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The Energy Metabolic Function and Biosynthetic Role of the Pentose Phosphate Pathway

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Abstract The pentose phosphate pathway (PPP) is an important branch in cellular metabolism. It is not only related to energy metabolism but also responsible for biosynthesis. PPP has two parts. Oxidative branches can produce NADPH, which is used to maintain the REDOX balance within cells. It can also support the synthesis of fatty acids and cholesterol, and help cells resist oxidative stress. Non-oxidizing branches provide some raw materials, such as ribo5-phosphoric acid, for the synthesis of nucleotides and amino acids. PPP is closely related to pathways such as glycolysis and the tricarboxylic acid cycle. They will cooperate with each other and adjust at any time to meet the needs of cells in different situations. In recent years, studies have found that PPP is often abnormally regulated in diseases such as tumors and diabetes. Meanwhile, it also has great application value in the field of biotechnology. This article mainly reviews the role of PPP in energy metabolism and biosynthesis, and points out its significant importance in health, disease and bioengineering. Finally, we also put forward a goal: in the future, we will regulate PPP more precisely through systems biology and new technologies. Further in-depth research on the regulatory mechanism of PPP may provide new ideas for disease treatment and industrial production.

Keywords Pentose phosphate pathway; Energy metabolism; Biosynthesis; NADPH; REDOX steady state

1 Introduction

The Pentose Phosphate Pathway (PPP) is an important branch in the cellular metabolic network. It is on par with glycolysis and the tricarboxylic acid cycle, and is also one of the earliest discovered metabolic pathways. PPP plays a significant role in maintaining carbon balance, providing raw materials for nucleotide and amino acid synthesis, offering reducing power (NADPH) for synthesis reactions, and helping cells resist oxidative stress. Meanwhile, it is also closely related to the growth, differentiation, aging of cells, as well as the occurrence of some diseases (such as cancer, diabetes, etc.) (Kruger and Von Schaewen, 2003; Stincone et al., 2014; Ge et al., 2020; Gupta and Gupta, 2021; Rashida and Laxman, 2021; TeSlaa et al., 2023). PPP consists of two parts: oxidized branches and non-oxidized branches. The oxidation branch mainly generates NADPH and ribose 5-phosphate. The non-oxidative branch provides different synthetic raw materials for cells through the transformation between sugar and phosphate, and is closely associated with other metabolic pathways such as glycolysis (Bertels et al., 2021; Sharkey, 2021).

The generation of NADPH not only supports the synthesis of fatty acids, cholesterol and deoxynucleotides, etc., but also helps maintain the REDOX balance of cells and participates in antioxidant protection and signal regulation (Chen et al., 2019; Fuentes-Lemus et al., 2023; TeSlaa et al., 2023). The intermediate products generated by PPP can also be used as raw materials to synthesize biological macromolecules such as nucleic acids, amino acids and vitamins (Stincone et al., 2014; Bertels et al., 2021; Gupta and Gupta, 2021). In addition, PPP has dynamic regulation in different environments, and this regulation is crucial for maintaining metabolic homeostasis and cellular adaptation to external changes (Masi et al., 2021; Rashida and Laxman, 2021).

The purpose of this study is to systematically organize the functions of the pentose phosphate pathway in energy metabolism and biosynthesis, with a focus on its regulatory modalities under different physiological and pathological conditions, as well as its connections with other metabolic pathways. Specific goals include

summarizing the role of PPP in energy metabolism and its interrelationship with pathways such as glycolysis and fatty acid metabolism; Explain the core role of PPP in biosynthesis, especially the generation of NADPH and ribose 5-phosphate and their subsequent reactions; Explore the connection between abnormal PPP function and the occurrence of diseases; And introduce the new progress in PPP regulation, metabolic engineering and biomedical applications in recent years. This review aims to provide theoretical support for a better understanding of the metabolic function and biosynthetic role of PPP, and also offer references for disease prevention and treatment as well as the improvement of metabolic engineering.

2 Overview of the Pentose Phosphate Pathway

2.1 Pathway structure

The pentose phosphate pathway (PPP) is an important branch of glucose metabolism in cells. It is divided into two parts: the oxidation branch and the non-oxidation branch. The oxidation branch starts with glucose-6-phosphate and undergoes a series of irreversible reactions to produce NADPH and ribose 5-phosphate. NADPH provides reducing power for cells, while ribose 5-phosphate is the raw material for synthesizing nucleotides (Alfarouk et al., 2020; Ge et al., 2020; Bertels et al., 2021; Sharkey, 2021). The non-oxidizing branch is composed of reversible reactions catalyzed by transketoolase and transaldoolase. It can convert pentose phosphates (such as ribose 5-phosphate, xylose 5-phosphate) into intermediate substances in glycolysis, such as fructose-6-phosphate and glyceraldehyde 3-phosphate, thereby interlinking with glycolysis. These two branches not only meet the cells' demands for reducing power and synthetic raw materials, but also flexibly regulate the flow direction of carbon by sharing intermediates with glycolysis to adapt to different physiological states.

2.2 Comparison with glycolysis

Both the Glycolysis and pentose phosphate pathways start with glucose-6-phosphate, but their products and functions are different. Glycolysis breaks down glucose into pyruvate and generates ATP and NADH for direct energy supply (Ge et al., 2020; Bertels et al., 2021). PPP does not produce ATP but generates NADPH and pentose sugar (Alfarouk et al., 2020; Ge et al., 2020) (Figure 1). There are intermediates between the two that can be converted into each other, such as glucose-6-phosphate, fructose-6-phosphate and glyceraldehyde 3-phosphate. The non-oxidizing branch of PPP can also convert pentose sugar back to these substances, thereby achieving dynamic regulation of carbon flow (Sharkey, 2021). Functionally, glycolysis mainly provides energy; PPP focuses more on providing NADPH and the raw materials required for the synthesis of nucleotides, amino acids, fatty acids, etc. It is particularly important during antioxidant stress and rapid cell division. In addition, the key enzymes of these two pathways are regulated by different metabolic signals, and cells allocate carbon flows according to energy, reducing power and synthetic requirements.

3 Energy Metabolic Function of the PPP

3.1 NADPH production

The core function of the pentose phosphate pathway (PPP) is to generate NADPH in the oxidation branch. Under the action of glucose-6-phosphate dehydrogenase (G6PD) and 6-phosphogluconate dehydrogenase (6PGDH), after two oxidation reactions, for each molecule of glucose-6-phosphate decomposed, two molecules of NADPH are obtained (Stincone et al., 2014; Chen et al., 2019; Ge et al., 2020; Bertels et al., 2021; Masi et al., 2021; Fuentes-Lemus et al., 2023; TeSlaa et al., 2023). NADPH is the main source of reducing power in cells. It participates in the synthesis of fatty acids, cholesterol, deoxynucleotides, etc., and also provides electrons for antioxidant systems such as glutathione reductase, helping to maintain the REDOX balance of cells (Cherkas et al., 2019; Qiao et al., 2025). Under conditions such as oxidative stress, rapid cell division or immune response, NADPH generated by PPP is particularly important for cells.

3.2 ATP linkages

Unlike glycolysis and the tricarboxylic acid cycle, PPP itself does not directly produce ATP. However, PPP and glycolysis share some intermediate products, such as fructose-6-phosphate and glyceraldehyde 3-phosphate. The intercommunication of these substances enables the carbon flow to be dynamically adjusted, thereby indirectly

affecting energy metabolism (Stincone et al., 2014; Morelli and Scholkmann, 2024; Qiao et al., 2025). New research suggests that a closed loop may form among PPP, glycolysis and oxidative phosphorylation outside mitochondria. The pentose sugars generated by PPP can return to glycolysis and participate in overall energy regulation. In addition, the alteration of PPP activity will affect the utilization mode of glucose, and thereby influence the generation efficiency of ATP. This situation is particularly evident during cellular stress or metabolic reprogramming (such as the Warburg effect in cancer cells) (Nagao et al., 2019).

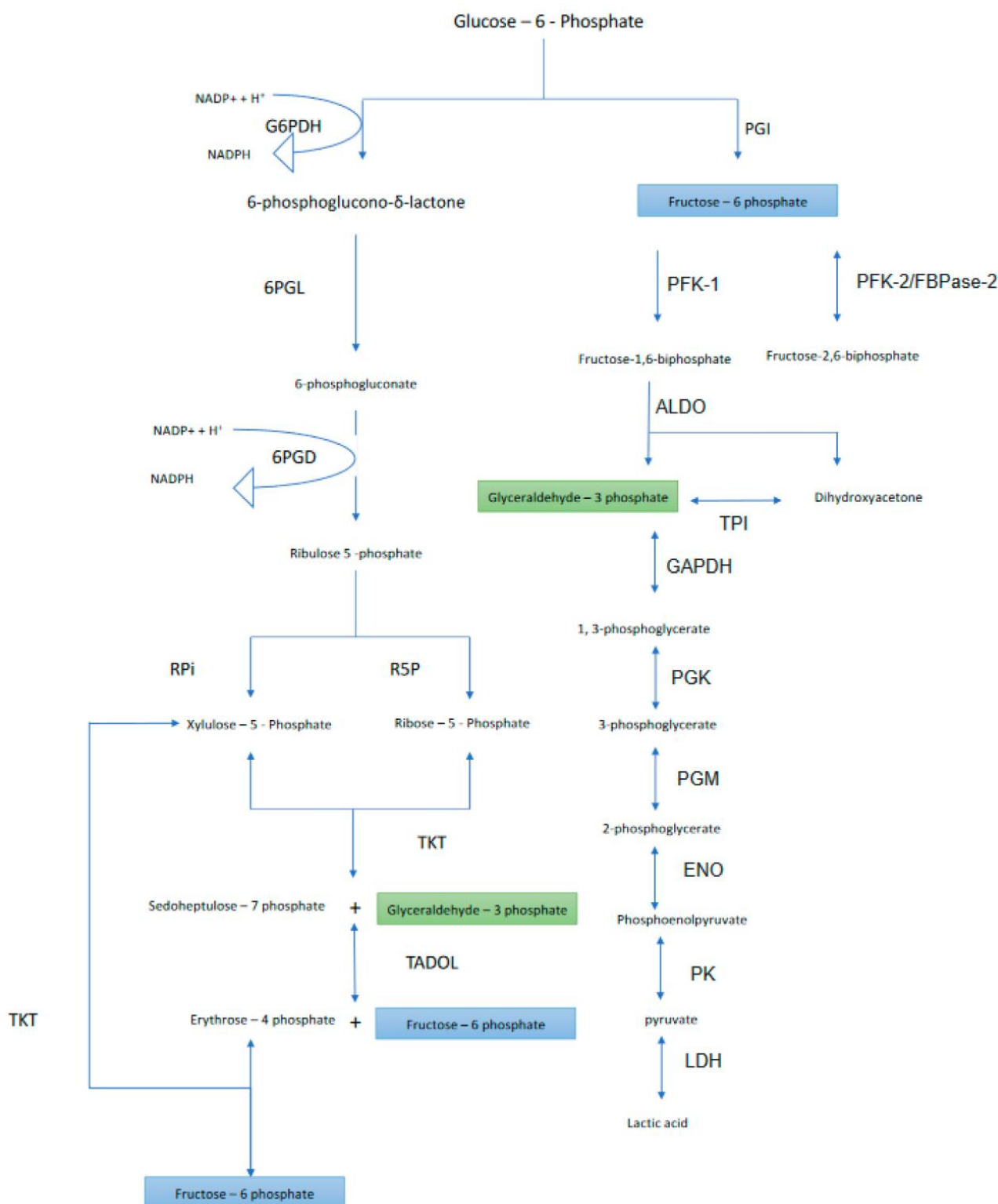


Figure 1 Scheme showing the interaction between glycolysis and PPP (Adopted from Alfarouk et al., 2020)

3.3 Redox homeostasis

PPP continuously generates NADPH, which is a key pathway for cells to maintain REDOX balance. NADPH can not only reduce oxidized glutathione (GSSG) to reduced glutathione (GSH) to protect cells from damage by reactive oxygen species (ROS) and reactive nitrogen species (RNS), but also regulate signaling pathways related to oxidative stress (Stincone et al., 2014; Chen et al., 2019; Cherkas et al., 2019; Ge et al., 2020; Masi et al., 2021; TeSlaa et al., 2023; Fuentes-Lemus et al., 2023; Qiao et al., 2025). During acute oxidative stress, cells rapidly shift glucose metabolism to PPP to quickly replenish NADPH and preferentially support the antioxidant system. The activity of PPP-related enzymes is regulated by oxidative modification. If these enzymes are damaged, NADPH production decreases and cells are more prone to oxidative damage. Furthermore, the dynamic regulation of PPP can also participate in a broader antioxidant response by influencing gene expression and signal transduction (Kruger et al., 2011).

4 Biosynthetic Role of the PPP

4.1 Nucleotide biosynthesis

The non-oxidizing branch of the pentose phosphate pathway (PPP) can generate ribose 5-phosphate (R5P). It is the direct raw material for the synthesis of nucleotides and nucleic acids. R5P is not only used in the synthesis of DNA and RNA, but also provides key substances during cell division and repair. PPP can be regulated as needed and can efficiently supply pentose sugars required for nucleotide synthesis during rapid cell proliferation or tumor growth (Stincone et al., 2014; Ge et al., 2020; Polat et al., 2021; TeSlaa et al., 2023; Qiao et al., 2025).

4.2 Amino acid metabolism

PPP can provide a variety of precursors for amino acid synthesis. For instance, its intermediate product, erythritol-4-phosphate (E4P), is an important substrate for the synthesis of aromatic amino acids (phenylalanine, tyrosine and tryptophan). PPP also indirectly regulates the synthesis of non-essential amino acids by influencing the direction of carbon flow and the supply of NADPH, and maintains the balance of the entire amino acid metabolic network (Bertels et al., 2021; Gupta and Gupta, 2021; Rashida and Laxman, 2021; Srivastava, 2024).

4.3 Lipid biosynthesis

The NADPH generated by PPP provides reducing power for the synthesis of lipids such as fatty acids, cholesterol and phospholipids. NADPH is a necessary coenzyme for fatty acid synthase and enzymes related to cholesterol synthesis. In tissues where lipid synthesis is active, such as the liver, adipose tissue and tumor cells, the activity of PPP is significantly enhanced. In addition, phospholipid synthesis is also related to nucleotide metabolism and NADPH generation, which further indicates that PPP is in a core position in lipid metabolism (Wasylenko et al., 2015; Gupta and Gupta, 2021; TeSlaa et al., 2023; Zhu et al., 2024).

4.4 Other anabolic processes

PPP also provides raw materials and reducing power for other anabolic processes, such as the synthesis of vitamins, coenzymes and cell wall components (such as lipopolysaccharides). Some intermediate products of PPP can also act as signaling molecules to regulate cell growth, differentiation and stress response. PPP exhibits diverse functions in plant, microbial and animal cells, indicating that it is an important hub in cellular anabolic metabolism (Rahman and Hasan, 2014; Stincone et al., 2014; Sharkey, 2021; Srivastava, 2024).

5 Regulatory Mechanisms

5.1 Enzymatic control

The key enzymes of the pentose phosphate pathway (PPP) are mainly controlled through allosteric regulation and feedback inhibition. Glucose-6-phosphate dehydrogenase (G6PD) is the rate-limiting enzyme of PPP. Its activity is affected by NADP^+ and NADPH. NADP^+ can activate it, while NADPH will inhibit it. In this way, NADPH forms a negative feedback to G6PD, thereby maintaining the balance of carbon flow in a steady state (Ramos-Martinez, 2017; TeSlaa et al., 2023). When cells are under oxidative stress, NADPH consumption accelerates, inhibition is lifted, and the flux of PPP will increase rapidly to replenish the reducing power (Christodoulou et al., 2018). In addition, enzymes in glycolysis, such as phosphoglucose isomerase (PGI) and

glyceraldehyde 3-phosphate dehydrogenase (GAPD), are also subject to oxidative modification or allosteric regulation. These changes allow more carbon to enter PPP (Hurbain et al., 2022). The collaboration of multiple enzymes enables cells to flexibly adjust PPP activity as needed (Christodoulou et al., 2018; Hurbain et al., 2022).

5.2 Hormonal regulation

Hormones can indirectly affect PPP by regulating gene expression and enzyme activity. Insulin can upregulate the expression of PPP-related enzymes such as G6PD, thereby promoting anabolic and antioxidant responses. This effect is particularly evident in the liver and adipose tissue. Glucocorticoids and growth hormones can also enhance PPP activity through transcriptional regulation to meet the requirements of cells for NADPH and synthetic substrates during growth, differentiation or stress states (Wu et al., 2018; TeSlaa et al., 2023). Furthermore, some transcription factors (such as YY1) can directly activate the transcription of the G6PD gene, further increase the flux of PPP, and support cell proliferation and antioxidant defense (Wu et al., 2018).

5.3 Cellular stress responses

Under stressful conditions such as oxidative stress, PPP will be rapidly activated as the first line of defense. Oxidative stress will accelerate the consumption of NADPH, thereby relieving the inhibition of G6PD and promoting the entry of glucose into PPP in order to replenish NADPH rapidly (Kuehne et al., 2015; Christodoulou et al., 2018; Hurbain et al., 2022). Meanwhile, intermediate products such as 6-phosphogluconic acid (6PG) can also inhibit glycolysis, further promoting carbon flow into PPP (Dubreuil et al., 2020). Genomic and metabolomics studies have shown that the dynamic regulation of PPP not only affects the generation of NADPH, but also coordinates the overall antioxidant response by regulating the antioxidant system (such as glutathione, catalase, etc.) and gene expression (Kruger et al., 2011; Hambardikar et al., 2022). Furthermore, PPP has a certain reserve capacity and can rapidly increase NADPH supply during acute stress, thereby enhancing the viability of cells.

6 PPP in Physiology and Pathophysiology

6.1 Normal physiology

The pentose phosphate pathway (PPP) plays many important roles under normal circumstances. It can generate ribose 5-phosphate, providing raw materials for the synthesis of nucleotides, thereby supporting cell division and the replication of genetic material. PPP also generates NADPH. These molecules not only provide reducing power for the synthesis of fatty acids and cholesterol, but also help maintain the REDOX balance of cells and enhance antioxidant capacity. NADPH participates in the glutathione and thioredoxin systems, eliminating reactive oxygen species (ROS) and reactive nitrogen species (RNS), and protecting cells from oxidative damage. In addition, PPP can also support the functions of immune cells. For instance, neutrophils and macrophages utilize NADPH oxidase to produce ROS, which is used to kill pathogens (TeSlaa et al., 2023). These functions are important for cell growth, differentiation, immune defense and overall metabolic balance (Ge et al., 2020).

6.2 Disease contexts

In many diseases, the functions and regulation of PPP will undergo significant changes.

In terms of genetic defects, glucose-6-phosphate dehydrogenase (G6PD) deficiency is the most common problem. This defect can reduce the antioxidant capacity of red blood cells, making them prone to hemolytic anemia. If the defect is severe, the oxidative burst of white blood cells will also be affected, resulting in a higher risk of infection (TeSlaa et al., 2023).

In tumors, cancer cells often upregulate PPP to meet the demands of rapid proliferation for nucleotides and NADPH. In this way, they can not only support synthesis but also enhance antioxidant capacity to resist metabolic stress. Therefore, inhibiting PPP is regarded as a potential direction for anti-cancer treatment (Ge et al., 2020).

In diabetes and metabolic syndrome, abnormal regulation of PPP can affect the REDOX balance and synthetic processes of cells. This is related to insulin resistance, chronic inflammation and the occurrence of complications (Ge et al., 2020).

In terms of immunity and infection, the NADPH produced by PPP can not only assist in antioxidant defense but also enable immune cells to generate ROS to kill bacteria. Those with G6PD deficiency are not only prone to hemolysis, but also more susceptible to infection due to the decline in immune cell function.

7 Case Study: PPP in Cancer Metabolism

7.1 Background

The metabolism of tumor cells is often reprogrammed, which is an important characteristic of cancer. Unlike normal cells that mainly rely on mitochondrial oxidative phosphorylation, cancer cells prefer to obtain energy and synthesize necessary substances through glycolysis and the pentose phosphate pathway (PPP) even under aerobic conditions. This is known as the Warburg effect. PPP can not only provide ribo5-phosphoric acid to meet the nucleotide demand during the rapid proliferation of tumor cells, but also generate NADPH to support reductive metabolism and antioxidant defense (Jiang et al., 2014; Nagao et al., 2019; Ghanem et al., 2021; Qiao et al., 2025).

7.2 PPP upregulation

In many cancers, the expression and activity of key enzymes of PPP (such as G6PD, 6PGD, TKT) will significantly increase, leading to an increase in the flux of PPP. The reasons for this upregulation include the activation of some tumor-related signaling pathways, such as PI3K/AKT, STAT3, HIF-1 α , NRF2, etc. These pathways promote the transcription, translation or modification of enzymes such as G6PD, thereby increasing the supply of NADPH and nucleotides, helping tumor cells resist oxidative stress, maintain growth, and may also enhance drug resistance (Rao et al., 2015; Sarfraz et al., 2020; Cheng et al., 2020).

7.3 Illustrative example

In hepatocellular carcinoma and lung adenocarcinoma, studies have found that PPP enzymes such as G6PD and 6PGD are highly expressed in tumor tissues, promoting cell proliferation, migration and anti-apoptosis (Sarfraz et al., 2020; Bai et al., 2024; Wu et al., 2024). In gastrointestinal tumors, PPP not only regulates the REDOX balance of the tumor microenvironment, but also supports continuous tumor growth and drug resistance development by providing raw materials for nucleotide and lipid synthesis (Qiao et al., 2025). In addition, some molecules such as TIGAR can promote more glucose to enter PPP, thereby increasing NADPH production, reducing ROS levels, and further protecting tumor cells (AlMaazmi et al., 2025) (Figure 2).

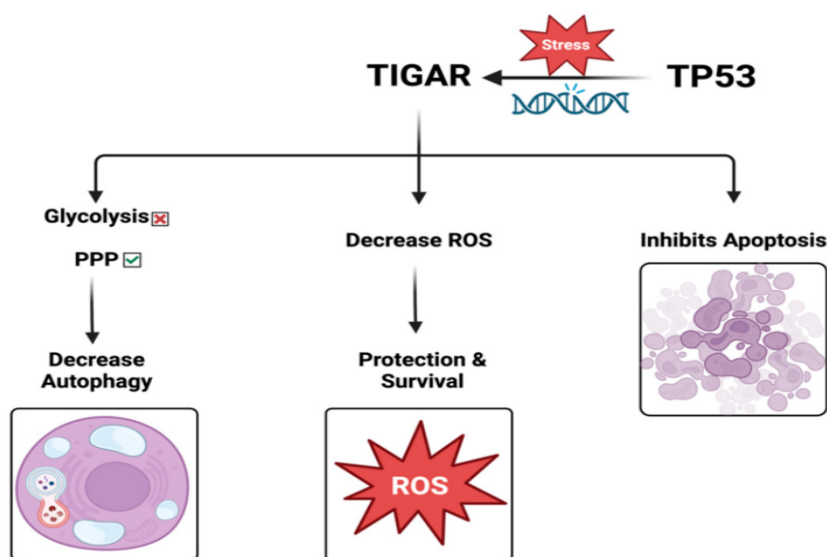


Figure 2 The role of TIGAR protein (Adopted from AlMaazmi et al., 2025)

7.4 Therapeutic implications

The high activity of PPP has brought new targets for tumor treatment. If the key enzymes of PPP (such as G6PD, 6PGD, TKT) are inhibited, it can significantly reduce the proliferation and drug resistance of tumor cells, and also

increase their sensitivity to chemotherapy and radiotherapy (Jiang et al., 2014; Sarfraz et al., 2020; Ghanem et al., 2021; Wu et al., 2024; Qiao et al., 2025). If PPP inhibitors are used in combination with traditional chemotherapy drugs, a synergistic effect can also be produced, inducing oxidative stress and apoptosis of tumor cells (Liu et al., 2020; Kaushik et al., 2021; Meskers et al., 2022). However, at present, PPP inhibitors still face many challenges in terms of toxicity, specificity and clinical application. In the future, safer and more effective targeted drugs need to be developed.

8 Biotechnological and Clinical Applications

8.1 Metabolic engineering

The pentose phosphate pathway (PPP) is a common modification target in metabolic engineering and is widely used in the industrial production of microorganisms and fungi. By regulating the expression of PPP-related enzymes, the supply of NADPH can be significantly increased, thereby enhancing the synthesis efficiency of various high-value products, such as polyols, biofuels, carotenoids and antibiotics, etc. In some industrial fungi, engineered PPP modification has been proven to increase yield, optimize carbon flow distribution, and enable cells to better adapt to different carbon sources and oxidative stress conditions (Bertels et al., 2021; Masi et al., 2021). In addition, computational models based on cohort theory have also been used to simulate the metabolic flow of PPP, providing new tools for drug development, which can accelerate the screening of new drugs and reduce the use of animal experiments (Kloska et al., 2022).

8.2 Therapeutics

PPP is a potential therapeutic target in a variety of diseases, especially cancer. Cancer cells usually up-regulate PPP to meet the demands of rapid proliferation and antioxidation. If the key enzymes of PPP (such as G6PD, 6PGD, TKT) are inhibited, the proliferation ability, drug resistance and resistance to radiotherapy or chemotherapy of cancer cells can be reduced (Rahman and Hasan, 2014; Cho et al., 2017; Ghanem et al., 2021; Polat et al., 2021; Qiao et al., 2025). The combined use of PPP inhibitors and traditional anti-cancer drugs (such as cisplatin) can also enhance the therapeutic effect. At present, some drug delivery systems have also been able to achieve targeting on tumor cells (Giacomini et al., 2020; Shimoni-Sebag et al., 2024). Furthermore, regulating PPP has also been studied for improving the efficacy of immunotherapy, enhancing antioxidant defense, and treating hemolytic diseases (Bories et al., 2020; TeSlaa et al., 2023; Markowitz et al., 2024).

8.3 Diagnostics

The changes in PPP activity also bring new methods for disease diagnosis and therapeutic effect monitoring. Metabolic imaging techniques (such as magnetic resonance spectroscopy MRS) can detect glucose entry into PPP, thereby enabling non-invasive monitoring of TERT expression and metabolic reprogramming in tumors (such as low-grade gliomas) (Viswanath et al., 2021). Furthermore, detecting the activity of PPP-related enzymes (such as G6PD) is helpful for determining hereditary hemolytic anemia, tumor subtypes, and drug sensitivity (Polat et al., 2021; Tang et al., 2023; TeSlaa et al., 2023). Metabolomics and systems biology methods have also shown application potential in early disease screening and individualized treatment (Rashida and Laxman, 2021).

9 Future Directions

9.1 Systems biology approaches

Systems biology provides a powerful tool for understanding the role of the pentose phosphate pathway (PPP) in cellular metabolism. In recent years, researchers have revealed the connections between PPP and multiple pathways such as amino acids and lipids by combining omics data, metabolic flow analysis and network modeling, and have also observed its overall role in cell growth, stress and synthesis processes (Bertels et al., 2021; Rashida and Laxman, 2021). For instance, computational models such as queue theory have been employed to simulate the changes in the concentration of PPP metabolites and verify their stability in complex environments like tumor cells. These results also provide a theoretical basis for drug development and metabolic engineering (Kloska et al., 2022). In the future, systems biology will continue to help us understand the overall regulatory mechanisms of PPP in different physiological and pathological states.

9.2 Emerging technologies

Some new technologies are accelerating the research on PPP. High-throughput gene editing (such as CRISPR screening), metabolomics, single-cell analysis and real-time metabolic imaging have all been used to discover the regulatory factors of PPP and its unconventional roles in oxidative stress and tumor metabolism (Dubreuil et al., 2020; Masi et al., 2021). In addition, synthetic biology methods such as automated carbon flow redirection and oxygen-responsive metabolic switches have also achieved precise regulation of PPP in microorganisms and fungi. These methods can significantly increase NADPH supply and the yield of the target product (Kobayashi et al., 2020). These technologies have brought new opportunities for metabolic engineering, disease treatment and biomanufacturing.

9.3 Open questions

Although significant progress has been made in the research of PPP, there are still many unknowns. First of all, the regulatory network of PPP is very complex and is not yet fully understood. Further research is needed on how signals such as carbon sources, nitrogen sources and oxidative stress jointly regulate PPP and its transcription factors (Masi et al., 2021; Rashida and Laxman, 2021). Secondly, the dynamic regulatory patterns of PPP in different cell types, developmental stages and disease states, as well as its relationship with other metabolic pathways, are not yet clear (Bertels et al., 2025). In addition, the sensitivity of PPP key enzymes to oxidative damage and their fine regulatory mechanisms in antioxidant defense also require more in-depth molecular-level studies (Fuentes-Lemus et al., 2023). Finally, how to combine systems biology with emerging technologies to achieve precise regulation and individualized intervention of PPP is an important issue to be solved in the future.

10 Conclusion

The pentose phosphate pathway (PPP) is an important branch in cellular metabolism, which is related not only to energy metabolism but also to biosynthesis. PPP has two parts. Oxidative branches generate NADPH, which can provide reducing power for the synthesis of fatty acids, cholesterol and other substances, and also maintain the REDOX balance of cells, helping to resist oxidative stress. The non-oxidizing branch provides substances such as ribose 5-phosphate, which are used to synthesize nucleotides and amino acids. This flexibility makes PPP important in cell proliferation, differentiation and immune defense, and also plays a key role when cells are under oxidative stress.

In a healthy state, PPP can support cell growth, assist in antioxidant defense, and also ensure the replication of genetic material. However, in some diseases, such as G6PD deficiency, diabetes or tumors, the regulation of PPP may encounter problems. It either weakens its function or becomes overly active, thereby affecting the survival, proliferation and response of cells to drugs. Especially in tumors, cells enhance the activity of PPP to meet the needs of rapid synthesis and antioxidation, which also makes PPP a new target for anti-cancer treatment. Meanwhile, PPP also has great value in biotechnology. Regulating PPP through metabolic engineering can enhance the product synthesis efficiency of industrial microorganisms and promote the development of biomanufacturing and green industries.

Although the role of PPP has been widely recognized, its regulatory network is very complex. How PPP is interrelated with other metabolic pathways and how it changes in different cell types and disease states remain to be studied. In the future, if systems biology can be combined with emerging technologies, it is expected to achieve precise regulation of PPP. This can not only promote the progress of disease treatment, but also facilitate industrial applications. Continuous and in-depth research on PPP will provide a solid foundation for the development of new treatment methods and efficient biomanufacturing platforms.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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