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Mini Review

Research Progress in the Biological Production of Vanillin

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Abstract

Vanillin is one of the most extensively used aromatic aldehydes in the food, flavor and fragrance, pharmaceutical, and fine chemical industries. However, production from vanilla pods is constrained by limited feedstock supply, long cultivation cycles, and high extraction costs, whereas conventional chemical synthesis faces increasing concerns over sustainability and compliance with "natural label" requirements. Accordingly, the biotechnological production of vanillin using microbial and enzymatic systems has attracted growing attention. Vanillin can be produced either by bioconversion of ferulic acid, eugenol/isoeugenol, and lignin-derived aromatics, or by de novo biosynthesis from glucose and related carbon sources. These routes differ markedly in substrate economics, pathway length, product toxicity, host compatibility, and downstream recovery demands. Ferulic acid bioconversion remains the most technically mature route, whereas lignin- and lignocellulose-based processes offer greater long-term potential for sustainable manufacturing. Current efforts to improve performance have focused on enhancing host tolerance, blocking competing pathways, strengthening key catalytic modules, optimizing precursor supply, and integrating in situ product recovery. This review summarizes two major aspects of vanillin biomanufacturing: (1) The principal substrate routes and their technical features, and (2) Host selection and engineering strategies. It further discusses four major barriers to industrial implementation, namely substrate heterogeneity, vanillin toxicity, insufficient coupling of reaction and separation, and the balance between high-value production and scalable manufacturing. Further advances in vanillin biomanufacturing will increasingly depend on the integrated optimization of host engineering, low-cost feedstock utilization, and process design.

Keywords: vanillin; substrate routes; technical characteristics; engineered hosts; metabolic engineering strategies

Introduction

Vanillin, chemically designated 4-hydroxy-3-methoxybenzaldehyde, is the principal component of natural vanilla flavor and one of the most commercially important flavor aldehydes worldwide [1,2]. Beyond its use in the food and beverage industries, vanillin is also employed in fragrances, pharmaceutical intermediates, household chemicals, and selected functional materials [3,4]. Although vanillin was originally sourced from vanilla pods, natural extraction cannot satisfy market demand because of its limited productivity [5]. As a result, industrial production has long relied on chemical routes, primarily based on guaiacol or lignin oxidation [6,7]. In recent years, growing interest in natural sourcing and green manufacturing has renewed attention to the biotechnological production of vanillin [8]. The significance of biomanufacturing lies not only in its potential to replace conventional chemical processes, but also in its capacity to connect agricultural by-products, aromatic biomass, and programmable microbial hosts, thereby providing a new biorefinery route for the production of high-value aromatic compounds [9].

From a technological perspective, vanillin biomanufacturing has evolved through three major stages.

The first stage was characterized by the screening of natural strains and substrate bioconversion, in which the inherent aromatic metabolism of microorganisms was exploited to convert ferulic acid, eugenol, isoeugenol, vanillic acid, and even related precursors present in agricultural wastes into vanillin [10].

The second stage involved metabolic engineering and the construction of microbial cell factories, where engineered Escherichia coli, Pseudomonas, and Actinomycete chassis were established through introduction of the fcs-ech module, blockade of vanillin degradation pathways, and optimization of cellular redox balance [11].

The third stage has been marked by system integration and sustainable biorefinery development, in which lignin/lignocellulose valorization, the development of non-model or food-grade hosts, and the integration of in situ product recovery with fed-batch process control have collectively shifted vanillin production from simple bioconversion toward a more sustainable biorefinery framework [12].

Based on current studies, this review summarizes the state of the art in vanillin biomanufacturing from two perspectives, namely substrate routes and their technical characteristics, and host selection and engineering strategies, followed by an overall assessment and future outlook. The analysis presented here is intended to provide a useful reference and technical basis for the green biomanufacturing of vanillin.

Substrate Routes and Technical Characteristics of Vanillin Biomanufacturing

At present, vanillin biomanufacturing can be broadly divided into three established substrate routes, each with distinct technical characteristics;

(i) The aromatic precursor route, which uses ferulic acid, eugenol, or isoeugenol as substrates and is characterized by short pathways, well-defined key reactions, and relatively high product selectivity;

(ii) The lignin route, which is attractive from a sustainability perspective but remains constrained by feedstock heterogeneity, limited depolymerization efficiency, and challenging downstream separation; and

(iii) The glucose route, which is conceptually more amenable to platform-based production but is generally limited by low flux and strong competition from intermediate metabolism [13].

The aromatic precursor route is currently the most technically mature route for vanillin biomanufacturing. Its principal advantage lies in the close structural relationship between the substrate and vanillin. Ferulic acid, in particular, can be converted to vanillin through only two core reactions, namely CoA activation and side-chain cleavage, which confers clear advantages in terms of pathway length, enzyme definition, and conversion selectivity [14]. In practice, however, the major limitation of this route is the further degradation of vanillin, as the product is often oxidized to vanillic acid or reduced to vanillyl alcohol by the host, thereby lowering net accumulation. Two main strategies have been developed to address this issue.

The first is to strengthen the fcs-ech core conversion module. In Amycolatopsis sp. ATCC 39116, deletion of vdh (encoding vanillin dehydrogenase), together with overexpression of fcs (encoding feruloyl-CoA synthetase) and ech (encoding enoyl-CoA hydratase/aldolase), increased the vanillin titer to 19.3 g/L.

The second is to block oxidative or reductive product-loss pathways.

In Amycolatopsis, simultaneous deletion of vdh and phdB increased the vanillin titer from 10.60 g/L to 20.44 g/L. In addition, this route has also been validated in E. coli, Pseudomonas putida, and lactic acid bacteria. These studies indicate that the aromatic precursor route, owing to its short pathway and clearly defined core module, is particularly suitable for high-level vanillin production through a combination of branch-pathway blocking and pathway strengthening [15].

The lignin route is the most technically challenging route currently explored for vanillin biomanufacturing. As a substrate, lignin fully reflects the potential of biomass valorization for the production of high-value aromatics. However, lignin originates from diverse sources, exhibits high structural heterogeneity, contains variable interunit linkages, and typically yields complex mixtures of aromatic monomers after depolymerization. These features complicate both subsequent bioconversion and product recovery [16]. To address these limitations, two major strategies have been developed.

The first involves pretreatment and directed conversion of lignin feedstocks. For example, alkaline wet oxidation combined with membrane separation and resin adsorption afforded a vanillin yield of 4.3% (w/w) from kraft lignin, together with a recovery rate of 71%. Subsequent optimization of oxidation conditions further increased the vanillin yield to 9.25% (w/w). In another study, electrochemical depolymerization of organosolv lignin achieved a maximum vanillin yield of 17.5% [17].

The second strategy is the construction of cell factories capable of aromatic monomer funneling and directed synthesis.

In S. cerevisiae, an artificial biological funneling pathway (ABFP) was established to channel lignin-derived monomers and sugar fractions simultaneously toward vanillin biosynthesis, resulting in a vanillin titer of 1.97 mmol/L and a yield of 10.5 mg/g. In Arthrobacter sp. C2, deletion of xylC (encoding benzaldehyde dehydrogenase) and overexpression of pchF (encoding vanillyl alcohol oxidase) enabled a vanillin productivity of 0.85 mg/g DCW/h from alkaline lignin. In Bacillus ligniniphilus L1, deletion of vdh increased the vanillin titer to 315 mg/L. In Rhodococcus jostii

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RHA1, deletion of vdh enabled vanillin titers of 13 mg/L and 96 mg/L when kraft lignin and wheat straw were used as substrates, respectively. Collectively, these studies show that the key challenge of the lignin route lies not only in improving depolymerization efficiency, but also in reconstructing metabolic networks to funnel structurally diverse aromatic intermediates toward a single target product [18].

The glucose route reflects the transition of vanillin production from bioconversion of specific precursors to platform-based microbial synthesis [19]. Compared with the aromatic precursor route, glucose is widely available, inexpensive, and more readily integrated into standardized fermentation processes. Its major limitation, however, is the extended pathway length. Vanillin biosynthesis from glucose requires the coordinated operation of central carbon metabolism, the shikimate pathway, and aromatic amino acid biosynthesis, and is therefore frequently constrained by insufficient precursor supply, limited cofactor regeneration, and strong competition from intermediate metabolism [20]. Current strategies to improve this route mainly include:

(i) Relieving feedback inhibition in aromatic amino acid biosynthesis

(ii) Enhancing tyrosine or upstream precursor supply

(iii) Optimizing hydroxylation and methylation steps; and

(iv) Blocking byproduct pathways leading to vanillyl alcohol and vanillic acid.

For instance, in E. coli, suppression of vanillyl alcohol/vanillic acid formation, reinforcement of tyrosine supply, and improvement of NADPH and SAM regeneration increased the vanillin titer to 279.17 mg/L, which was further improved to 465.81 mg/L through a co-culture strategy [21]. These results indicate that the principal technical challenge of the glucose route lies in coordinating carbon flux between central metabolism and aromatic secondary metabolism, thereby minimizing flux loss along the extended biosynthetic pathway.

Host Selection and Engineering Strategies for Vanillin Biomanufacturing

Host selection defines the engineering boundaries of vanillin biomanufacturing [22]. This is largely because vanillin, as a reactive aromatic aldehyde, can impair both cell growth and metabolic homeostasis [23].

Accordingly, chassis evaluation should not rely on a single criterion, but rather consider at least five factors:

(i) product tolerance;

(ii) The ease of genetic manipulation

(iii) Compatibility with modular pathway assembly

(iv) Intrinsic aromatic metabolic capacity; and

(iv) Adaptability to bioprocess engineering.

At present, vanillin-producing chassis can be broadly classified into two groups:

(i) model microorganisms, represented by E. coli, S. cerevisiae, and P. putida, whose major advantages lie in mature genetic tools, well-characterized metabolic networks, and suitability for modular pathway construction; and

(ii) non-model microorganisms, represented by Amycolatopsis, which display higher intrinsic tolerance to aromatic substrates and vanillin itself and are therefore more compatible with high-level accumulation and process scale-up [24].

Model microorganisms provide highly programmable platforms for vanillin pathway engineering, but three major constraints remain [25]. First, product tolerance is often insufficient, because vanillin, as a reactive aromatic aldehyde, perturbs cellular physiology and metabolic stability [26]. Second, the product is readily degraded, since hosts with strong aromatic metabolic capacity frequently convert vanillin further to vanillyl alcohol or other byproducts, thereby reducing net accumulation [27]. Third, precursor limitation and feedback inhibition remain major bottlenecks. Vanillin biosynthesis in these hosts typically requires integration of the shikimate pathway, aromatic amino acid supply, hydroxylation and methylation steps, and is therefore constrained by insufficient precursor flux and endogenous regulatory control. To address these limitations, several strategies have been developed [28].

One approach is to employ resting cells for non-growing bioconversion: under optimized substrate and biomass concentrations, E. coli achieved a vanillin titer of 2.52 g/L with a molar yield of 70.6% [29].

A second strategy is to block degradation pathways: genomic and functional analyses identified PP_2426 in P. putida as encoding a reductase involved in the conversion of vanillin to vanillyl alcohol; deletion of this gene reduced the vanillyl alcohol byproduct fraction from 17% to 1% [30]. A third strategy is to overexpress key pathway genes and relieve feedback inhibition: in S. cerevisiae, integration of sam8, CYP199A2, comt, fcs, and ech, together with the introduction of the feedback-resistant mutants ARO4K229L and ARO7G141S, increased the vanillin titer to 700 μg/L [31].

In contrast, non-model microorganisms are distinguished by their intrinsic tolerance and process compatibility, but their engineering remains limited by three major factors [32]. First, genetic manipulation is often difficult, because these organisms generally exhibit low transformation efficiency for exogenous DNA, poor homologous recombination efficiency, and a limited range of selectable antibiotic markers. Second, their genetic toolboxes remain underdeveloped, with relatively few standardized expression parts and regulatory elements available for metabolic engineering. Third, their metabolic pathways are less programmable, because the underlying regulatory networks have not yet been systematically characterized, which restricts rational strain design [33,34] Several targeted strategies have been proposed to address these limitations.

One is the development of high-efficiency genome editing tools for non-model hosts: in Amycolatopsis, establishment of a CRISPR-

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Cas12a system enabled deletion of the byproduct-related genes vdh and phdB, reducing vanillic acid accumulation from 2.45 g/L to 0.15 g/L35.

A second strategy is to expand the genetic engineering toolbox for these hosts: based on the constitutive promoter PermE*, the expression plasmid p6permE was constructed, and overexpression of ech and fcs increased the vanillin titer of the engineered strain to 22.3 g/L after process optimization. A third strategy is to analyze host-specific metabolic features in order to identify regulatory bottlenecks: RT-PCR analysis showed that the adaptation phase observed in Amycolatopsis sp. ATCC 39116 during early vanillin production was associated with ferulic acid-induced expression of the key gene ech [36].

Overall, model and non-model microorganisms represent two complementary engineering logics in vanillin biomanufacturing [37]. Model hosts offer superior programmability and are better suited for pathway design, modular assembly, and mechanistic analysis, whereas non-model hosts provide higher intrinsic tolerance and stronger process compatibility for vanillin accumulation [38]. Future progress will depend not only on improving individual hosts, but also on narrowing the gap between designability and production robustness through integrated development of genetic tools, regulatory understanding, and process-oriented strain engineering [39].

Conclusions and Perspectives

From the current landscape of substrate routes, bioconversion of ferulic acid remains the most mature process for vanillin production. The development of systems metabolic engineering has, in parallel, accelerated the construction of engineered production strains. Among these, model microorganisms such as E. coli, P. putida, and S. cerevisiae offer high metabolic programmability for modular design, pathway reconstruction, and substrate expansion, whereas non-model chassis represented by Amycolatopsis provide higher product tolerance and greater industrial relevance. In contrast, lignin- and lignocellulose-derived routes, although attractive in terms of feedstock sustainability and compatibility with integrated biorefinery concepts, are still constrained by feedstock heterogeneity, insufficient selectivity in depolymerization, and the high cost of downstream separation [40].

Four directions merit particular attention in future studies.

First, systematic elucidation and targeted engineering of host tolerance mechanisms remain necessary. Vanillin toxicity has been repeatedly shown to affect membrane homeostasis, redox balance, and overall cellular metabolism; however, most current studies still rely primarily on process-level mitigation, with limited efforts devoted to transporter engineering, membrane lipid remodeling, stress-regulatory networks, or aldehyde detoxification mechanisms [41].

Second, metabolic engineering should move beyond local pathway strengthening toward coordinated network-level optimization. Current evidence indicates that overexpression of fcs and ech alone is insufficient to further improve vanillin biosynthesis; more effective strain development will require integrated strategies that simultaneously suppress byproduct formation, enhance precursor supply, improve cofactor regeneration, and facilitate product export [42].

Third, bioprocess optimization should be regarded as an integral part of vanillin production systems. For an aromatic aldehyde with pronounced product toxicity, in situ adsorption, fed-batch operation, and reaction–separation coupling are critical not only for increasing the overall titer, but also for maintaining process stability [43].

Fourth, the compatibility of low-cost renewable feedstocks will define the future industrial boundary of vanillin biomanufacturing. Whether through efficient release of ferulic acid from agricultural by-products or selective funneling of lignin-derived aromatic monomers, the extent to which feedstock pretreatment can be matched with chassis performance will directly determine process economics [44]. Taken together, vanillin biomanufacturing is likely to evolve toward an integrated production framework that combines feedstock pretreatment, aromatic monomer funneling, microbial cell factory conversion, and online product recovery.

Competing interests

The authors declare no competing financial interests.

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