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Metabolic Engineering of Yeast for Enhanced Production of Terpenoid-Based Biofuels

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ABSTRACT

Background: Terpenoid hydrocarbons such as farnesene, bisabolene, amorphadiene, and limonene are promising drop-in biofuel precursors, and yeast is the leading chassis for their microbial production via the mevalonate pathway. Objective: This narrative review synthesizes published metabolic engineering strategies used to raise terpenoid titers in Saccharomyces cerevisiae and Yarrowia lipolytica. Methods: Peer-reviewed studies describing precursor-supply enhancement, pathway pull, and competing-flux blocking were identified and organized within a push-pull-block framework; no new experiments were performed. Findings: Deregulated HMG-CoA reductase, rebalanced central carbon and cofactor metabolism, dynamic and subcellularly targeted control of squalene synthase (ERG9), and CRISPR/Cas9-enabled multiplex genome engineering together improved titers from milligram-per-liter shake-flask levels to industrial farnesene production exceeding 130 g/L, with intermediate advances documented for amorphadiene, santalene, and limonene in both yeast hosts. Conclusions: Two decades of incremental, individually validated strain modifications have converged into a reusable engineering framework; further titer gains for fuel-relevant terpenoids will likely depend on integrating dynamic regulation, compartmentalization, and fed-batch process design already demonstrated separately across the literature.

Keywords: *terpenoid biofuels; metabolic engineering; yeast; mevalonate pathway; Saccharomyces cerevisiae*

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Introduction

Terpenoids constitute the largest and most structurally diverse class of natural products, and several members—farnesene, bisabolene, amorphadiene, and limonene among them—possess energy densities and combustion properties that make them attractive as "drop-in" advanced biofuels or as precursors that can be hydrogenated into diesel- and jet-fuel-range hydrocarbons [1,2]. Because terpenoid backbones share the universal five-carbon isoprenoid units synthesized via the mevalonate (MVA) pathway, the engineering lessons first developed for pharmaceutical isoprenoids such as artemisinin have become the template for biofuel-precursor strain construction. *Saccharomyces cerevisiae* remains the dominant chassis for this work owing to its genetic tractability, native and highly active MVA pathway, and long industrial fermentation record, while the oleaginous yeast *Yarrowia lipolytica* has emerged as a complementary host whose intrinsically high acetyl-CoA and NADPH flux favors lipophilic terpenoid accumulation [3,4].

The single greatest obstacle to economically viable microbial terpenoid biofuels is titer: whereas fine chemicals and pharmaceutical intermediates can justify milligram-to-gram-per-liter production costs, biofuel precursors must ultimately be produced at tens of grams per liter to approach cost parity with petroleum-derived fuels. Achieving such titers requires simultaneously (i) increasing carbon and cofactor flux into the MVA pathway ("push"), (ii) redirecting flux at the farnesyl diphosphate (FPP) branch point toward the terpenoid synthase of interest ("pull"), and (iii) restricting flux loss into competing native pathways, chiefly the sterol pathway consuming FPP via squalene synthase (ERG9) ("block")—the so-called push-pull-block framework that now organizes most reported strain designs [5]. This framework was first crystallized and named in the context of taxadiene overproduction in bacteria, but its constituent logic—relieve feedback-regulated bottlenecks, amplify the terminal committed enzyme, and suppress competing consumption of the shared precursor pool—maps directly onto decades of yeast MVA pathway engineering carried out independently and, in several cases, well before the term itself was coined [2]. This review synthesizes two

decades of published metabolic engineering studies that established and refined this framework in yeast, traces its application to specific biofuel-relevant terpenoids, and summarizes the titers so far reported in the primary literature. No new experimental work is presented; all data and strategies discussed are drawn from previously published, peer-reviewed studies, and the reported titers should be read as reflecting the specific strain backgrounds, media, and cultivation modes of the individual publications rather than as directly interchangeable benchmarks.

Engineering Precursor Supply and Enzyme Bottlenecks ("Push")

Flux into the MVA pathway in yeast is rate-limited principally by 3-hydroxy-3-methylglutaryl-CoA reductase (HMG-CoA reductase, encoded by *HMG1*/*HMG2*), and truncation or overexpression of the catalytic domain of this enzyme, removing its sterol-mediated feedback degradation, was among the earliest and most broadly reused interventions in the field. Overexpression of a truncated, feedback-resistant HMG-CoA reductase was shown more than two decades ago to markedly increase squalene accumulation in engineered *S. cerevisiae*, establishing HMGR deregulation as a cornerstone push strategy still used in essentially every subsequent terpenoid-producing strain [6]. Complementary work rerouted central carbon metabolism itself: replacing the native, NADH-generating pyruvate dehydrogenase bypass with pathways that better balance acetyl-CoA and NADPH supply increased sesquiterpene precursor availability [7], while systems-level, in-silico-guided redesign identified additional non-obvious gene targets—including disruption of mitochondrial α-ketoglutarate dehydrogenase and heterologous expression of ATP-citrate lyase—that improved cytosolic acetyl-CoA and terpenoid titers when validated experimentally [8]. A genome-wide carotenoid-based phenotypic screen of the yeast deletion collection subsequently uncovered numerous previously unannotated genes influencing isoprenoid flux, considerably expanding the catalogue of validated push targets beyond the canonical MVA enzymes [9]. In parallel, model-driven combinatorial engineering of precursor supply together with cofactor (NADPH) regeneration enzymes was used to systematically raise sesquiterpene (cubebol) titers in a stepwise, quantitatively predictable manner [10]. Because many terpenoid synthases and their substrates are cytotoxic or poorly soluble in the cytosol, an important refinement of the push strategy has been subcellular re-routing of MVA-pathway enzymes into peroxisomes or mitochondria, which increases local precursor concentration while limiting exposure of the rest of the cell to toxic intermediates and has proven effective for several plant terpenoids expressed in yeast [11]. This compartmentalization logic complements, rather than replaces, classical push engineering: relocating a truncated HMG-CoA reductase or a terpenoid synthase to an organelle with its own acetyl-CoA and NADPH pools effectively creates a second, semi-independent precursor-generating compartment, reducing competition with cytosolic sterol biosynthesis for the same enzyme pool and substrate. Collectively, these push-oriented interventions—feedback-resistant HMG-CoA reductase, rebalanced central carbon and cofactor metabolism, genome-scale identification of auxiliary flux-controlling genes, and subcellular re-routing—now form a standard, largely interchangeable engineering module that is combined with pathway-specific pull and block modifications depending on the terpenoid target.

Table 1: Representative push-pull-block metabolic engineering strategies applied to yeast terpenoid pathways.

Strategy category	Representative gene target(s)	Effect reported	Key reference(s)
Push: precursor supply	Truncated, feedback-resistant HMG-CoA reductase (HMG1)	Increased squalene/isoprenoid precursor accumulation	Polakowski et al. 1998
Push: central carbon/cofactor rebalancing	Pyruvate dehydrogenase bypass enzymes	Increased acetyl-CoA and NADPH supply for isoprenoid synthesis	Shiba et al. 2007
Push: genome-scale target discovery	Deletion collection screen (multiple genes)	Identified novel genes improving isoprenoid/carotenoid output	Ozaydin et al. 2013
Push: subcellular compartmentalization	Peroxisomal/mitochondrial targeting of MVA enzymes	Increased local precursor pools, reduced cytotoxicity	Farhi et al. 2011
Pull: terpenoid synthase expression	Amorphadiene synthase, farnesene/bisabolene synthases	Redirected FPP flux to target terpenoid	Ro et al. 2006; Peralta-Yahya et al. 2011
Block: static squalene synthase repression	ERG9 (methionine-repressible promoter)	Reduced competing sterol flux	Ro et al. 2006
Block: dynamic squalene synthase control	ERG9 (growth-phase-dependent promoters)	Improved biomass and terpenoid titer versus constitutive repression	Westfall et al. 2012; Yuan and Ching 2015
Pull-block co-tuning	ERG20 and ERG9 dynamic co-expression	Balanced FPP/GPP supply against consumption	Callari et al. 2018
Multiplex genome engineering	Simultaneous multi-locus editing	Accelerated combination of push/pull/block edits	Jakociunas et al. 2015

Redirecting and Blocking Flux at the FPP Branch Point ("Pull-Block")

Farnesyl diphosphate sits at the metabolic branch point between sterol biosynthesis (essential for viability) and heterologous sesquiterpenoid synthesis, making squalene synthase (ERG9) the principal "block" target. Early work producing the antimalarial precursor artemisinic acid combined heterologous expression of amorphadiene synthase and a cytochrome P450 with downregulation of ERG9, together with HMG-CoA reductase deregulation, to give engineered yeast capable of secreting the acid at titers on the order of 100 mg/L in shake-flask culture, a proof of concept that catalyzed the entire field [12]. Because constitutive ERG9 repression impairs growth by starving the cell of ergosterol, later strategies replaced static knockdown with dynamic, growth-phase-dependent control: methionine-repressible or glucose/ethanol diauxic-shift promoters were used to fully express ERG9 during a growth phase and repress it only during a subsequent production phase,

substantially improving both biomass accumulation and final amorphadiene titer relative to constitutive downregulation approaches [13,14]. Stress- and quorum-responsive promoters have similarly been harnessed to autonomously time the transition from growth to production without exogenous inducers, a strategy validated for isoprenoid pathways in bacteria and subsequently adapted conceptually to yeast dynamic pathway regulation [15]. Related work has shown that simultaneous dynamic tuning of both ERG20 (farnesyl diphosphate synthase) and ERG9 expression, rather than ERG9 alone, further improves flux into heterologous diterpenoids such as casbene by better balancing FPP/GPP supply against consumption [16]. Multiplexed, single-step genome engineering using CRISPR/Cas9 has made it practical to combine numerous push, pull, and block modifications simultaneously in one transformation, dramatically accelerating the design-build-test cycle for mevalonate pathway strains [17]. Together, these push-pull-block refinements culminated in the fully engineered artemisinin production strain, in which more than a dozen genetic modifications spanning the MVA pathway, cytochrome P450 chemistry, and cofactor engineering were integrated to enable industrial-scale semi-synthetic artemisinin manufacture [18]. Although artemisinin itself is not a fuel molecule, the strain construction logic used to reach that milestone—layering push, pull, and block modifications sequentially and verifying flux improvements at each step before adding the next—has been adopted essentially unchanged by subsequent biofuel-precursor engineering efforts, making the artemisinin programme the de facto engineering blueprint for the terpenoid biofuel strains discussed below.

Case Studies in Biofuel-Relevant Terpenoids and Titer Progress

Applying this cumulative toolkit to biofuel-relevant molecules rather than pharmaceutical intermediates has produced some of the highest terpenoid titers reported to date. Sesquiterpene olefins bisabolene and farnesene were identified and produced heterologously as diesel- and jet-fuel-precursor candidates, with subsequent hydrogenation yielding a fungible diesel-range fuel, establishing the biofuel relevance of the sesquiterpene synthase toolbox [1]. Industrial-scale rewriting of yeast central carbon metabolism—rebalancing glycolytic, pentose phosphate, and MVA pathway flux together with ERG9 control—enabled farnesene production at commercially relevant titers exceeding 130 g/L, demonstrating that push-pull-block principles established in laboratory strains can translate to industrial fermentation performance [19]. Fed-batch, respiratory-quotient-controlled cultivation further improved farnesene and α-santalene titers over shake-flask benchmarks, underscoring that bioprocess optimization is as consequential as genetic design once a pathway is functional [20,21]. The oleaginous host *Y. lipolytica* has been engineered analogously for α- and β-farnesene and, separately, for amorphadiene via debottlenecking of its native MVA pathway, exploiting its naturally lipogenic acetyl-CoA flux as an alternative push mechanism to that used in *S. cerevisiae* [4,22,3]. Monoterpenes such as limonene remain comparatively difficult targets owing to volatility and cytotoxicity, but combinatorial engineering strategies in *Y. lipolytica* have recently improved limonene synthesis substantially over earlier benchmarks [23]. Screening of farnesene synthase homologs combined with pathway balancing has likewise improved α-farnesene titers in *S. cerevisiae* [24], while heterologous expression in the alternative host *Pichia pastoris* has extended the push-pull-block paradigm to sesquiterpenoids such as nootkatone, illustrating the generality of the approach across yeast chassis [25]. Comprehensive reviews of yeast fermentation strategies for terpenoids reinforce that titer, yield, and productivity must be co-optimized with genetic design to approach the volumetric productivities needed for fuel-scale economics, and that batch, fed-batch, and continuous cultivation modes each impose distinct trade-offs on strain performance that are not captured by shake-flask screening alone [26]. Foundational carotenoid pathway work, including successive transformation with carotenogenic genes to achieve high-level β-carotene production, further demonstrates that terpenoid pathway capacity in yeast, once precursor supply and flux-blocking are addressed, can reach substantial titers even for downstream, highly oxidized isoprenoid products, and that carotenoid pathways can serve as convenient visual reporters for optimizing the same upstream MVA modules subsequently reused for colorless biofuel-precursor terpenoids [27]. Taken together, the case studies summarized in Table 1 and Table 2 show a clear, if uneven, trajectory: titers for oxidized, pharmaceutical-grade sesquiterpenoids plateaued in the tens of grams per liter by the early 2010s, while titers for simpler, more volatile hydrocarbon terpenoids relevant to fuels have taken longer to approach comparable levels, reflecting the additional toxicity and volatility challenges that fuel-like terpenoids pose relative to their oxygenated pharmaceutical counterparts.

Figure 1: Reported titers of representative isoprenoid intermediates and terpenoid biofuel precursors in engineered Saccharomyces cerevisiae across selected published studies, illustrating the order-of-magnitude gains achieved between early proof-of-concept strains and industrially optimized fed-batch production.

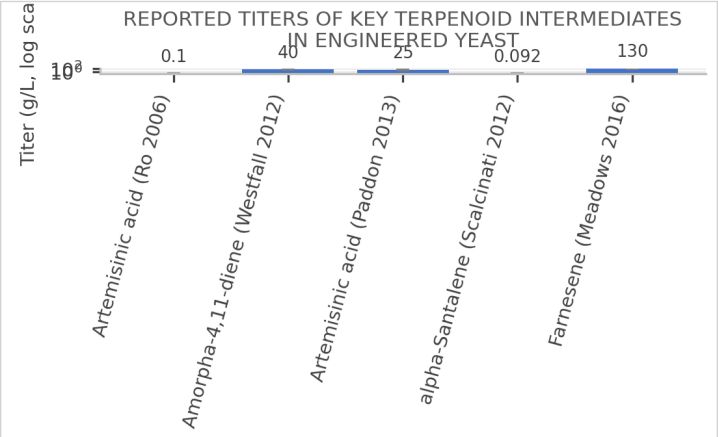
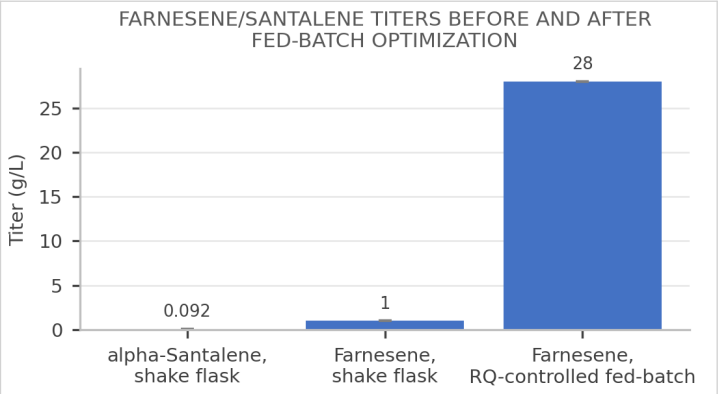


Figure 2: Effect of moving from shake-flask to respiratory-quotient-controlled fed-batch cultivation on sesquiterpene titers in engineered Saccharomyces cerevisiae, showing that bioprocess optimization can amplify titer gains achieved through strain engineering alone.



Conclusion

Two decades of published metabolic engineering studies in *Saccharomyces cerevisiae* and, increasingly, *Yarrowia lipolytica* have converged on a coherent push-pull-block engineering framework for terpenoid production: deregulating HMG-CoA reductase and rebalancing central carbon and cofactor metabolism to push flux into the mevalonate pathway, expressing and often protein-engineering terpenoid synthases to pull flux toward a target molecule, and dynamically or subcellularly restricting competing sterol biosynthesis to block flux loss. Applied initially to the antimalarial precursor artemisinin, this framework has since been redirected toward biofuel-relevant sesquiterpenes and monoterpenes—farnesene, bisabolene, amorphadiene, santalene, and limonene—yielding titers that in the best documented industrial case exceed 130 g/L. Closing the remaining gap between laboratory and biofuel-scale economics will likely depend less on discovering new individual gene targets than on the continued integration of dynamic regulatory circuits, multiplexed genome engineering, subcellular compartmentalization, and process-level fed-batch optimization already validated, individually, across the literature reviewed here.

Table 2: Selected terpenoid biofuel precursors produced in engineered yeast hosts.

Terpenoid	Host organism	Reported titer / outcome	Reference
Farnesene	Saccharomyces cerevisiae (industrial fed-batch)	>130 g/L	Meadows et al. 2016
Amorpha-4,11-diene	Saccharomyces cerevisiae	~40 g/L	Westfall et al. 2012
Artemisinic acid	Saccharomyces cerevisiae	~25 g/L (full semi-synthetic pathway)	Paddon et al. 2013
alpha-Santalene	Saccharomyces cerevisiae (shake flask)	~92 mg/L	Scalcinati et al. 2012
Bisabolene	Saccharomyces cerevisiae / Escherichia coli	Sub-gram-per-liter, diesel-precursor proof of concept	Peralta-Yahya et al. 2011
alpha-/beta-Farnesene	Yarrowia lipolytica	Gram-per-liter-scale, lipid-flux-based production	Liu et al. 2019; Shi et al. 2021
Limonene	Yarrowia lipolytica (combinatorial engineering)	Substantially improved over earlier low benchmarks	Park et al. 2024
Nootkatone	Pichia pastoris	De novo sesquiterpenoid production established	Wriessnegger et al. 2014

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Butkute E conceived the review, conducted the literature search, and drafted the manuscript. Liepa K contributed to the literature screening and technical framing and critically revised the manuscript for important intellectual content. Chevalier M contributed additional context and approved the final version for submission.

Ethics Statement

Not applicable. This is a narrative review of previously published literature and did not involve new experimental data, human participants, or animal subjects.

Data Availability

No new data were generated or analyzed for this review. All sources synthesized are cited in the reference list and are available through their original publishers.

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