/L	Ferulic acid	Lemongrass leaves	[104]
<i>Phanerochaete chrysosporium</i>	Vanillin	93 mg/L	Ferulic acid	Lemongrass leaves	[105]
<i>Phanerochaete chrysosporium</i>	Vanillin	1.3 mg/L	Ferulic acid	Palm oil	[106]
<i>Phanerochaete chrysosporium</i>	Vanillin	0.192 g/L	Ferulic acid	Lemongrass leaves	[107]
<i>Phanerochaete chrysosporium</i>	Vanillin	52.5 µg/g	Ferulic acid	Green coconut residue	[103]
<i>Phanerochaete chrysosporium</i>	Vanillin	55 µg/mL	Ferulic acid	Groundnut shell	[108]
<i>Pycnoporus cinnabarinus</i>	Vanillin	141 mg/L	Ferulic acid	Pineapple waste	[109]
<i>Pycnoporus cinnabarinus</i>	Vanillin	2.8 g/L	Vanillic acid	Rice bran oil residues	[110]
<i>Pycnoporus cinnabarinus</i>	Vanillin	725 mg/L	Vanillic acid	-	[111]
<i>Pycnoporus cinnabarinus</i>	Vanillin	767 mg/L	Vanillic acid	Autoclaved corn bran	[112]
<i>Pycnoporus cinnabarinus</i>	Vanillin	>100 mg/L	Ferulic acid	Sugar beet pulp	[113]
<i>Pycnoporus cinnabarinus</i>	Vanillin	90 mg/L	Ferulic acid	Wheat bran	[114]
<i>Pycnoporus cinnabarinus</i>	Vanillin	300 mg/L	Ferulic acid	Beet pulp	[114]
<i>Pleurotus pulmonarius</i>	<i>p</i> -Anisaldehyde	134.1 µM	<i>p</i> -Anisyl alcohol	Lignin and straw	[115]
<i>Fomitopsis betulina</i>	(5 <i>E</i> / <i>Z</i> ,7 <i>E</i> ,9)-decatrien-2-ones	1.1 mg/L	-	Cabbage residue extract	[116]
<i>Tyromyces chioneus</i>	3-phenylpropanal	290 µg/L	(<i>E</i>)-cinnamic acid	Apple pomace	[12]
<i>Tyromyces chioneus</i>	3-phenyl-1-propanol	270 µg/L	(<i>E</i>)-cinnamic acid	Apple pomace	[12]
<i>Tyromyces chioneus</i>	Benzyl alcohol	100 µg/L	-	Apple pomace	[12]
<i>Fistulina hepatica</i>	1-Octen-3-ol	1000 µg/kg	-	Oak wood dust	[117]
<i>Pleurotus pulmonarius</i>	1-Octeno-3-ol	700 µg/g	Linoleic acid	Soy flour and soy oil	[118]

Lemongrass leaves were also used as substrates for the production of vanillin in the presence of *Phanerochaete chrysosporium*. The influence of the pH in the culture medium for the production of vanillin was investigated, and a higher production of vanillin (124 mg/L) was found with a molar yield of 32% in the culture at a constant pH 6.0. However, a decrease in pH to 3.5 resulted in a decrease in *Phanerochaete chrysosporium* growth and vanillin production. The two-stage controls improved the vanillin production to 131 mg/L and cell concentration to 13.0 g/L [104]. Lemongrass leaves hydrolysates were also used as source of ferulic acid for one-step vanillin bioconversion using *P. chrysosporium*. The bioconversion process was affected by the interaction of the initial concentration of ferulic acid, incubation temperature, incubation time and initial pH; the values of these parameters, optimized for greater production of biovanillin, were 0.5 g/L, 35 °C, 72h and 6, respectively, showing a vanillin production of 93 ± 3 mg/L with a molar yield of 23% [105]. Even higher concentrations of vanillin were obtained after studies using different nitrogen sources in the production of vanillin with *Phanerochaete chrysosporium*. The maximum biotransformation of ferulic acid (from hydrolyzed lemongrass leaves) to vanillin was obtained using ammonium chloride and yeast extract as organic and inorganic nitrogen, respectively, and the optimum nitrogen and temperature conditions resulted in a production of 192 mg/L vanillin with 24.5% molar yield [107].

Currently, the annual quantity of residues generated by the Malaysian palm oil industry is about 49 million tons, and these residues can be used as raw material for the generation of high-value products due to their availability throughout the year and at low cost. Thus, the alkaline hydrolyzate from the degradation of lignin present in these residues was studied as a potential substrate for the production of vanillin via biotransformation in two stages. In the first step, the fungus *A. niger* was used, which converted ferulic acid into 41% vanillic acid, and later, this was biotransformed with the basidiomycete fungus *P. chrysosporium* into 39% vanillin. The highest production of vanillin with *P. chrysosporium* was found to be 1.3 mg/L, after 42 h of fermentation [106].

The basidiomycete *P. chrysosporium* was able to produce up to 55 µg/mL of vanillin after 72 h of fermentation using peanut shell as substrate. Glucose supplementation with peanut husks produced a vanillin production of 37 µg/mL in 96 h, while starch supplementation produced up to 21 µg/mL of vanillin in 96 h [108]. In another study, solid-state fermentation parameters were optimized for the single-step production of vanillic acid, a vanillin precursor, using the fungus *P. chrysosporium* and peanut husk as

substrate. The most significant variables of the fermentation process were *L*-asparagine, pH and moisture content of the solid medium and the optimization of these variables resulted in a maximum 10-fold increase in the yield of vanillic acid (73.69 mg/g) after 8 days of solid-state fermentation compared to that observed under suboptimal conditions (7.2 mg/g) [119].

The fungus *P. cinnabarinus* was found to be another basidiomycete with the potential to produce the vanillin compound from agro-industrial residues, such as pineapple residues, rice bran oil residues, corn bran, wheat bran and sugar beet pulp residues. Using pineapple residue, *P. cinnabarinus* was able to bioconvert vanillic acid from ferulic acid present in pineapple residue, along with *A. niger* to vanillin (36.5 mg/L). The biotransformation of vanillic acid into vanillin was also found to increase with the addition of Amberlite XAD-4 resin, producing 141.00 mg/L of vanillin from 5 g of pineapple residue [109]. The resin adsorbed the produced vanillin and prevented its deterioration to vanillic alcohol and vanillic acid, thereby reducing the high rate of degradation of vanillin [120]. Rice bran oil residues were also used as a source of ferulic acid for biotransformation into vanillic acid and subsequently into vanillin, in the presence of the combined *A. niger* strain and the basidiomycete *P. cinnabarinus*. The results of the study showed that a maximum yield of 2.2 g/L of vanillic acid was found in the filtrate from the *A. niger* culture in a 25 L fermenter when the concentration of ferulic acid was 4 g/L; under these conditions, the filtrate was concentrated and vanillic acid was biotransformed into vanillin with *P. cinnabarinus*. The vanillin yield reached values even higher than 2.8 g/L, when 5 g/L of glucose and 25 g of HZ802 resin were supplemented in the biotransformation medium [110].

Enzymatic and fungal treatments allowed the production of vanillin from autoclaved corn bran, without any purification step. Vanillic acid from the biotransformation of ferulic acid was obtained from the enzymatic degradation of autoclaved corn bran, which was recovered and efficiently biotransformed into vanillin using *P. cinnabarinus* in the presence of cellobiose and XAD-2 resin, with a production of 767 mg/L of vanillin. Another study of producing vanillin using corn bran used 3-day-old high-density cultures of *P. cinnabarinus* fed with autoclaved corn bran as a source of ferulic acid and with *A. niger* culture filtrate as a source of extracellular enzyme. Under these conditions, *P. cinnabarinus* directly biotransformed the free ferulic acid released from autoclaved corn bran by *Aspergillus niger* enzymes into 584 mg/L vanillin [112]. Other studies have also used the basidiomycete *P. cinnabarinus* in the production of vanillin from the biotransformation of ferulic acid derived from beet pulp into vanillic acid. The study was found to produce more than 100 mg/L of vanillin, and the results of the sensory analysis of the vanillin revealed a predominant flavor of vanillin with a slight chocolate odor as a secondary organoleptic sensation [113]. The basidiomycete *P. cinnabarinus* converted ferulic acid, releasing vanillin (90 and 300 mg/L) in the presence of cellobiose and enzymatically from wheat bran and beet pulp, respectively. This process was carried out in two stages involving the addition of *P. cinnabarinus* and *A. niger* along with complementary transformation capabilities [114].

The agro-industrial substrates also include different by-products from the food industry, namely apple pomace, cracked waffles, broken cake, cocoa husks, cocoa powder, ground coffee and wine pomace as a carbon source. A previous study showed that, when *Tyromyces chioneus* was cultivated in a freeze-dried apple pomace as substrate, it yielded compounds such as 3-phenylpropanal, 3-phenyl-1-propanol and benzyl alcohol at concentrations of 290 µg/L, 270 µg/L and 100 µg/L, respectively. Thus, the fungal strain was able to biotransform food by-products into pleasant mixtures of complex flavors [12]. Grosse et al. [116] used cabbage cuttings as a substrate in a fermentation medium submerged with the edible basidiomycete *Fomitopsis betulina*. They reported that the fermented product presented a fruity odor, strongly reminiscent of pineapple. The olfactory analysis showed that this impression was mainly caused by the two (5*E*/*Z*,7*E*,9)-decatrien-2-one compounds [116,121].

Volatile compounds were also produced by cultures of *Fistulina hepatica* using oak wood powder as substrate. Surface cultures produced 53 main volatile compounds, mostly

composed of aldehydes, methoxybenzenes and terpenes. The most abundant compounds found in their study were 2-methyl-1-propanol, hexadecanoic acid, linoleic acid and its methyl ester at approximate concentrations of 1000–5000 µg/kg. Similarly, the fungal strain also yielded high amounts of 1-octen-3-ol, 1,2,3,4-tetramethoxybenzene and elemicin, which are the main flavor compounds of Puer tea (*Camellia sinensis*) with insecticidal and antioxidant properties. Various terpenoids such as menthol, α -terpineol, terpinen-4-ol, α -pinene, (*Z*)-linalool oxide, *D*-fenchol, (*E*)-nerolidol, biformene and isopulegol have also been identified in this study [117].

The basidiomycete *P. ostreatus* also showed the potential for aroma production using various agro-industrial residues as substrate. The strains of *P. ostreatus*, as well as *F. tenuiculus*, were cultivated by solid-state fermentation using residues from *Eucalyptus cinerea* leaves. The two mushrooms were able to transform 1,8-cineole, a remaining component of the *Eucalyptus cinerea* residue leaves, into new compounds, namely 1,3,3-trimethyl-2-oxabicyclo[2.2.2]octan-6-ol and 1,3,3-trimethyl-2-oxabicyclo[2.2.2]octan-6-one, in addition to increasing the concentration of other aromatic compounds such as 1,8-cineole, β -caryophyllene and drimenol present in the substrate [122]. The production of aroma by the mycelium of *P. ostreatus* growing on sugarcane bagasse solid support has been found as an excellent alternative method in industrial culture, as it grew in a shorter period of time than the fruiting bodies and hence recorded lower costs during production. Several aromatic profiles were produced under liquid, surface and solid-state conditions; however, the best aromatic similarities with the fruit body of *P. ostreatus* were obtained from the mycelium cultivated in sugarcane bagasse enriched with nutrient solution. The aroma produced by the fruit body was essentially due to the presence of octan-3-one and, to a lesser extent, octan-3-ol. Oct-1-en-3-ol, 2-methylbutanol and α -pinene were also found in low concentrations. The main aromatic compounds present in the fruit body and mycelium of *P. ostreatus* were produced in the same proportions on the agar surface and in the solid support culture with sugarcane bagasse, but not under submerged conditions [123]. Earlier studies identified a variety of aromatic compounds in liquid cultures of the basidiomycetes, namely, *P. cornucopiae*, *P. eryngii*, *P. floridanus*, *P. pulmonarius*, *P. ostreatus* and *P. sajor-caju* in media containing lignin and straw. Of these species, *P. pulmonarius* synthesized the greatest amount and diversity of compounds, mostly anisyls and hydroxybenzyls, such as alcohols, aldehydes and acids, wherein *p*-anisaldehyde was the most characteristic extracellular metabolite synthesized by these ligninolytic fungi, in addition to small amounts of 3-chloro-*p*-anisaldehyde detected in several species [115]. *P. pulmonarius* was also used for the production of 1-octen-3-ol in substrates rich in nitrogen and fatty acids. The addition of soy flour and soy oil to the growth medium increased the production of 1-octen-3-ol (700 µg/g) by about seven times compared to that grown in defined synthetic medium [118].

Studies have also investigated the use of 31 basidiomycete fungi in must fermentation. The main pleasant odors included fruity notes obtained from *Lentinula edodes*, *Polyporus umbellatus* and *Trametes versicolor*, toast from *Agrocybe aegerita* and *Pleurotus cornucopiae* and honey notes from *Trametes versicolor* and *Panellus serotinus*. The cultures produced a wide variety of different odors in a short fermentation time of about 48 h, and this rapid formation of compounds may be related to the available nutrients and aroma precursors in the must, which provided an adequate environment for the growth of basidiomycetes. Among the species studied, shiitake (*Lentinula edodes*) and its fermented product possessed a pleasant aroma with fruity notes which were similar to plums. In addition, odorous compounds such as 2-phenylethanol, methyl 2-methylbutanoate, 2-phenylethanol acetate and (*E*)-methyl cinnamate were also produced by shiitake. These compounds were found to be responsible for the overall flavor, and compounds, namely, methyl 3-methylbutanoate, hexanol and 1-octanol, produced in lower concentrations, were also identified [13].

6. Conclusions

In the foreseeable future, the production of bioflavors and bioaromas through biotechnological processes is expected to replace the traditional and chemical processes used in

producing these compounds. However, the production of bioaromas also represents a challenge for academic and industrial research, in order to make it a very attractive alternative through the utilization of residues/agro-industrial wastes left after food processing. Basidiomycetes ease this process, as they have a great potential to produce a wide variety of aromatic compounds, where the use of some precursors improves the production yield of these compounds. Thus, the compilation of various research studies in this review indicates that agro-industrial residues constitute a potential substrate for the generation of aroma compounds, thus making the biotechnological process economically viable and ecologically suitable. Furthermore, the biotechnological processes known today are in full development, with the aim of discovering even newer bioaromas with the combination of microorganisms and substrates/residues, consequently improving results with higher yields and enabling the production of volatile compounds in a natural and sustainable way with greater industrial relevance.

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