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INHIBITORS OF LIGNOCELLULOSIC BIOMASS: MECHANISMS OF ACTION AND IMPACT ON THE EFFICIENCY OF BIOLOGICAL HYDROGEN PRODUCTION (REVIEW)

Abstract: *The work is devoted to the study of inhibitory factors limiting the yield of biohydrogen during the processing of lignocellulosic biomass (LCB). In this context, dark fermentation is considered one of the most promising biological methods for producing hydrogen, since it does not require an external energy source, is compatible with modern reactor technologies and allows the use of a wide range of substrates. The main barrier to its industrial application remains the accumulation of toxic compounds formed during the pre-*

treatment of LCB and during fermentation. The work summarizes information on the composition and action of the main inhibitors. The results of the analysis showed that the yield of H_2 during TF reaches 2-4 mol/mol sugar (maximum ~3.8 mol/mol hexose), but drops significantly in the presence of: (i) furans (furfural 0.03-8.23 g/l; 5-HMF 0.09-1.59 g/l), (ii) phenolic compounds of lignin (vanillin, syringaldehyde), (iii) organic acids (formic, acetic, levulinic), (iv) inorganic ions and heavy metals (Zn, Cu, Cr, Ni, etc.), (v) ammonia and sulfates. Dose-dependent effects and changes in microbial community composition are also discussed, such as the effect of pH, the reduction in Clostridium abundance due to furfural, or the increase in Clostridium and Ruminococcaceae abundance with the addition of 5-HMP. Thus, understanding the mechanisms of action of inhibitors and finding ways to reduce their impact are key areas for improving the efficiency of dark fermentation and its implementation as a sustainable technology for converting lignocellulosic biomass into biohydrogen.

Key words: *dark fermentation, biohydrogen, lignocellulosic biomass, inhibitors, furan compounds, phenolic compounds, volatile fatty acids, heavy metals.*

Introduction

In recent decades, the production of molecular hydrogen (H_2) using lignocellulosic biomass (LCB) has attracted considerable attention from researchers. Both primary plant resources - wheat straw, rice husks and straw, herbaceous vegetation - and agro-industrial waste, including sugar beet pulp, sunflower residues, rapeseed and other oilseeds, are studied as substrates [1-3]. The potential of this direction is confirmed by the scale of available raw materials: the annual global volume of LCB is estimated at more than 220 billion tons [4, 5], which makes it a virtually inexhaustible and renewable source for biotechnological processing.

Among all alternative energy sources, molecular hydrogen is considered the most promising, since it has a high specific heat of combustion, is environmentally friendly (when used, only water is formed without CO_2 emissions), can be produced from agricultural waste and lignocellulosic biomass, facilitates the utilization of by-products and the creation of closed bioeconomy cycles, is used in the food industry for the hydrogenation of fats and oils [6], saturation of water and drinks in order to give them antioxidant properties [7], extending the shelf life of meat, dairy and fat products, and also ensures the energy autonomy of enterprises and a reduction in the carbon footprint of products [8, 9].

According to Jain R. et al. (Fig. 1) [9], biological pathways for producing hydrogen are divided into three main directions: fermentation processes, biophotolysis and bioelectrochemical systems. Fermentation methods include dark fermentation and photofermentation, carried out by mesophilic and thermophilic microorganisms, as well as sulfur-containing and sulfur-independent phototrophic bacteria. Biophotolysis, in turn, is divided into direct and indirect and is implemented with the participation of microalgae and cyanobacteria. Bioelectrochemical systems are represented by microbial electrolysis cells, the functioning of which is ensured by exoelectrogenic microorganisms. Each of these approaches is based on specific biochemical reactions, the end result of which is the formation of molecular hydrogen [9].

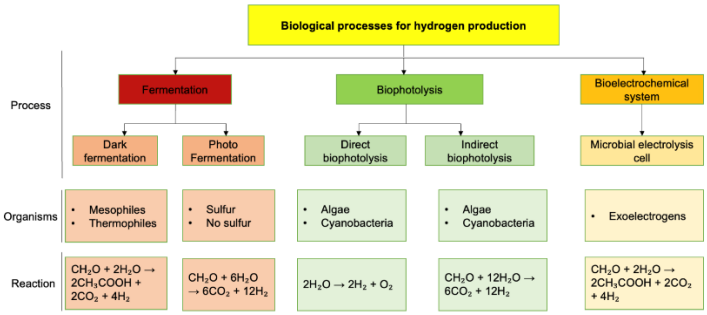

Figure 1. Brief description of processes, organisms and reactions in biohydrogen production [9]

It is worth noting that each of these technologies has its own advantages and difficulties depending on its feasibility, sustainability and energy efficiency.

Photobiological approaches to hydrogen production, including biophotolysis, appear attractive because they use sunlight and water. However, their efficiency is limited by low H_2 yields and the high sensitivity of hydrogenases to oxygen.

In contrast, dark fermentation exhibits a higher hydrogen production rate, does not require an external energy source, and can be implemented using a wide range of substrates, including LCB.

In addition, TF is compatible with existing reactor technologies, making it the most practical method for biological hydrogen production [10, 11].

The yield of hydrogen in TF reaches up to 3.8 mol H_2/mol hexose (using Bacillus, Clostridium, Thermotoga, etc. cultures), while in photofermentation it is limited to 0.5-2 mol/mol. It is believed that the theoretical yield limit is 2-4 mol H_2/mol sugar depending on the by-products – acetic or butyric acid. The highest yield values are achieved using simple carbohydrates, while lignocellulosic materials require special pre-treatment [12, 13].

Despite the obvious advantages of dark fermentation and the wide availability of lignocellulosic biomass, the key problem holding back industrial implementation of the technology remains the low yield of hydrogen. As numerous studies in recent years have shown, the main reason for this is the formation and accumulation of inhibitory compounds that arise during the pre-treatment of lignocellulosic biomass and the fermentation itself.

This review study systematically analyzes and summarizes various inhibitory factors affecting DF hydrogen production. Among them are:

• inorganic inhibitors: heavy and light metal ions, ammonia, sulfates and hydrogen.
• organic inhibitors: volatile fatty acids, furan derivatives and phenolic compounds.
• biological inhibitors: bacteriocins and thiosulfinates.

Inhibitor concentrations and mechanisms of action are discussed in detail. Strategies to reduce their impact are also presented and analyzed. The article suggests directions for further research aimed at scaling up and commercializing the DF hydrogen production technology [14-16].

1. Main inhibitors of dark fermentation

Despite the advantages of TF, the key problem remains the low yield of H2 when using lignocellulosic hydrolysates. This is due to the accumulation of by-products formed both at the pre-treatment stage and during the fermentation itself. The most common inhibitors include furan derivatives (furfural, 5-hydroxymethylfurfural), phenolic compounds, organic acids, and inorganic substances - heavy metals, ammonia and sulfates (Fig. 2) [17-20].

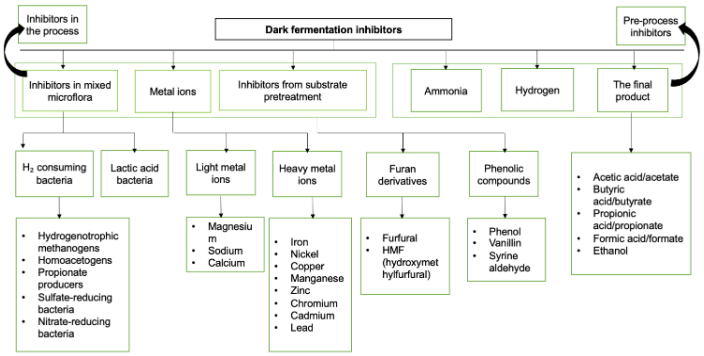

Figure 2 – Inhibitors of DF biohydrogen production [17-20]

The main groups of dark fermentation inhibitors that can act at different stages of the process – from the composition of the initial substrate and microbial community to the accumulation of final products – can be classified as follows:

Inhibitors in mixed microflora are H2-consuming microorganisms (methanogens, homoacetogens, propionate producers, sulfate- and nitrate-reducing bacteria), as well as lactic acid bacteria, which compete for substrates and shift metabolism.

Metal ions – light metals in excess cause osmotic stress, heavy metals block enzymes and damage cells. Inhibitors from pre-treatment of substrates – furan derivatives inhibit glycolysis, phenolic compounds damage membranes and reduce cell viability.

Additional inhibitors – ammonia and its derivatives cause nitrogen stress; high H_2 levels inhibit its further formation; accumulation of organic acids and ethanol reduces pH and inhibits producers. The end products (acetic, butyric, propionic and formic acids, ethanol) when accumulated cause self-suppression of the process due to a decrease in pH and toxicity to producers [21, 22].

1.1 Inhibition by lactic acid bacteria

Lactic acid bacteria are well known for their antimicrobial properties and are able to partially or completely inhibit the process of dark fermentation. The mechanisms of suppression of the activity of hydrogen-producing microorganisms by lactic acid bacteria include several pathways:

(a) acidification of the environment due to the formation of lactic acid;

(b) production of antimicrobial compounds, such as reactive oxygen species (e.g. hydrogen peroxide);

(c) secretion of polypeptide antibiotics – bacteriocins [23].

LAB species such as Lactobacillus sp. produce lactic acid as the primary product of fermentation of carbohydrate-containing substrates, although they can also utilize amino acids and nucleotides. When mixed microflora are used in dark fermentation (DF) processes, the presence of LAB acts as a factor suppressing biohydrogen producers (HPB) by competing for substrates or releasing toxins. LAB compete with HPB for pyruvate and produce lactic acid at the expense of biohydrogen formation, which leads to a decrease in its yield. In addition, LAB produce toxins that have a damaging effect on HPB, as a result of which the process is inhibited and biohydrogen production is reduced.

As for lactic acid itself, its production increases with increasing organic load or substrate concentration. Some studies report an inhibitory effect of lactic acid on dark fermentative H_2 production. Crigler J et al. recorded a decrease in biohydrogen yield from 0.071 to 0.049 m^3/kg volatile solids with an increase in lactic acid concentration from 2345.6 to 4425.6 mg/L [24]. However, Wang et al. noted that micro-addition of lactic acid, on the contrary, resulted in an increase in biohydrogen production to 138.9 ml/g dry matter compared to 101.5 ml/g without the additive [25]. Thus, unlike LAB, the effect of lactic acid itself on DF hydrogen production requires further study before definitive conclusions can be drawn.

1.2 Inhibitors formed during pretreatment of substrates

Pretreatment of lignocellulosic materials is an important step in the transformation of biomass into fermentable sugars. It prepares the material for the hydrolysis stage, which breaks down the lignin and hemicellulose, releasing the cellulose inside [26, 27].

Pretreatment can be applied to both inoculum and substrates. While inoculum pretreatment aims to enrich H_2 producers and suppress H_2 consumers, substrate pretreatment aims to destroy the lignin «barrier» of lignocellulosic materials, release cellulose molecules into solution, destroy the crystalline structure of cellulose and promote depolymerization, which ultimately improves hydrolysis and biohydrogen production [28].

In addition to these positive aspects, pre-treatment of lignocellulose also results in the formation of toxic by-products such as phenolic compounds, furan derivatives and weak acids, which can inhibit the dark fermentation process in biohydrogen production [29-31].

Furan derivatives. Acid hydrolysis, which is the most common method, can lead to the formation of furan derivatives, including 5-hydroxymethylfurfural (5-HMF) and furfural [11].

Furan derivatives are formed mainly as a result of dehydration of pentoses and hexoses. According to the literature, the concentration of furans formed during substrate pretreatment varies from 0.12 to 9.82 g/l (furfural – 0.03-8.23 g/l, 5-HMF – 0.09-1.59 g/l). Such concentrations can have an inhibitory effect on hydrogen production. With a furan derivative content of about 1 g/l, hydrogen production decreases by 17.9-76.05%, and bacterial growth is not observed at concentrations up to 2.0 g/l. In a continuous hydrogen production system, furfural at a concentration of 1-4 g/l reduced hydrogen yield by 21-62% compared to the control group [32].

However, the inhibitory effect of furans is highly dependent on the inoculum used. Thus, in the case of anaerobic reactor sludge, furfural at concentrations of 0.10, 0.50, and 1.00 g/L was completely decomposed and, therefore, had no inhibitory effect on hydrogen production. It is possible that some members of the microbial consortium are less sensitive to furans, allowing the entire community to overcome this limitation. In addition, the addition of HMF can lead to an increase in the proportion of bacteria of the genus Clostridium and the family Ruminococcaceae. This confirms that the effect of furans is highly dependent on the inoculum.

The mechanisms of inhibition by furans can be diverse. It has been reported that furans are capable of changing the structure of the microbial community, inducing the formation of reactive oxygen species, destroying DNA and inhibiting the synthesis of proteins and RNA, slowing down cell growth, disrupting the work of glycolytic and enzymatic enzymes, and reducing the permeability of cell membranes. Also, the main mechanism of inhibition by furans is the disruption of the synthesis of glycolytic enzymes and the suppression of biomass growth [33-35].

Phenolic compounds. Phenolic compounds are formed during the degradation of lignin during pretreatment or acid hydrolysis of biomass, and the most typical representatives of this group are vanillin and syringaldehyde. These substances have a destructive effect on the cell membranes of

microorganisms: they change their structure, increase permeability or directly damage the lipid layer. As a result, the cytoplasm loses its protective barrier, becoming vulnerable to extracellular toxins. Such a violation of membrane integrity is accompanied by a leakage of intracellular components (proteins, potassium and phosphate ions), which leads to a decrease in the growth rate of bacteria, inhibition of metabolic activity and changes in fermentation pathways [36].

Aromatic carboxylic acids, which also belong to phenolic compounds, attract special attention of researchers. Among them are phenolic acids (for example, ferulic and 4-hydroxybenzoic) and non-phenolic aromatic acids, such as cinnamic. They are usually considered in a single row with other phenolic compounds, rather than with aliphatic acids, which is due to their structural features. Thus, the presence of S-(syringyl), G-(guaiacyl) and H-(4-hydroxyphenyl) fragments indicates their origin from lignin or products of hydrolysis of esterified phenols. Despite the fact that their concentrations in lignocellulose hydrolysates are relatively low compared to aliphatic acids, they demonstrate a significantly more pronounced inhibitory effect. For example, up to 6.6 mg/l (0.033 mM) of ferulic acid was detected in corn stover hydrolysates, and up to 210 mg/l in sugarcane bagasse hydrolysates [37].

Thus, phenolic compounds, including aromatic acids, even in low concentrations are capable of significantly suppressing the growth of microorganisms, slowing down fermentation processes and reducing the yield of biohydrogen. Their combined effect with other inhibitors makes it necessary to develop effective methods for detoxifying hydrolysates to increase the efficiency of bioconversion of lignocellulosic biomass.

1.3 Organic acids

It is known that anaerobic digestion is a complex biochemical process that proceeds through successive stages of hydrolysis, acidogenesis, acetogenesis and methanogenesis. During the stages of hydrolysis and acidogenesis, complex organic substances are broken down into short-chain volatile fatty acids (VFAs), such as acetic, propionic, butyric, lactic and valeric acids. These reactions are catalyzed by acidogenic or fermentative bacteria.

At the acetogenesis stage, organic acids are further converted into acetic acid and hydrogen (H_2), which serve as precursors of methane for methanogenic microorganisms. Acetic acid can be used directly by methanogens, with about 75% of methane being formed from its degradation.

However, excessive accumulation of VFA (i.e. acidification of the environment) causes an imbalance between the acidogenic and methanogenic stages [38, 39].

Organic acids are formed by deep degradation of monosaccharides. At low concentrations, short-chain organic acids may have no effect or even stimulate acidogenic H_2 formation. However, as high levels of organic acids accumulate, the pH decreases, which negatively affects hydrogenase activity and reduces the overall yield of H_2.

The pKa of acetic and butyric acids is 4.75 and 4.82, respectively. At low pH, undissociated volatile fatty acids (VFA) penetrate bacterial cell membranes and dissociate inside the cell (where the pH is close to neutral), releasing protons and lowering the cytosolic pH. The accumulation of protons has a negative effect on bacterial growth and metabolism. To restore normal pH, ATPases pump protons out, spending ATP, which leads to the depletion of cellular energy reserves. Continuation of this process causes the cessation of microbial growth. In addition, the accumulation of VFA anions increases the osmolarity of the cytosol, which leads to the development of turgor pressure and disruption of the integrity of the cell membrane [40].

Volatile fatty acids (VFA). Accumulation of volatile fatty acids (VFA) during processing of lignocellulosic biomass can significantly inhibit the process of anaerobic decomposition, which leads to a decrease in biogas yield. It has been shown that the concentration of VFA affects all stages of anaerobic decomposition, especially hydrolysis and acidogenesis. Inhibition of methanogenic bacteria activity under the influence of VFA is associated with a drop in pH, which causes a loss of activity of acid-sensitive enzymes [41].

In addition, significant amounts of undissociated acids are able to penetrate the cell membranes of microorganisms, destroying macromolecules and disrupting their metabolism. The optimal concentration of VFA for stable metabolic activity is 2000-3000 mg/l.

At a VFA concentration of about 2 g/l, cellulolytic activity is suppressed, which is especially critical for the processing of lignocellulosic biomass. At a concentration above 4 g/l, biogas production is significantly reduced due to the inhibition of glucose fermentation and the slowing down of cellulose hydrolysis. Local accumulation of VFA in a reactor operating on lignocellulosic waste

can lead to disruption of the microbial community structure, which causes inhibition of the process and subsequently leads to its failure [42, 43].

1.4 Inorganic compounds

Inorganic ions present in lignocellulose hydrolysates originate from the lignocellulosic feedstock itself, from chemicals added during pretreatment, conditioning and hydrolysis, and possibly from process equipment .

Addition of salts increases osmotic pressure, which may have an inhibitory effect. At moderate concentrations, it is possible that inorganic ions will enhance ethanol formation similar to aliphatic acids at low doses. The proposed mechanism is an increased cellular demand for ATP due to increased transport across the plasma membrane. Additional ATP is formed due to increased ethanol synthesis, but at the expense of biomass formation [29].

1.5 Inhibition by metals

Microbial cell growth, enzyme activity, and metabolic pathways involved in hydrogen production by bacteria are highly dependent on low concentrations of trace elements. However, elevated concentrations of these metal ions can inhibit hydrogen production during dark fermentation. High metal levels reduce nutrient availability and impair cell membrane function. The degree of inhibition is influenced by factors such as pH, organic matter concentration, and the presence of chelating agents [44-46].

Of particular importance is iron, which is necessary for the functioning of hydrogenase. In the process of enzymatic hydrogen production, ferredoxin, an iron-sulfur protein, plays a key role as an electron carrier, participating in the oxidation of pyruvate to acetyl-CoA and CO_2, as well as in the reduction of protons to molecular hydrogen. Additional iron intake can have a positive effect on the growth of microorganisms and the rate of hydrogen biosynthesis. However, at excessive concentrations, deterioration of the physiological state of cells and a tendency of cultures to form aggregates are observed, which leads to a limitation of mass transfer.

It is known that iron deficiency limits the growth of Clostridium pasteurianum, and a decrease in iron concentration to 5.7 mmol/l leads to a shift in metabolism towards the formation of lactate instead of butyrate, without reducing the yield of hydrogen in continuous culture. With sufficient iron supply (up to 25 mmol/l), Clostridium acetobutylicum exhibits an acidogenic type of metabolism with the dominance of hydrogen as the main product [38].

Inhibitors of dark fermentation of lignocellulosic biomass include Cd, Cr, Zn, Cu, Ni, Pb. Their toxicity for biohydrogen producers is manifested in a decrease in hydrogenase activity and damage to cellular structures.

It was found that the relative toxicity of heavy metals for enzymatic hydrogen production is distributed in the order: Zn > Cu > Cr. It was found that a 50% decrease in the activity of H_2 producers is observed at concentrations of 4.5 mg Zn/l, 6.5 mg Cu/l and 60 mg Cr/l. Other studies have shown that the degree of toxicity can vary and is presented in the sequence: Cu > Ni > Zn > Cr > Cd > Pb. Copper had the greatest inhibitory effect, leading to a 50% decrease in biological activity already at a concentration of 30 mg/l, while lead showed the least effect (>5000 mg/l) [43, 47].

Light metals such as calcium, sodium and magnesium are also essential elements for microbial growth. Moderate concentrations stimulate growth and metabolic activity, while excess causes inhibition and toxic effects. For Clostridium cultures with glucose substrate, it has been established that sodium concentrations in the range of 3,000-20,000 mg/L do not significantly affect hydrogen yield. However, with a significant increase in Na^+ concentration, the osmotic pressure of the medium increases, which can lead to cell inactivation and death. Maintaining sodium concentration below 20 g/L is considered optimal [14, 48].

Calcium plays an important role in the formation of extracellular polysaccharides, biofilm formation, cell granulation and biomass sedimentation. It is also a cofactor of alpha-amylase and proteases, and participates in the structural organization of proteins and the extracellular polymer matrix. Low concentrations of Ca^{2+} improve the processes of adsorption, adhesion and cell proliferation during sediment granulation, and also enhance hydrogen biosynthesis. At concentrations of up to 150 mg/l, calcium does not have an inhibitory effect, providing a hydrogen yield of up to 3.6 mol/mol.

Magnesium (Mg^{2+}) is one of the most common elements in cells and plays a key role in metabolism. It is necessary for the functioning of many enzymes, in particular kinases and phosphatases, and is involved in glycolysis reactions. Mg^{2+} concentrations up to 200 mg/L do not

inhibit hydrogen formation (yield up to 2.84 mol/mol), but at a concentration of 1000 mg/L, a decrease in yield to 1.72 mol/mol is observed [18].

The effect of nickel in low concentrations (up to 0.1 mg/l) does not have an inhibitory effect, which is confirmed by the high yield of hydrogen, exceeding 3 mol/mol.

Strategies for controlling metal inhibition in dark fermentation processes remain poorly understood. Promising approaches include pretreatment methods such as electrodialysis, biosorption, sulfide precipitation, and co-fermentation to reduce the negative impact of metal ions.

1.6 Ammonia inhibition

As mentioned earlier, ammonia can be produced during dark fermentation (DF) as a result of nitrate reduction by nitrate-reducing bacteria (NRB) using H_2 as an electron donor.

Ammonia nitrogen exists as free ammonia (NH_3) or ammonium ions (NH_4^+). Although nitrogen (in the form of NH_3 or NH_4^+) is a nutrient source for bacterial growth, high concentrations of both NH_3 and NH_4^+ have been shown to be toxic and inhibitory to anaerobic digestion processes as well as dark fermentation processes [49].

Among the two forms of ammonia nitrogen (NH_3 and NH_4^+), free or unionized ammonia is considered the major inhibitor because it can easily diffuse across the cell membrane.

When NH_3 penetrates the cell membrane, it reacts with a proton to form NH_4^+, which causes an imbalance in intracellular pH. To compensate for this pH change, the K^+/H^+ antiporter is activated, resulting in an influx of protons and an efflux of potassium ions K^+. The resulting accumulation of NH_4^+ within the cell membrane can cause inhibition of bacterial activity, such as for enzymes involved in methanogenesis.

The concentration of free ammonia depends on the total nitrogen content (TAN), as well as on the pH and temperature of the environment: the higher the pH and temperature, the greater the proportion of NH_3. Therefore, at the same TAN, conditions with a pH of 5.5-6.0 can be safe, while at a pH above 6.5, noticeable inhibition begins. According to literature, critical TAN values are about 1.5-3.0 g N/l, and the concentration of free ammonia above 80-100 mg N/l already causes inhibition of the process. At the same time, moderate amounts of NH_3 can even have a stimulating effect due to partial inhibition of competing microorganisms, which confirms the nonlinear nature of the action of ammonia.

The mechanisms of inhibition are diverse: from disruption of the proton-motive force to the shift of metabolic flows towards by-products (ethanol, lactic acid), which reduces the stoichiometric yield of hydrogen. Therefore, managing the ammonia level is one of the key engineering parameters. Practice shows that maintaining pH in the range of 5.2-6.0, adjusting the C/N ratio within 20-40 and limiting TAN below 1.5 g/l can reduce the risks of inhibition [30, 50].

There are a number of technical approaches to mitigate the effect of ammonia. The most common of these are co-fermentation of protein waste with carbon-rich lignocellulosic feedstock (which equalizes C/N), the use of zeolites or biochar to adsorb ammonium ions, and its precipitation in the form of struvite. In some cases, ammonia stripping or two-stage schemes are used to avoid the accumulation of toxic concentrations [36].

Ammonia is thus a dual factor: in small quantities it can contribute to process stability, but when threshold values are exceeded it becomes a serious inhibitor of dark fermentation. For work with lignocellulosic substrates poor in nitrogen, it is especially relevant when using mixed feeds, where it is the C/N balance and pH control that determine the stability and efficiency of biohydrogen production.

2. Conclusion

The efficiency of dark fermentation as a technology for biological hydrogen production is largely limited by the action of inhibitory factors. The most important role is played by the products of pre-treatment of lignocellulosic substrates - furan derivatives, phenolic compounds and organic acids, as well as inorganic ions, heavy metals and microbial competitors, including lactic acid bacteria and H_2-utilizing microorganisms. Their presence leads to a violation of the enzymatic balance, a change in the structure of microbial communities and a decrease in hydrogen yield.

Despite significant efforts to study the mechanisms of toxic action and develop detoxification methods, the issues of adaptation of microbial consortia and the formation of their resistance to inhibitors still remain open. Modern strategies for minimizing negative impact include optimization of pre-treatment modes, the use of sorption technologies and co-fermentation, as well as regulation of cultivation parameters.

Engineering control of the process requires an integrated approach based on: (i) gentle pre-treatment followed by detoxification of hydrolysates (overliming, biocatalytic oxidation, use of adsorbents – biochar, zeolites); (ii) maintaining optimal conditions (pH 5.2-6.0; C/N = 20-40; TAN <1.5 g N/l) to reduce ammonia stress; (iii) control of microelement composition of the environment to ensure a sufficient level of Fe and exclusion of toxic metals; (iv) reduction of partial pressure of H_2 (gas stripping, recirculation, inert gases) to prevent reverse suppression; (v) selection and enrichment of microbial cultures to suppress H_2 consumers and limit the activity of lactic acid bacteria.

Prospects for further research are related to the development of stable microbial consortia, integration of dark fermentation with other biotechnological processes and the introduction of combined methods for suppressing inhibitors. The implementation of these areas will improve the stability and energy efficiency of the process, increase the hydrogen yield and bring dark fermentation closer to industrial operation, ensuring the rational use of renewable resources and reducing the carbon footprint in the energy and agricultural sectors.

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ЛИГНОЦЕЛЛЮЛОЗАЛЫҚ БИОМАССАНЫҢ ИНГИБИТОРЛАРЫ: ӘСЕР ЕТУ МЕХАНИЗМДЕРІ ЖӘНЕ СУТЕГІНІ БИОЛОГИЯЛЫҚ ӨНДІРУ ТИІМДІЛІГІНЕ ӘСЕРІ (ШОЛУ)

Бұл мақалада лигноцеллюлозалық биомассаны (ЛЦБ) өңдеу кезінде биосутегінің тиімді өндірілуіне кедергі келтіретін ингибиторлық факторлар талданады. Бұл тұрғыда қараңғы ферментация сутегін алудың ең перспективалы биологиялық әдістерінің бірі болып саналады, себебі ол сыртқы энергия көзін қажет етпейді, заманауи реакторлық технологиялармен үйлесімді және субстраттардың кең спектрін пайдалануға мүмкіндік береді. Оны өнеркәсіпте қолданудағы негізгі кедергі ЛЦБ алдын ала өңдеу және ферментация кезінде түзілетін улы қосылыстардың жинақталуы болып табылады. Мақалада негізгі ингибиторлардың құрамы мен әрекеті туралы ақпарат жинақталған. Талдау нәтижелері көрсеткендей, қараңғы ферментацияда H_2 шығымы 2-4 моль/моль қантқа жетеді (максималды ~3,8 моль/моль гексоза), бірақ (i) фурандар (фурфурол 0,03–8,23 г/л; 5-ГМФ 0,09-1,59 г/л), (ii) лигниндік фенолдар (ванилин, сирингальдегид), (iii) органикалық қышқылдар (құмырсқа, сірке, левулин қышқылы), (iv) бейорганикалық иондар мен ауыр металдар (Zn, Cu, Cr, Ni және т.б.), (v) аммиак пен сульфаттар болған кезде айтарлықтай төмендейді.

Сондай-ақ дозаға тәуелді әсерлер мен микробтық қауымдастықтың құрамындағы өзгерістер, мысалы, pH әсері, фурфуролдың Clostridium санының азаюына ықпалы немесе 5-HMP қосылғанда Clostridium мен Ruminococcaceae санының артуы талқыланады. Осылайша, ингибиторлардың әсер ету механизмдерін түсіну және олардың әсерін азайту жолдарын табу қараңғы ашытудың тиімділігін арттыру және оны лигноцеллюлозалық биомассаны биосутекке айналдырудың тұрақты технологиясы ретінде жүзеге асырудың негізгі бағыттары болып табылады.

Түйін сөздер: *қараңғы ферментация, биосутек, лигнецеллюлозалық биомасса, ингибиторлар, фуран қосылыстары, фенолды қосылыстар, ұшпа май қышқылдары, ауыр металдар.*

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ИНГИБИТОРЫ ЛИГНОЦЕЛЛЮЛОЗНОЙ БИОМАССЫ: МЕХАНИЗМЫ ДЕЙСТВИЯ И ВЛИЯНИЕ НА ЭФФЕКТИВНОСТЬ БИОЛОГИЧЕСКОГО ПОЛУЧЕНИЯ ВОДОРОДА (ОБЗОР)

В данной статье проводится анализ ингибирующих факторов, которые препятствуют эффективному производству биоводорода при переработке лигноцеллюлозной биомассы (ЛЦБ). В этом контексте темная ферментация рассматривается как один из наиболее перспективных биологических методов получения водорода, поскольку не требует внешнего источника энергии, совместимо с современными реакторными технологиями и позволяет использовать широкий спектр субстратов. Основным препятствием для его промышленного применения является накопление токсичных соединений, образующихся в процессе предварительной обработки и самой ферментации ЛЦБ. В статье обобщена информация о составе и действии основных ингибиторов. Результаты анализа показывают, что при темной ферментации выход H_2 достигает 2-4 моль/моль сахара (максимум ~3,8 моль/моль гексозы), но значительно снижается в присутствии: (i) фуранов (фурфурол 0,03-8,23 г/л; 5-ГМФ 0,09-1,59 г/л), (ii) лигновых фенолов (ванилин, сиреневый альдегид), (iii) органических кислот (муравьиная, уксусная, левулиновая кислота), (iv) неорганических ионов и тяжелых металлов (Zn, Cu, Cr, Ni и др.), (v) аммиака и сульфатов. Также обсуждаются дозозависимые эффекты и изменения в составе микробного сообщества, такие как влияние pH, снижение численности Clostridium из-за фурфурола или увеличение численности Clostridium и Ruminococcaceae при добавлении 5-HMP. Таким образом, понимание механизмов действия ингибиторов и поиск способов снижения их воздействия являются ключевыми направлениями для повышения эффективности темной ферментации и её внедрения в качестве устойчивой технологии преобразования лигноцеллюлозной биомассы в биоводород.

Ключевые слова: *тёмная ферментация, биоводород, лигноцеллюлозная биомасса, ингибиторы, фурановые соединения, фенольные соединения, летучие жирные кислоты, тяжёлые металлы.*

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ИССЛЕДОВАНИЕ ПИЩЕВОЙ И БИОЛОГИЧЕСКОЙ ЦЕННОСТЕЙ КОМПОЗИТНОЙ МУКИ ИЗ ЛЬНЯНОГО И КОНОПЛЯНОГО ЖМЫХА

Аннотация: *В современных исследованиях функциональных продуктов питания особое внимание уделяется разработке композитных ингредиентов, способных обогащать рацион белком, витаминами, минералами и биологически активными соединениями. В настоящей работе проведён комплексный анализ композитной муки, полученной из льняного и конопляного жмыха в соотношении 1:1, с целью оценки её физико-химических характеристик, витаминного и минерального состава, аминокислотного профиля и антиоксидантной активности, а также определения потенциала применения в функциональных и обогащённых продуктах питания.*

Результаты исследования продемонстрировали, что композитная мука обладает существенно более высоким содержанием пищевых волокон – 11,03 ± 0,13 %, по сравнению с пшеничной мукой высшего сорта (0,1–0,15 ± 0,02 %). Анализ витаминного состава показал наличие значительных количеств витамина Е (92,02 ± 0,96 мг/100 г) и витаминов группы В (В1, В2, В3, В5, В6, фолиевая кислота), содержание которых многократно превышает показатели пшеничной муки. Минеральный профиль характеризуется повышенным содержанием железа (11,70 ± 0,14 мг/100 г), магния (256,7 ± 3,1 мг/100 г), кальция (200,17 ± 2,41 мг/100 г), фосфора (582,10 ± 6,98 мг/100 г) и цинка (3,56 ± 0,04 мг/100 г), а наличие йода (0,0069 ± 0,0001 мг/100 г) расширяет спектр микроэлементов.

Аминокислотный анализ показал высокое содержание незаменимых и условно незаменимых аминокислот, включая аргинин, лизин, лейцин, изолейцин, валин и метионин, что подтверждает высокую биологическую ценность белка. Композитная мука также обладает выраженной антиоксидантной активностью, обеспечивая защиту липидных и белковых структур от окислительных процессов.

Полученные результаты свидетельствуют о целесообразности использования композитной муки из льняного и конопляного жмыха в рецептурах функциональных, обогащённых и профилактических продуктов питания, включая мясорастительные изделия, с целью повышения нутритивной ценности, улучшения технологических свойств и пролонгации срока хранения.

Ключевые слова: *композитная мука; конопляный жмых; льняной жмых; пищевая ценность; биологическая ценность; аминокислотный состав; функциональные продукты питания.*

Введение

В последние годы растет интерес к созданию функциональных продуктов питания с использованием растительных компонентов, способных улучшать здоровье человека и компенсировать недостаток отдельных нутриентов [1, 2]. Льняной и конопляный жмых представляют собой богатые источники белка, пищевых волокон, витаминов, минералов и биологически активных соединений. Совместное использование этих компонентов позволяет получить композитные продукты с повышенной питательной и биологической ценностью [3].