

Research Insight into the Genetic Regulation of Photosynthesis in Sweet Potato

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Abstract In sweet potato (*Ipomoea batatas*), improvements in photosynthetic capacity have significant implications for increasing yield, starch production, and resilience under environmental stress. This study explores the genetic regulation of photosynthesis in sweet potato, focusing on key genes, transcription factors, and pathways that enhance photosynthetic efficiency and carbohydrate metabolism. Genes such as *IbVPI* and *IbMIPSI* play pivotal roles in optimizing photosynthesis, while transcription factors like *IbBBX29* and *IbC3H18* are critical for stress tolerance and efficient light utilization. Recent advancements in genetic engineering, including CRISPR/Cas9 applications, provide new avenues for precisely modifying photosynthetic traits to boost productivity. Additionally, insights from high-photosynthetic sweet potato varieties and their genetic profiles offer valuable guidance for future breeding programs aimed at achieving higher yield and better adaptability. Understanding the molecular mechanisms behind these genetic factors can facilitate the development of resilient, high-yield sweet potato cultivars, contributing to food security and sustainable agriculture.

Keywords Sweet potato (*Ipomoea batatas*); Photosynthesis; Genetic regulation; CRISPR/Cas9; Crop improvement

1 Introduction

Photosynthesis is the fundamental process driving plant growth and productivity, converting light energy into chemical energy stored in carbohydrates. This process is crucial for the biosphere, fixing over 100 billion tons of CO₂ annually, which forms the basis of crop production and, consequently, animal and human food supply (Baslam et al., 2020). Enhancing photosynthetic efficiency has been identified as a key strategy to increase crop yields, especially under varying environmental conditions. Genetic modifications and breeding strategies targeting photosynthetic traits have shown promise in improving crop productivity by optimizing the capture and utilization of solar energy (Theeuwens et al., 2022; Keller et al., 2023).

Sweet potato (*Ipomoea batatas*) is a vital crop for food security and nutrition, particularly in developing countries. The efficiency of photosynthesis in sweet potato directly influences its yield and starch production, which are critical for its role as a staple food. Recent studies have highlighted the potential of genetic interventions to enhance photosynthetic efficiency and, consequently, crop yield. For instance, overexpression of the H⁺-pyrophosphatase gene (*IbVPI*) in sweet potato has been shown to improve photosynthesis and sucrose content in source leaves, leading to increased starch content and total yield in storage roots (Fan et al., 2021). This underscores the importance of photosynthetic efficiency in maximizing the productivity of sweet potato (Long et al., 2022; Vijayakumar et al., 2023; Tao and Han, 2024).

This study investigates the genetic regulation of photosynthesis in sweet potato, identifying key gene targets for manipulation, elucidating the role of specific genes (such as *IbVPI*) in regulating photosynthesis and carbohydrate metabolism, and exploring the genetic variation of photosynthetic traits and their impact on yield under different environmental conditions. By developing genetic engineering and breeding strategies to improve photosynthetic performance and stress resistance in sweet potato varieties, this study aims to contribute to the development of high-yield, stress-resistant cultivars, thereby enhancing food security and agricultural sustainability.

2 Overview of Photosynthesis in Sweet Potato

Sweet potato (*Ipomoea batatas*) is a significant crop known for its high starch content and adaptability to various environmental conditions. Photosynthesis in sweet potato, like in other plants, involves the conversion of light energy into chemical energy, which is then used to produce carbohydrates. This process is crucial for the growth and yield of sweet potato, particularly in its storage roots, which are the primary sink organs for photoassimilates and energy (Fan et al., 2021).

2.1 Photosynthetic pathways and efficiency in sweet potato

Photosynthesis in sweet potato involves both the light-dependent reactions and the Calvin cycle. The efficiency of these pathways can be influenced by various genetic and environmental factors. For instance, the overexpression of the H⁺-pyrophosphatase gene (IbVP1) in sweet potato has been shown to enhance photosynthetic ability and sucrose content in source leaves, leading to increased starch content and yield in storage roots (Fan et al., 2021). Additionally, transcription factors such as BBX21 have been found to improve photosynthetic rates and water use efficiency under both optimal and drought conditions, further highlighting the genetic regulation of photosynthetic efficiency (Crocco et al., 2018; Ocampo et al., 2021).

2.2 Key components and enzymes involved in photosynthesis

Several key components and enzymes are involved in the photosynthetic process in sweet potato. These include chlorophyll-binding proteins, photosystem I and II, and enzymes involved in the Calvin cycle. The expression of genes encoding these components can be regulated by various transcription factors. For example, the transcription factor StABI5 has been shown to negatively regulate chloroplast development and photosynthesis by downregulating genes involved in photosynthesis and carbon fixation (Zhu et al., 2020). Similarly, the overexpression of IbBBX29 has been linked to increased flavonoid accumulation and improved leaf development, which can indirectly affect photosynthetic efficiency (Gao et al., 2022).

2.3 Genetic factors influencing photosynthetic performance

Genetic factors play a crucial role in determining the photosynthetic performance of sweet potato. Variations in transcription factors and photosynthesis-related genes can significantly impact photosynthetic traits. For instance, genetic variation in transcription factors and light-reaction genes has been shown to regulate photosynthetic traits by affecting the expression of multiple genes involved in the photosynthetic pathway (Wang et al., 2018). Additionally, the overexpression of genes such as IbMIPS1 and IbNAC43 has been found to influence photosynthetic performance by modulating stress responses and leaf development, respectively (Zhai et al., 2016; Sun et al., 2023). Furthermore, the identification of genetic variations in starch biosynthesis and sucrose metabolism genes provides insights into the molecular mechanisms regulating photosynthesis and carbohydrate metabolism in sweet potato (Zhang et al., 2020).

In summary, the genetic regulation of photosynthesis in sweet potato involves a complex interplay of various transcription factors, enzymes, and genetic variations. Understanding these regulatory mechanisms can provide valuable insights into improving photosynthetic efficiency and crop yield in sweet potato. Further research in this area can lead to the development of genetically engineered sweet potato cultivars with enhanced photosynthetic performance and stress tolerance.

3 Genetic Regulation of Photosynthesis

3.1 Regulatory genes and transcription factors

The genetic regulation of photosynthesis in sweet potato involves several key genes that influence various aspects of the photosynthetic process. For instance, the H⁺-pyrophosphatase gene (IbVP1) has been shown to enhance photosynthesis and sucrose content in source leaves, thereby increasing starch content and yield in storage tissues (Fan et al., 2021). Additionally, the IbMIPS1 gene, which is involved in myo-inositol biosynthesis, has been found to upregulate genes related to photosynthesis and stress responses, thereby improving photosynthetic efficiency under stress conditions (Zhai et al., 2016).

Transcription factors (TFs) play a crucial role in regulating the expression of photosynthetic genes. The NAC transcription factor IbNAC43, for example, negatively impacts photosynthetic efficiency by causing leaf curling and reducing chlorophyll content (Figure 1) (Sun et al., 2023). Conversely, the B-box transcription factor IbBBX29 enhances leaf biomass and flavonoid accumulation, which are associated with improved photosynthetic performance (Gao et al., 2022). Another important TF, IbC3H18, has been shown to enhance abiotic stress tolerance and regulate genes involved in photosynthesis and reactive oxygen species (ROS) scavenging (Zhang et al., 2019).

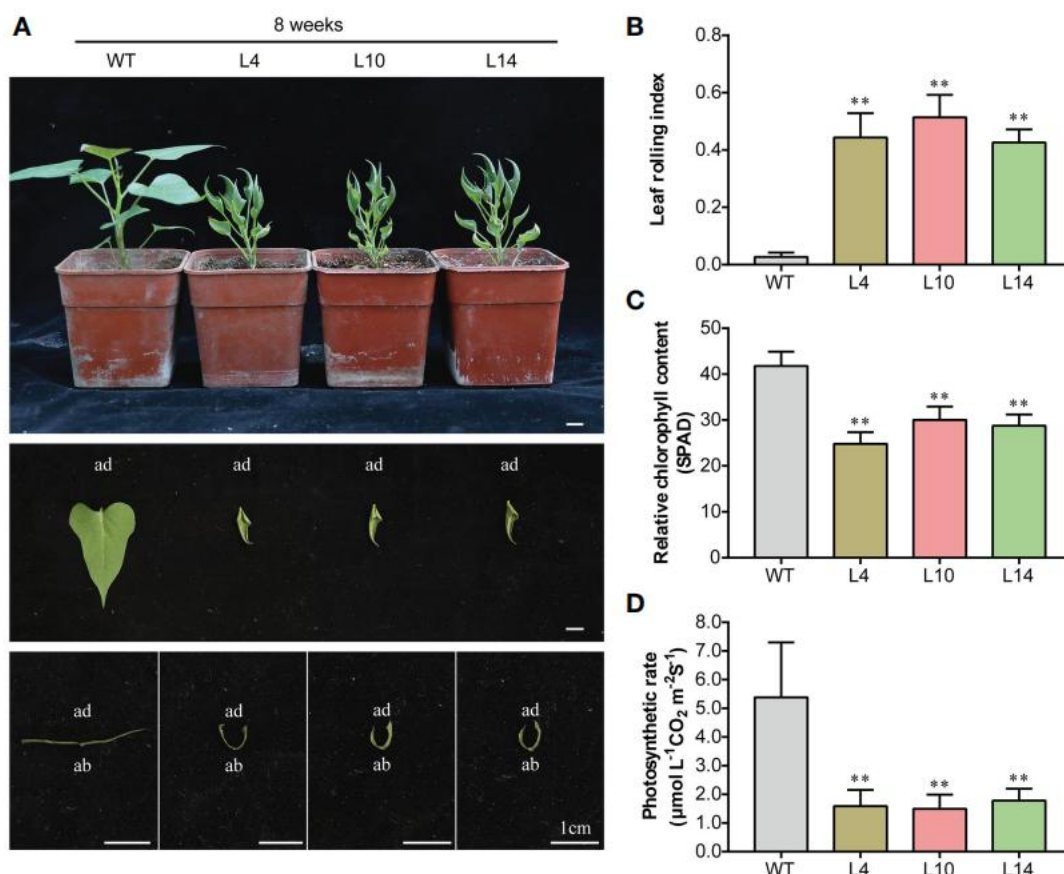


Figure 1 Phenotypes of transgenic and wild-type (WT) sweet potato plants in the greenhouse (Adopted from Sun et al., 2023)
 Image caption: (A) Plant stature and leaf phenotypes of both WT and transgenic plants. Scale bar, 1 cm. ad, adaxial side; ab, abaxial side. (B) Leaf rolling index (LRI). Data are presented as the mean \pm SE (n = 6). (C) Relative chlorophyll content. (D) Photosynthetic rate. Data are presented as the mean \pm SE (n = 3). Asterisks denote significant differences based on a Student's t-test. **p < 0.01 (Adopted from Sun et al., 2023)

3.2 Signal transduction pathways affecting photosynthesis

Signal transduction pathways are integral to the regulation of photosynthesis, particularly under stress conditions. The overexpression of IbMIPS1, for instance, activates phosphatidylinositol (PI) and abscisic acid (ABA) signaling pathways, which are crucial for maintaining photosynthetic efficiency under salt and drought stress (Zhai et al., 2016). Additionally, the non-tandem CCCH-type zinc-finger protein IbC3H18 regulates abiotic stress-responsive genes through ABA signaling, thereby enhancing photosynthetic performance under adverse conditions (Zhang et al., 2019).

Photoreceptors and hormones significantly influence photosynthetic regulation. The transcription factor IbBBX29, which is induced by the hormone auxin (IAA), modulates the expression of genes involved in auxin signaling and flavonoid biosynthesis, thereby enhancing photosynthetic efficiency (Gao et al., 2022). Furthermore, the symbiotic relationship with *Piriformospora indica* has been shown to increase photosynthetic pigments and efficiency, partly through the regulation of jasmonic acid (JA)-mediated defense mechanisms (Li et al., 2020).

3.3 Molecular mechanisms enhancing photosynthetic efficiency

Several molecular mechanisms have been identified that enhance photosynthetic efficiency in sweet potato. The overexpression of antioxidant enzyme genes, such as Cu/Zn SOD and APX, has been shown to maintain higher photosynthetic capacity under drought stress by improving light energy conversion efficiency and reducing photorespiration (Lu et al., 2015). Additionally, genetic variations in starch biosynthesis and sucrose metabolism genes, such as IbAGPb3 and IbGBSS1-1, contribute to the regulation of starch properties, which are essential for efficient photosynthesis and energy storage (Zhang et al., 2020). The vacuolar invertase gene Ib β fruct2-1 also plays a role in regulating starch and glucose content, further influencing photosynthetic efficiency (Zhang et al., 2023).

The genetic regulation of photosynthesis in sweet potato is a complex process involving multiple genes, transcription factors, and signaling pathways. Key regulatory genes such as IbVP1 and IbMIPS1, along with transcription factors like IbNAC43 and IbBBX29, play significant roles in modulating photosynthetic efficiency. Signal transduction pathways, including those mediated by PI and ABA, as well as the influence of photoreceptors and hormones, are crucial for maintaining photosynthesis under stress conditions. Understanding these molecular mechanisms provides valuable insights for improving photosynthetic efficiency and crop yield in sweet potato.

4 Recent Advances in Genetic Manipulation for Enhanced Photosynthesis

4.1 Approaches to enhance photosynthetic efficiency

Recent advancements in genome-editing technologies, particularly CRISPR/Cas9, have revolutionized plant genetic engineering. CRISPR/Cas9 allows for precise, targeted modifications in plant genomes, which can be used to enhance photosynthetic efficiency. This technology has been successfully applied to various crops, including sweet potato, to improve traits such as starch quality and resistance to biotic and abiotic stresses (Figure 2) (Chen et al., 2019; Wang et al., 2019; Ahmad et al., 2022). The CRISPR/Cas9 system is favored for its simplicity, high efficiency, and cost-effectiveness compared to earlier genome-editing tools like zinc finger nucleases (ZFNs) and transcription activator-like effector nucleases (TALENs) (Wang et al., 2015; Razzaq et al., 2019; Zhou et al., 2023). Additionally, the development of base-editing tools and DNA-free delivery systems has further enhanced the precision and applicability of CRISPR/Cas9 in crop improvement.

Traditional breeding methods have long been used to improve crop traits, but they are often time-consuming and less precise. In contrast, molecular breeding techniques, including CRISPR/Cas9, offer a more targeted approach to genetic improvement. Molecular breeding can rapidly introduce desirable traits by directly modifying specific genes, bypassing the lengthy process of crossbreeding and selection (Razzaq et al., 2019; Wang et al., 2022). For instance, CRISPR/Cas9 has been used to create transgene-free, genome-edited plants with enhanced traits, such as improved starch quality in sweet potato and increased resistance to environmental stresses in other crops (Wang et al., 2019; Tussipkan and Manabayeva, 2021; Ahmad et al., 2022). These advancements highlight the potential of molecular breeding to complement and enhance traditional breeding efforts.

4.2 Genetic engineering of photosynthetic pathways in other crops: lessons for sweet potato

The application of genetic engineering to enhance photosynthetic pathways has been extensively studied in various crops, providing valuable insights for sweet potato improvement. For example, CRISPR/Cas9 has been used to modify genes involved in starch biosynthesis in potato, leading to improved tuber quality and yield (Wang et al., 2015; Ahmad et al., 2022). These studies demonstrate the potential of genome editing to enhance photosynthetic efficiency and overall crop performance. By leveraging these lessons, similar strategies can be applied to sweet potato to optimize its photosynthetic pathways and improve its productivity and nutritional value (Wang et al., 2019; Tussipkan and Manabayeva, 2021; Wang et al., 2022).

4.3 Potential challenges and risks in genetic modification for photosynthetic efficiency

While genetic modification holds great promise for enhancing photosynthetic efficiency, it also presents several challenges and risks. One major concern is the off-target effects of genome editing, which can lead to unintended genetic changes and potential ecological impacts (Chen et al., 2019; Razzaq et al., 2019; Zhou et al., 2023).

Additionally, the regulatory landscape for genetically modified organisms (GMOs) varies globally, posing challenges for the commercialization and acceptance of genome-edited crops (Wang et al., 2022). There are also technical challenges, such as optimizing gene-editing efficiency and ensuring stable expression of the modified traits. Addressing these challenges requires ongoing research and the development of more precise and reliable genome-editing tools, as well as robust regulatory frameworks to ensure the safe and effective use of genetic modification in agriculture.

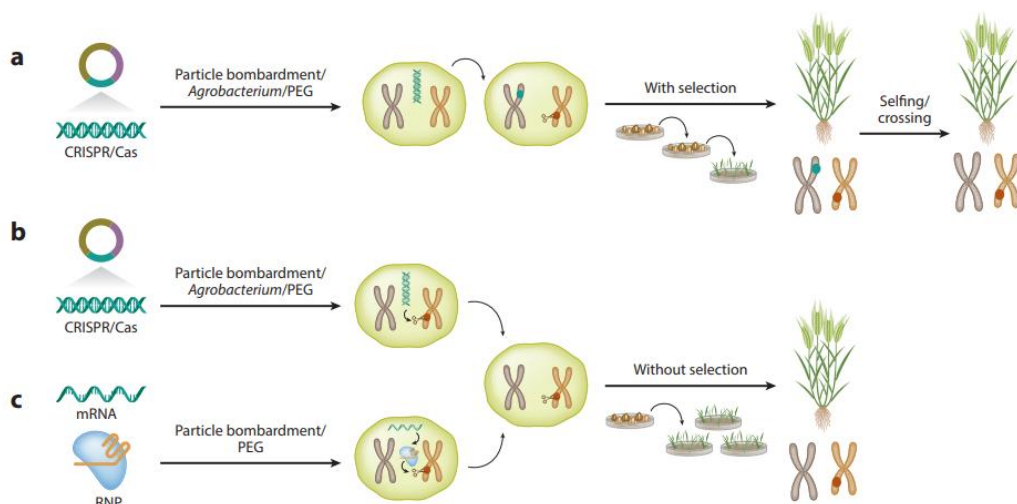


Figure 2 Delivery strategies for CRISPR/Cas systems to plants (Adopted from Chen et al., 2019)

Image caption: (a) Traditional delivery methods for CRISPR/Cas DNA combined with herbicide or antibiotic selection. Transgene-free plants can be obtained through genetic segregation by selfing and crossing. (b,c) Transient delivery systems for transgene-free and DNA-free genome editing. CRISPR reagents include DNA, mRNA, and RNP. After transient expression, CRISPR/Cas DNA, mRNA, or RNP will be degraded, and the edited plants can be regenerated without selection pressure. Abbreviations: mRNA, messenger RNA; PEG, polyethylene glycol; RNP, ribonucleoprotein (Adopted from Chen et al., 2019)

The integration of advanced genome-editing technologies, particularly CRISPR/Cas9, into sweet potato breeding programs offers significant potential for enhancing photosynthetic efficiency and overall crop performance. By learning from the successes and challenges of genetic engineering in other crops, researchers can develop targeted strategies to improve sweet potato traits. However, careful consideration of the potential risks and regulatory challenges is essential to ensure the safe and sustainable application of these technologies in agriculture.

5 Case Study: Genetic Insights from High-Photosynthetic Sweet Potato Varieties

5.1 Selection criteria for high-photosynthetic sweet potato varieties

The selection of high-photosynthetic sweet potato varieties involves identifying genotypes that exhibit superior photosynthetic efficiency and related traits. Key criteria include enhanced chlorophyll content, efficient carbon flux, and improved leaf anatomical morphology. For instance, overexpression of the H⁺-pyrophosphatase gene (IbVP1) in sweet potato has been shown to improve photosynthesis and sucrose content in source leaves, leading to increased starch content and yield in sink tissues (Figure 3) (Fan et al., 2021). Additionally, the identification of genetic loci associated with photosynthetic traits, such as the quantum yield of photosystem II (ΦPSII), can aid in selecting varieties with superior photosynthetic performance (Prinzenberg et al., 2018).

5.2 Comparative genetic analysis of high-photosynthetic and standard varieties

Comparative genetic analysis between high-photosynthetic and standard sweet potato varieties reveals significant differences in gene expression and genetic loci. For example, high-throughput sequencing has identified numerous single nucleotide polymorphisms (SNPs) and insertions/deletions (InDels) in genes involved in starch biosynthesis and sucrose metabolism, which are critical for photosynthetic efficiency (Zhang et al., 2020). Furthermore, expression quantitative trait locus (eQTL) analysis has uncovered regulatory networks that control gene expression variations in storage roots, highlighting the role of master regulators like IbMYB1-2 in anthocyanin biosynthesis and potentially influencing photosynthetic traits (Zhang et al., 2020).

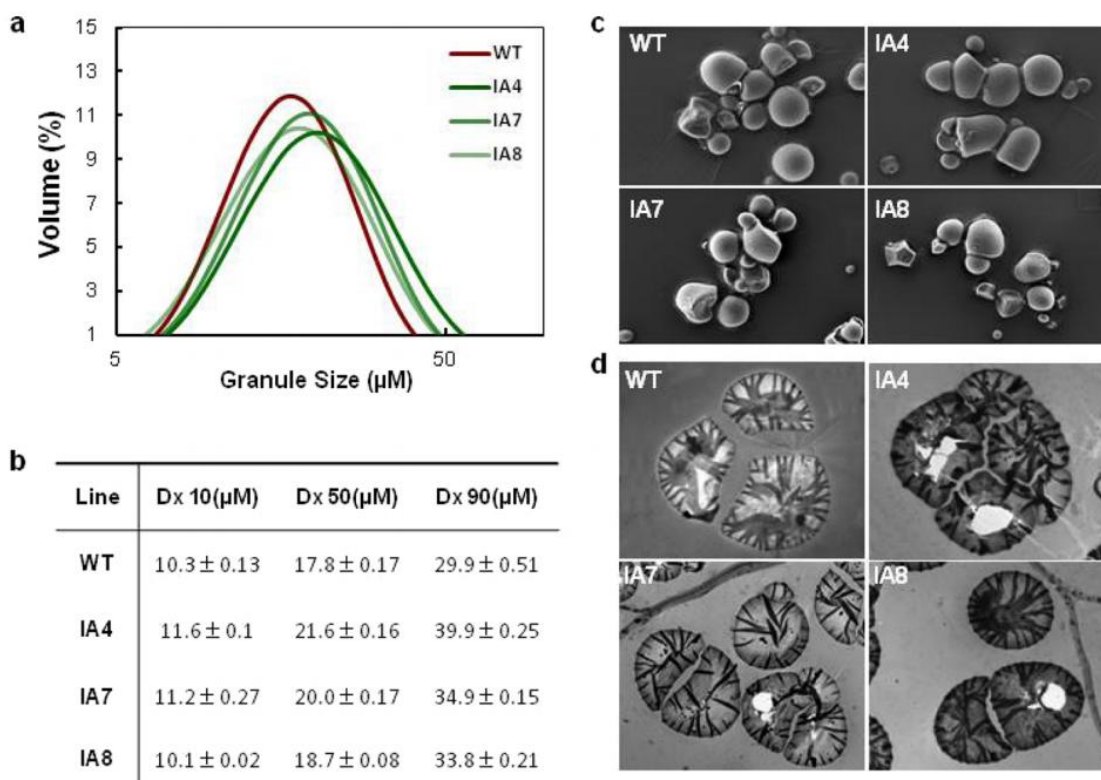


Figure 3 Starch granules from sweet potato storage roots (Adopted from Fan et al., 2021)

Image caption: a Starch granule size distribution. b Descriptive diameters Dx10, Dx50, and Dx90 of starch granules. Dx10, Dx50, and Dx90 are the projected equivalent diameters below which 10%, 50, and 90% of the total volume of all particles analyzed is represented. c Scanning electron microscopy images of extracted starch. d Transmission electron microscopy images of starch granules in storage roots. WT wild type; IA4, IA7, and IA8 are three independent IbVP1 transgenic lines. Five-month-old storage roots harvested from the field were used for analysis (Adopted from Fan et al., 2021)

5.3 Observed genetic traits contributing to improved photosynthesis

Several genetic traits have been observed to contribute to improved photosynthesis in sweet potato. Overexpression of the IbVP1 gene enhances phloem loading and sucrose transport, upregulating starch biosynthesis pathway genes such as AGPase and GBSSI, which are crucial for efficient photosynthesis and starch production (Fan et al., 2021). Additionally, the TCP transcription factors, particularly those targeted by miR319, play significant roles in leaf anatomical morphology, which directly impacts photosynthetic rates (Ren et al., 2021). The regulation of leaf polarity and development by transcription factors like IbNAC43 also affects photosynthetic efficiency, as seen in transgenic plants with altered leaf structure and reduced photosynthetic rates (Sun et al., 2023).

5.4 Implications for future breeding programs

The insights gained from genetic studies on high-photosynthetic sweet potato varieties have significant implications for future breeding programs. By leveraging genetic markers and regulatory networks identified through eQTL and SNP analyses, breeders can develop new varieties with enhanced photosynthetic efficiency and yield. The overexpression of key genes such as IbVP1 and IbMYB1 can be employed to improve starch production and antioxidant capacity under various environmental conditions (Park et al., 2015; Fan et al., 2021). Additionally, understanding the genetic basis of leaf anatomical traits and their impact on photosynthesis can guide the selection of genotypes with optimal leaf morphology for improved photosynthetic performance (Ren et al., 2021). These strategies will enable the development of sweet potato varieties that are more resilient to stress and have higher productivity, contributing to food security and agricultural sustainability.

6 Environmental and Physiological Influences on Photosynthesis in Sweet Potato

6.1 Effects of light intensity and quality

Light intensity and quality significantly influence the photosynthetic efficiency and overall growth of sweet potato. Shading experiments have shown that reduced light conditions can decrease the net photosynthetic rate, soluble sugar, starch, and sucrose content in sweet potato leaves. However, moderate shading (30%-50%) can increase chlorophyll concentrations and enhance the efficiency of light interception and absorption, which may help the plant adapt to low light environments (Jing et al., 2023). Additionally, the expression of genes related to photosynthesis and chlorophyll synthesis is upregulated under shading, indicating a complex regulatory mechanism to optimize light utilization.

6.2 Impact of temperature and water availability

Temperature and water availability are critical factors affecting photosynthesis in sweet potato. High temperatures can cause photo-oxidative damage to the photosynthetic machinery, but the *Orange* gene (IbOr) in sweet potato helps maintain carotenoid homeostasis and stabilizes photosystem II, thereby enhancing tolerance to heat stress (Kim et al., 2018). Water availability also plays a crucial role; drought conditions can reduce photosynthetic rates and water use efficiency. However, overexpression of certain genes, such as *BBX21*, can improve photosynthesis and water use efficiency under moderate drought by enhancing mesophyll conductance and electron transport capacity (Ocampo et al., 2021). Additionally, the StCDF1-StFLORE locus in potato, which regulates water loss and stomatal conductance, highlights the importance of genetic factors in managing water use under drought conditions (Gonzales et al., 2020).

6.3 Interaction of genetic regulation with environmental factors

Epigenetic regulation plays a significant role in the adaptation of photosynthesis to environmental changes. Epigenetic mechanisms, such as histone acetylation and DNA demethylation, mediate the expression of key photosynthetic genes like RuBisCO and PEPC in response to light, temperature, and drought conditions. For instance, euchromatin configuration can enhance drought tolerance by optimizing stomatal conductance and gas exchange, suggesting that epigenetic modifications are crucial for photosynthetic plasticity and stress adaptation (Duarte-Aké et al., 2019). Additionally, the overexpression of epigenetic modifiers like StMSI1 and StE[z]2 in potato has been shown to induce tuber formation and improve plant architecture under varying photoperiods, further emphasizing the role of epigenetics in environmental adaptation (Kondhare et al., 2021).

The interaction between genetic regulation and environmental factors significantly impacts the yield of sweet potato. Overexpression of the H⁺-pyrophosphatase gene (IbVP1) in sweet potato enhances photosynthesis and sucrose content in leaves, leading to increased starch content and total yield in storage roots (Fan et al., 2021). Similarly, the *BBX21* gene improves photosynthetic rates and water use efficiency under drought conditions, resulting in higher tuber yield (Ocampo et al., 2021). However, not all genetic modifications lead to positive outcomes; for example, the overexpression of VPZ genes in potato, which accelerates non-photochemical quenching, did not improve photosynthetic rates or yield under fluctuating light conditions, highlighting the complexity of genetic-environmental interactions (Lehretz et al., 2022). These findings underscore the importance of understanding and optimizing genetic regulation to enhance crop yield under diverse environmental conditions.

7 Prospects and Future Directions

7.1 Emerging technologies in photosynthesis research

Recent advancements in photosynthesis research have opened new avenues for enhancing the efficiency of this critical process in sweet potatoes. One promising approach involves the use of kinetic modeling to identify and optimize key photosynthetic enzymes. For instance, a study on potato demonstrated that manipulating the expression of enzymes such as Rubisco, FBP aldolase, and SBPase could significantly increase photosynthetic rates, suggesting similar strategies could be applied to sweet potatoes (Vijayakumar et al., 2023). Additionally, the heterologous expression of transcription factors like AtBBX21 has shown potential in improving photosynthetic efficiency and reducing photoinhibition under high-irradiance conditions, which could be beneficial for sweet

potato cultivation in diverse environments (Crocco et al., 2018; Ocampo et al., 2021). Furthermore, chlorophyll fluorescence imaging has emerged as a powerful tool for non-invasive assessment of photosynthetic traits, enabling rapid identification of genetic variations that can be targeted for crop improvement (Prinzenberg et al., 2018).

7.2 Future opportunities for enhancing photosynthetic efficiency through genetic improvement

Genetic engineering offers substantial opportunities to enhance photosynthetic efficiency in sweet potatoes. Overexpression of genes such as IbVP1 has been shown to improve photosynthesis and sucrose content in source leaves, leading to increased starch content and yield in sweet potato storage roots (Fan et al., 2021). Similarly, the IbOr gene, which regulates carotenoid homeostasis, has been found to enhance plant tolerance to environmental stress, thereby stabilizing photosystem II and potentially improving photosynthetic efficiency under stress conditions (Kim et al., 2018). Another promising approach involves the manipulation of non-photochemical quenching (NPQ) mechanisms to optimize light energy utilization, as demonstrated in transgenic potato plants expressing VPZ genes (Lehretz et al., 2022). These genetic improvements could be further accelerated by leveraging natural allelic variations found in crop germplasm collections, as well as employing gene editing technologies to introduce beneficial traits into elite sweet potato cultivars (Sharwood et al., 2022).

7.3 Implications for global sweet potato production and food security

Enhancing the photosynthetic efficiency of sweet potatoes through genetic improvements has significant implications for global food security. As the demand for food continues to rise, improving the yield potential of staple crops like sweet potatoes is crucial. By increasing photosynthetic rates and optimizing carbohydrate metabolism, it is possible to achieve higher yields and better resilience to environmental stresses, thereby contributing to more stable food supplies (Long et al., 2022). Moreover, the application of advanced genetic technologies and the identification of key photosynthetic traits can help bridge the gap between current yield levels and the potential biological limits of sweet potatoes, ensuring that this vital crop can meet future food demands (Long et al., 2015). Overall, these advancements not only promise to enhance sweet potato production but also offer a model for improving other major crops, thereby supporting global efforts to achieve food security.

8 Concluding Remarks

The genetic regulation of photosynthesis in sweet potato has been extensively studied, revealing several key insights. Overexpression of the H⁺-pyrophosphatase gene IbVP1 significantly enhances photosynthesis and sucrose content in source leaves, leading to increased starch content and yield in storage roots. Conversely, the NAC transcription factor IbNAC43 negatively impacts photosynthesis by causing leaf curling and reducing chlorophyll content. The B-box transcription factor IbBBX29 has been shown to increase leaf biomass and flavonoid accumulation, which are crucial for plant growth and stress resistance. Additionally, the myo-inositol-1-phosphate synthase gene IbMIPS1 enhances photosynthesis and stress tolerance, further supporting the importance of genetic regulation in sweet potato. The transcription factor IbC3H18 also plays a significant role in enhancing abiotic stress tolerance and regulating photosynthesis. Moreover, the colonization of sweet potato by *Piriformospora indica* improves photosynthesis and growth, highlighting the potential of symbiotic relationships in enhancing photosynthetic efficiency.

The findings from these studies have significant implications for breeding and crop improvement in sweet potato. The overexpression of genes such as IbVP1 and IbMIPS1 can be utilized to develop sweet potato varieties with higher photosynthetic efficiency and stress tolerance, leading to improved yield and resilience under adverse conditions. The identification of transcription factors like IbBBX29 and IbC3H18 provides potential targets for genetic engineering to enhance leaf development and stress responses, which are critical for maintaining high photosynthetic rates. Additionally, understanding the negative regulatory roles of genes like IbNAC43 can help in developing strategies to mitigate their effects, thereby improving overall plant growth and photosynthetic efficiency. The use of symbiotic relationships, such as with *Piriformospora indica*, offers a novel approach to enhance photosynthesis and growth through natural means.

The genetic regulation of photosynthesis is crucial for the sustainable cultivation of sweet potato. By leveraging genetic insights and biotechnological advancements, it is possible to develop sweet potato varieties that are not only high-yielding but also resilient to environmental stresses. The integration of genes that enhance photosynthesis and stress tolerance can lead to more robust crops, ensuring food security and sustainability. Furthermore, the exploration of symbiotic relationships and natural growth promoters offers additional avenues for improving sweet potato cultivation. Overall, the continued research into the genetic regulation of photosynthesis will play a pivotal role in achieving sustainable agricultural practices and meeting the growing demands for food production.

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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.

References

- Ahmad D., Zhang Z., Rasheed H., Xu X., and Bao J., 2022, Recent advances in molecular improvement for potato tuber traits, *International Journal of Molecular Sciences*, 23(17): 9982.
<https://doi.org/10.3390/ijms23179982>
- Baslam M., Mitsui T., Hodges M., Priesack E., Herritt M., Aranjuelo Í., and Sanz-Saez A., 2020, Photosynthesis in a changing global climate: scaling up and scaling down in crops, *Frontiers in Plant Science*, 11: 882.
<https://doi.org/10.3389/fpls.2020.00882>
- Chen K., Wang Y., Zhang R., Zhang H., and Gao C., 2019, CRISPR/Cas genome editing and precision plant breeding in agriculture, *Annual review of plant biology*, 70: 667-697.
<https://doi.org/10.1146/annurev-arplant-050718-100049>
- Crocco C., Ocampo G., Ploschuk E., Mantese A., and Botto J., 2018, Heterologous expression of AtBBX21 enhances the rate of photosynthesis and alleviates photoinhibition in *Solanum tuberosum* L., *Plant Physiology*, 177: 369-380.
<https://doi.org/10.1104/pp.17.01417>
- Duarte-Aké F., Us-Camas R., Cancino-García V., and De-la-Peña C., 2019, Epigenetic changes and photosynthetic plasticity in response to environment, *Environmental and Experimental Botany*, 159: 108-120.
<https://doi.org/10.1016/j.envexpbot.2018.12.010>
- Fan W., Zhang Y., Wu Y., Zhou W., Yang J., Yuan L., Zhang P., and Wang H., 2021, The H⁺-pyrophosphatase IbVP1 regulates carbon flux to influence the starch metabolism and yield of sweet potato, *Horticulture Research*, 8: 20.
<https://doi.org/10.1038/s41438-020-00454-2>
- Gao X., Zhang H., Li X., Bai Y., Peng K., Wang Z., Dai Z., Bian X., Zhang Q., Jia L., Li Y., Liu Q., Zhai H., Gao S., Zhao N., and He S., 2022, The B-box transcription factor IbBBX29 regulates leaf development and flavonoid biosynthesis in sweet potato, *Plant Physiology*, 191(1): 496-514.
<https://doi.org/10.1093/plphys/kiac516>
- Gonzales L., Shi L., Bergonzi S., Oortwijn M., Franco-Zorrilla J., Solano-Tavira R., Visser R., Abelenda J., and Bachem C., 2020, Potato CYCLING DOF FACTOR 1 and its lncRNA counterpart StFLORE link tuber development and drought response, *The Plant Journal*, 105: 855-869.
<https://doi.org/10.1111/tpj.15093>
- Jing X., Chen P., Jin X., Lei J., Wang L., Chai S., and Yang X., 2023, Physiological, photosynthetic, and transcriptomics insights into the influence of shading on leafy sweet potato, *Genes*, 14(12): 2112.
<https://doi.org/10.3390/genes14122112>
- Keller B., Soto J., Steier A., Portilla-Benavides A., Raatz B., Studer B., Walter A., Muller O., and Urban M., 2023, Linking photosynthesis and yield reveals a strategy to improve light use efficiency in a climbing bean breeding population, *Journal of Experimental Botany*, 75(3): 901-916.
<https://doi.org/10.1093/jxb/erad416>
- Kim H., Ji C., Lee C., Kim S., Park S., and Kwak S., 2018, Orange: a target gene for regulating carotenoid homeostasis and increasing plant tolerance to environmental stress in marginal lands, *Journal of Experimental Botany*, 69: 3393-3400.
<https://doi.org/10.1093/jxb/ery023>
- Kondhare K., Kumar A., Patil N., Malankar N., Saha K., and Banerjee A., 2021, Development of aerial and belowground tubers in potato is governed by photoperiod and epigenetic mechanism, *Plant Physiology*, 187(3): 1071-1086.
<https://doi.org/10.1093/plphys/kiab409>

- Lehretz G., Schneider A., Leister D., and Sonnewald U., 2022, High non-photochemical quenching of VPZ transgenic potato plants limits CO₂ assimilation under high light conditions and reduces tuber yield under fluctuating light, *Journal of Integrative Plant Biology*, 64(9): 1821-1832.
<https://doi.org/10.1111/jipb.13320>
- Long S., Marshall-Colón A., and Zhu X., 2015, Meeting the global food demand of the future by engineering crop photosynthesis and yield potential, *Cell*, 161: 56-66.
<https://doi.org/10.1016/j.cell.2015.03.019>
- Long S., Taylor S., Burgess S., Carmo-Silva E., Lawson T., Souza A., Leonelli L., and Wang Y., 2022, Into the shadows and back into sunlight: photosynthesis in fluctuating light, *Annual Review of Plant Biology*, 73: 617-648.
<https://doi.org/10.1146/annurev-arplant-070221-024745>
- Lu Y.Y., Ma H.C., and Li H.M., 2015, Light response characteristics of photosynthetic of transgenic sweet potato under drought stress, *Acta Ecologica Sinica*, 35(7): 2155-2160.
<https://doi.org/10.5846/stxb201306041308>
- Ocampo G., Ploschuk E., Mantese A., Crocco C., and Botto J., 2021, BBX21 reduces ABA sensitivity, mesophyll conductance and chloroplast electron transport capacity to increase photosynthesis and water use efficient in potato plants cultivated under moderated drought, *The Plant Journal : For Cell and Molecular Biology*, 108(4): 1131-1144.
<https://doi.org/10.1111/tpj.15499>
- Park S., Kim Y., Kim S., Jeong Y., Kim C., Lee J., Bae J., Ahn M., Jeong J., Lee H., and Kwak S., 2015, Overexpression of the IbMYB1 gene in an orange-fleshed sweet potato cultivar produces a dual-pigmented transgenic sweet potato with improved antioxidant activity, *Physiologia Plantarum*, 153(4): 525-537.
<https://doi.org/10.1111/ppl.12281>
- Prinzenberg A., Viquez-Zamora M., Harbinson J., Lindhout P., and Heusden S., 2018, Chlorophyll fluorescence imaging reveals genetic variation and loci for a photosynthetic trait in diploid potato, *Physiologia Plantarum*, 164(2): 163-175.
<https://doi.org/10.1111/ppl.12689>
- Razzaq A., Saleem F., Kanwal M., Mustafa G., Yousaf S., Arshad H., Hameed M., Khan M., and Joyia F., 2019, Modern trends in plant genome editing: an inclusive review of the CRISPR/Cas9 toolbox, *International Journal of Molecular Sciences*, 20(16): 4045.
<https://doi.org/10.3390/ijms20164045>
- Ren L., Wu H., Zhang T., Ge X., Wang T., Zhou W., Zhang L., Ma D., and Wang A., 2021, Genome-wide identification of TCP transcription factors family in sweet potato reveals significant roles of miR319-Targeted TCPs in leaf anatomical morphology, *Frontiers in Plant Science*, 12: 686698.
<https://doi.org/10.3389/fpls.2021.686698>
- Sharwood R., Quick W., Sargent D., Estavillo G., Silva-Pérez V., and Furbank R., 2022, Mining for allelic gold: finding genetic variation in photosynthetic traits in crops and wild relatives, *Journal of Experimental Botany*, 73(10): 3085-3108.
<https://doi.org/10.1093/jxb/erac081>
- Sun S., Li X., Nie N., Chen Y., Gao S., Zhang H., He S., Liu Q., and Zhai H., 2023, Sweet potato NAC transcription factor NAC43 negatively regulates plant growth by causing leaf curling and reducing photosynthetic efficiency, *Frontiers in Plant Science*, 14: 1095977.
<https://doi.org/10.3389/fpls.2023.1095977>
- Theeuwens T., Logie L., Harbinson J., and Aarts M., 2022, Genetics as a key to improving crop photosynthesis, *Journal of Experimental Botany*, 73: 3122-3137.
<https://doi.org/10.1093/jxb/erac076>
- Tussipkan D., and Manabayeva S., 2021, Employing CRISPR/Cas technology for the improvement of potato and other tuber crops, *Frontiers in Plant Science*, 12: 747476.
<https://doi.org/10.3389/fpls.2021.747476>
- Tao J., and Han J.Q., 2024, Physiological mechanisms of photosynthesis and antioxidant system in rice under high temperature stress, *Rice Genomics and Genetics*, 15(1): 36-47.
<https://doi.org/10.5376/rgg.2024.15.0005>
- Vijayakumar S., Wang Y., Lehretz G., Taylor S., Carmo-Silva E., and Long S., 2023, Kinetic modeling identifies targets for engineering improved photosynthetic efficiency in potato, (*Solanum tuberosum* cv. Solara), *The Plant Journal : For Cell and Molecular Biology*, 117(2): 561-572.
<https://doi.org/10.1111/tpj.16512>
- Wang H., Wu Y., Zhang Y., Yang J., Fan W., Zhang H., Zhao S., Yuan L., and Zhang P., 2019, CRISPR/Cas9-based mutagenesis of starch biosynthetic genes in sweet potato (*Ipomoea batatas*) for the improvement of starch quality, *International Journal of Molecular Sciences*, 20(19): 4702.
<https://doi.org/10.3390/ijms20194702>
- Wang L., Du Q., Xie J., Zhou D., Chen B., Yang H., and Zhang D., 2018, Genetic variation in transcription factors and photosynthesis light-reaction genes regulates photosynthetic traits, *Tree Physiology*, 38: 1871-1885.
<https://doi.org/10.1093/treephys/tpy079>
- Wang S., Zhang S., Wang W., Xiong X., Meng F., and Cui X., 2015, Efficient targeted mutagenesis in potato by the CRISPR/Cas9 system, *Plant Cell Reports*, 34: 1473-1476.
<https://doi.org/10.1007/s00299-015-1816-7>
- Wang Y., Zafar N., Ali Q., Manghar H., Wang G., Yu L., Ding X., Ding F., Hong N., Wang G., and Jin S., 2022, CRISPR/Cas genome editing technologies for plant improvement against biotic and abiotic stresses: advances, limitations, and future perspectives, *Cells*, 11(23): 3928.
<https://doi.org/10.3390/cells11233928>

- Zhai H., Wang F., Si Z., Huo J., Xing L., An Y., He S., and Liu Q., 2016, A myo-inositol-1-phosphate synthase gene, IbMIPS1, enhances salt and drought tolerance and stem nematode resistance in transgenic sweet potato, *Plant Biotechnology Journal*, 14(2): 592-602.
<https://doi.org/10.1111/pbi.12402>
- Zhang H., Gao X., Zhi Y., Li X., Zhang Q., Niu J., Wang J., Zhai H., Zhao N., Li J., Liu Q., and He S., 2019, A non-tandem CCCH-type zinc-finger protein, IbC3H18, functions as a nuclear transcriptional activator and enhances abiotic stress tolerance in sweet potato, *The New Phytologist*, 223(4): 1918-1936.
<https://doi.org/10.1111/nph.15925>
- Zhang K., Luo K., Li S., Peng D., Tang D., Lu H., Zhao Y., Lv C., and Wang J., 2020, Genetic variation and sequence diversity of starch biosynthesis and sucrose metabolism genes in sweet potato, *Agronomy*, 10(5): 627.
<https://doi.org/10.3390/agronomy10050627>
- Zhang K., Wu Z., Wu X., Han H., Ju X., Fan Y., Yang C., Tang D., Cao Q., Wang J., and Lv C., 2023, Regulatory and functional divergence among members of Ibβfruct2, a sweet potato vacuolar invertase gene controlling starch and glucose content, *Frontiers in Plant Science*, 14: 1192417.
<https://doi.org/10.3389/fpls.2023.1192417>
- Zhang L., Yu Y., Shi T., Kou M., Sun J., Xu T., Li Q., Wu S., Cao Q., Hou W., and Li Z., 2020, Genome-wide analysis of expression quantitative trait loci (eQTLs) reveals the regulatory architecture of gene expression variation in the storage roots of sweet potato, *Horticulture Research*, 7: 90.
<https://doi.org/10.1038/s41438-020-0314-4>
- Zhou J., Luan X., Liu Y., Wang L., Wang J., Yang S., Liu S., Zhang J., Liu H., and Yao D., 2023, Strategies and methods for improving the efficiency of CRISPR/Cas9 gene editing in plant molecular breeding, *Plants*, 12(7): 1478.
<https://doi.org/10.3390/plants12071478>
- Zhu T., Li L., Feng L., and Ren M., 2020, StABI5 Involved in the regulation of chloroplast development and photosynthesis in potato, *International Journal of Molecular Sciences*, 21(3): 1068.
<https://doi.org/10.3390/ijms21031068>

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