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Harnessing natural variation for photosynthetic improvement in next-generation crop breeding[FA]

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ABSTRACT

Because agriculture is confronted with escalating climatic and resource challenges, next-generation breeding requires innovative strategies to sustain and enhance crop productivity. As the foundation of carbon fixation in plants, photosynthesis strongly affects crop yield potential. Therefore, improving photosynthetic performance remains a central goal for crop improvement. Plants show substantial natural genetic variation in photosynthetic traits, arising from heritable differences in physiology, including metabolism and regulation, which represent valuable genetic resources for crop breeding. Meanwhile, advances in synthetic biology and photosynthetic genetic engineering provide complementary avenues for enhancing photosynthetic capacity and productivity. In this review, we analyze and synthesize recent progress in research on (i) natural variation in photosynthetic traits across physiological, developmental, and canopy scales; (ii) molecular and genetic regulatory mechanisms underlying photosynthetic diversity and adaptations; (iii) links between photosynthetic efficiency, source–sink coordination, and yield formation; and (iv) emerging strategies for engineering photosynthesis. We also outline remaining challenges and future perspectives. Collectively, these insights provide a strategic framework for leveraging natural genetic diversity and modern biotechnologies to optimize photosynthesis, enhance yield potential, and improve crop resilience under future climate scenarios, further supporting global food security.

Keywords: crop yield improvement, genetic regulation, natural variation, photosynthesis, photosynthetic efficiency, photosynthetic engineering

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INTRODUCTION

Global food demand continues to increase under intensifying climatic changes and environmental stress, exerting sustained strains on agricultural production systems (OECD/FAO, 2025). To sustain the growing population under these constraints, increasing crop productivity remains a fundamental objective of agricultural production. Although modern breeding programs and agronomic innovations have substantially boosted yields over the past decades (Lawson et al., 2012; Hickey et al., 2019; Wang et al., 2021; Gu and Han, 2024), many conventional high-yielding strategies are now approaching their physiological limits (Li et al., 2025b). Improving photosynthetic efficiency has therefore been recognized as a promising avenue for further yield improvement (Flood et al., 2011; Yin and Struik, 2015; Yin et al., 2022).

Photosynthesis is the fundamental process driving global carbon fixation and energy flow, contributing 90%–95% of plant dry matter accumulation and directly determining yield potential (Xu et al., 2022). Despite extensive efforts to improve photosynthetic performance through crop management practices—including fertilizer application, irrigation, and canopy manipulation—the actual solar energy conversion efficiency of modern annual crops at the canopy level remains low, approximately 2.2% in C_3 crops and 3.0% in C_4 crops, far below their theoretical maxima of 3.6% and 4.1%, respectively (Yin and Struik, 2015). This gap indicates the vast untapped potential for further improvement. However, photosynthesis is a highly complex trait governed by interactions among biochemical, physiological, developmental, genetic, environmental, and agronomic management factors. In field environments, the photosynthetic performance of healthy crops is dynamically influenced by fluctuating light, temperature variation, and water and nutrient availability. Consequently, improving photosynthesis requires not only enhanced steady-state efficiency but also optimized dynamic responses to variable environmental conditions.

To further improve photosynthetic performance, natural variation represents an essential resource, serving as the fundamental driver of plant adaptation and evolution while providing valuable genetic resources for crop improvement (Meyer and Purugganan, 2013; Hickey et al., 2019). Natural variation could be defined as heritable phenotypic and genetic diversity that arises spontaneously within or among populations without intentional human manipulation, including allele differences, *cis*-regulatory polymorphisms, small- and large-effect structural variants, and stable epigenetic states shaped by long-term environmental selection that can be exploited for future crop breeding (Flood et al., 2011; Flood, 2019; Liang et al., 2021; López et al., 2022; Taylor et al., 2023). We further distinguish intra-specific natural variation, referring to phenotypic or genetic differences within a single species (Alonso-Blanco et al., 2009), from interspecific natural variation, which refers to the divergence among species.

In photosynthesis research, conventional studies have primarily focused on physiological traits such as leaf chlorophyll content and photosynthetic rate, while the underlying genetic and molecular mechanisms governing photosynthetic efficiency have remained comparatively unexplored. Recent advances in molecular biology, genomics, high-throughput phenotyping, and biotechnology now enable the precise identification and manipulation of alleles directly associated with enhanced photosynthetic efficiency. Consequently, over the past two decades, numerous natural and synthetic variants have been uncovered, offering new opportunities for improving crop productivity and stress resilience.

Natural variation in photosynthesis not only contributes to environmental adaptation but also provides important opportunities for modern crop improvement (Croce et al., 2024). In this review, we first summarize current knowledge regarding natural variation in photosynthesis across physiological, developmental, and genetic scales, together with current strategies for photosynthetic engineering, and highlight the potential of harnessing natural variation for crop improvement. We further examine representative natural alleles and their responses to environmental fluctuations and evaluate the relationships between photosynthetic variation and crop yield. Finally, we highlight major challenges and future opportunities for integrating natural photosynthetic variation into next-generation crop improvement. Together, this review provides a systematic and conceptual foundation that connects natural variation to functional mechanisms and breeding applications, emphasizing that coordinated improvements across dynamic regulation, tissue-specific performance, and molecular networks are essential for developing resilient and high-efficiency crops.

NATURAL VARIATION IN PHOTOSYNTHETIC TRAITS

Photosynthetic natural variations across multiple biological scales collectively shape carbon assimilation, resource use efficiency, stress resilience, and ultimately crop productivity. Understanding how photosynthetic traits and their limitations vary across spatial and temporal scales is therefore essential for improving photosynthetic efficiency under realistic field conditions (Figure 1).

Variation in dynamic photosynthetic regulation

Plants growing under natural conditions experience continuous fluctuations in irradiance, temperature, humidity, and water availability. Consequently, plants must coordinate light absorption, electron transport, and stomatal response dynamically to maintain photosynthetic performance under field conditions (Slattery et al., 2018; Tanaka et al., 2019).

Natural variation in leaf structural and physiological traits strongly affects photosynthetic responses to fluctuating light environments. Studies have shown that Arabidopsis grown under fluctuating light conditions often develops thinner leaves with reduced light absorption compared with plants grown under stable light conditions. Although their steady-state photosynthetic rate per unit leaf area is similar, their early vegetative growth tends to be slower (Vialet-Chabrand et al., 2017). Similar observations have been reported in crops: in rice, plant height and growth rate were reduced under fluctuating light, associated with increased non-photochemical quenching (NPQ) components and decreased electron transport rate (Wei et al., 2021). Notably, substantial intra-specific variation has also been reported, with *japonica* cultivars generally demonstrating superior NPQ induction capacities compared to *indica* cultivars (Kasajima et al., 2011). Crucially, challenges of fluctuating light extend beyond photoprotection to interactions with water relations. Growth inhibition is influenced by stomatal dynamics: Although rapid stomatal opening promotes gas exchange, it reduces water use efficiency (WUE), reflecting a critical balance between light response and water management in variable environments

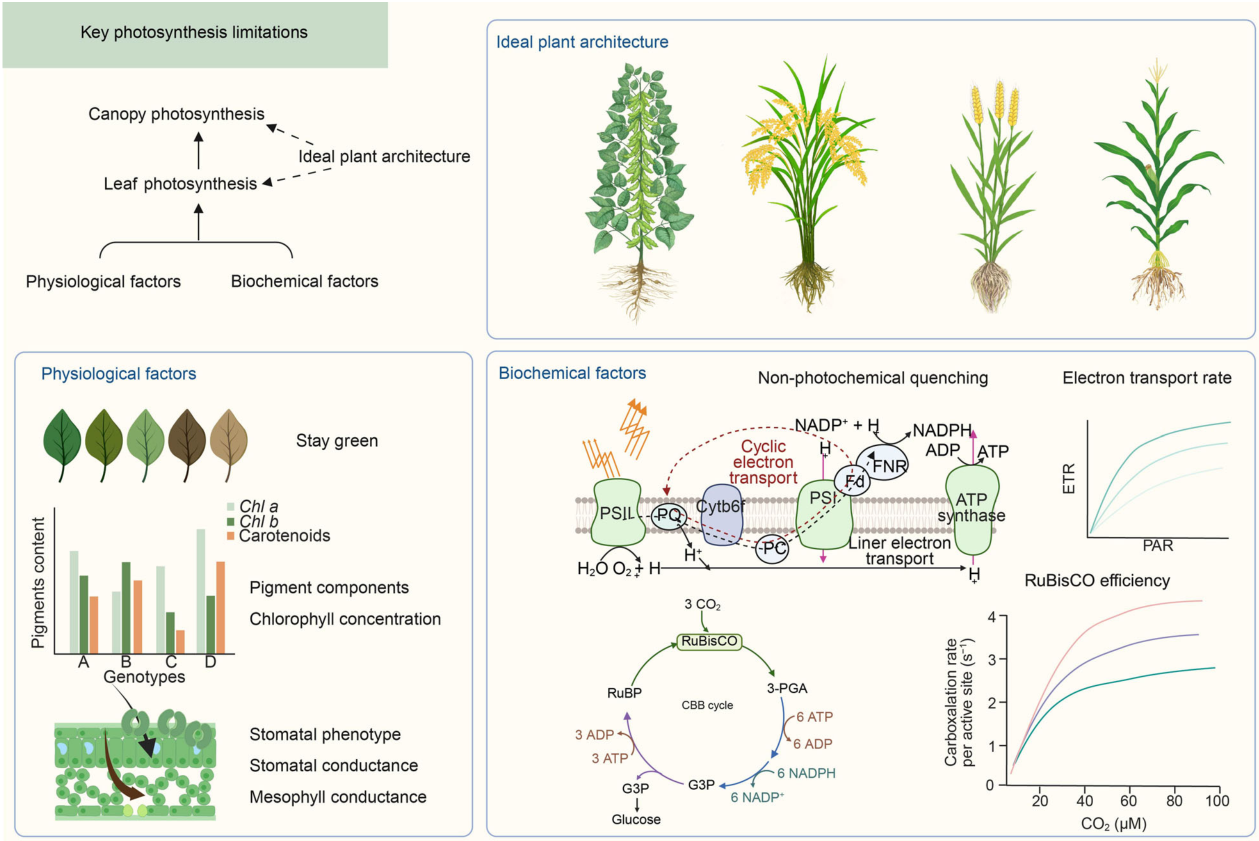

Figure 1. Key limitations to photosynthesis

Photosynthesis, the foundation of plant growth and yield formation, is constrained by multiple limiting factors. At the physiological level, these include leaf color, stay-green ability, duration of photosynthetic activity, stomatal conductance (g_s), and mesophyll conductance (g_m). Structural features such as leaf anatomy and canopy architecture significantly influence the overall photosynthetic capacity. At the molecular level, limiting factors include the efficiency of photosynthetic electron transport rate (ETR) and its relation to NPQ (non-photochemical quenching), the catalytic efficiency of RuBisCO to fix CO_2 (which is the limiting step of the Calvin–Benson–Bassham (CBB) cycle), and the coordination among photosynthetic components.

(Vialet-Chabrand et al., 2017; Eyland et al., 2021). This variation highlights that the dynamic regulation is not only a response of photosynthetic components to fluctuating light but also emerges from coordinated multi-scale processes that sustain higher overall photosynthetic performance rather than steady-state photosynthetic capacity alone.

Photosynthetic midday depression further illustrates another natural variation in dynamic photosynthetic regulation. While substantial differences in midday depression have been observed between photosynthetic types (e.g., C_3 vs. C_4 plants), considerable variation also occurs within species (Huang et al., 2006; Kumagai et al., 2009; Gu et al., 2017; Verma et al., 2020; Al-Salman et al., 2023). Even among C_3 genotypes, some show a pronounced midday decline associated with stomatal closure, enhanced NPQ, and increased photorespiration, while others maintain stable assimilation. The underlying genetic and molecular mechanisms of photosynthetic midday depression remain incompletely understood, but several systematic investigations point to variation in stomatal sensitivity, hydraulic regulation, and photoprotective responses. This makes midday depression a physiologically meaningful and promising phenotype for future genetic dissection to identify alleles that confer superior performance under high-light or water-limited conditions.

Variation in tissue- and developmental-specific photosynthesis

Photosynthetic variation also occurs across tissues and contributes to whole-plant carbon balance (Dehigaspitiya et al., 2019). Beyond leaves, non-foliar tissues such as stems and reproductive organs can contribute significantly to whole-plant carbon assimilation, energy partitioning, and stress resilience (Simkin et al., 2020), and their relative importance varies across species and genotypes.

Stem photosynthesis contributes to carbon gain through assimilation of atmospheric CO_2 and re-assimilation of respired CO_2, while its association with chlorophyll content, non-structural carbohydrates (NSC) levels, and gas exchange measurement highlights its functional complementarity to leaf photosynthesis (Bloemen et al., 2014; Valverdi et al., 2025). Species such as *Laurus nobilis* strongly depend on stem photosynthesis for growth, whereas *Populus alba* is strongly associated with it for hydraulic recovery (Trifilò et al., 2021), illustrating interspecific diversity in functional roles.

Moreover, natural variation in tissue-level photosynthesis is closely linked to developmental stages and plant growth. Specifically, photosynthesis in reproductive organs plays a key role in grain filling, contributing 12%–60% of the total yield and compensating for reduced leaf photosynthesis during leaf senescence or stress conditions in cereals (Maydup et al., 2010; Sanchez-Bragado et al., 2016; Zhang et al., 2022). Its efficiency depends on both genetic and anatomical characteristics. For example, panicle photosynthesis in rice is associated with vascular structure (Zhang et al., 2022), while in chickpea, pod wall photosynthesis accounts for the majority of recapturing respired CO_2, and pod walls function as primary photosynthetic tissues (Furbank et al., 2004; Zhang et al., 2025). These differences suggest that optimization of non-foliar photosynthesis should consider the distinct roles of different tissues in internal carbon recycling and direct carbon assimilation.

Interestingly, natural variation can also occur between vegetative and reproductive tissues, with some reproductive tissues showing photosynthetic characteristics that differ from those of the whole plant. Such cases reflect a partial decoupling of tissue-specific metabolic function from the dominant whole-plant photosynthetic type. For instance, maize husk tissues display a C_3-like characteristic despite the plant being a typical C_4 type (Langdale et al., 1988; Pengelly et al., 2011). Conversely, in wheat (*Triticum aestivum*), a C_3 species, C_4-like photosynthetic enzymes can be transcriptionally induced in spike bracts under drought stress, suggesting tissue-specific metabolic plasticity (Rangan et al., 2016; Zhang et al., 2019a), although this remains debated due to the limited biochemical and physiological validation (Busch and Farquhar, 2016).

Collectively, these findings indicate that photosynthesis is regulated differently across tissues and developmental stages, with important consequences for carbon allocation, stress adaptation, and yield stability. The molecular basis underlying these variations is discussed in a later section on molecular and genetic mechanisms.

Variation in canopy architecture and whole-plant photosynthesis

Photosynthesis measured at the single-leaf scale cannot reflect the whole-plant performance or yield potential. Thus, natural variations in plant and canopy architecture, which govern how light is intercepted, distributed, and utilized throughout the canopy, require systematic investigation. Early frameworks such as Donald's crop ideotype (Donald, 1968) emphasized coordinated interactions among different tissues and plants, whereas the more recent "smart canopy" concept highlights the importance of harmonized light capture across canopy layers rather than maximizing photosynthesis in individual leaves (Ort et al., 2015).

These ideas have guided the identification of allelic variation underlying canopy architecture in crops. In maize, diversity at loci such as the B3-domain transcription factor *ABI3/VP1-Like 1* (*ZmRAVL1*) and *leaf angle architecture of smart canopy 1* (*lac1*) contributes to differences in leaf angle and canopy structure that enhance light distribution and biomass production under dense planting (Tian et al., 2019, 2024). An optimized canopy architecture promotes functional coordination between upper and lower canopy layers, improving whole-canopy photosynthetic efficiency (Yan et al., 2024).

Beyond structural traits, Li et al. (2025b) recently proposed the concept of "physiotype", emphasizing that variation in photoassimilate partitioning and the coordination between internal physiology and metabolism, and external canopy architecture also contribute to whole plant photosynthetic efficiency. These findings suggest that future crop improvement should consider not only plant architecture but also physiological and metabolic traits, as both collectively influence canopy photosynthesis and overall crop productivity.

Natural variation in photosynthetic acclimation and resource allocation

Substantial natural variation exists in the capacity of plants to acclimate to environmental gradients. In particular, genotypic differences in photosynthetic plasticity, assimilate partitioning, and resource-use strategies play critical roles in determining stress tolerance and yield stability, making these traits important targets for breeding.

Natural variation in photosynthetic acclimation is closely associated with differences in water-use strategies (Gjindali and Johnson, 2023). Genotypes differ in their regulation of stomatal conductance, leading to contrasting trade-offs between carbon assimilation and water conservation, with nitrogen status further modulating these responses (Gong et al., 2010). Under drought stress, genotypes also vary in their ability to maintain assimilate transport and utilize NSCs to buffer reductions in carbon supply, reflecting natural diversity in xylem–phloem coordination and metabolic resilience (Prats et al., 2023). Variation also occurs at different developmental stages when plants respond to drought. For instance, mild drought during the early or mid-grain filling stage can promote the remobilization of pre-anthesis assimilates toward grains, enhancing both water use efficiency and yield (Liu et al., 2016). Furthermore, the existence of substantial genotypic variation in carbon accumulation and remobilization efficiency leads to contrasting drought responses (Liu et al., 2016; Prats et al., 2023; Fang et al., 2024). These differences illustrate naturally occurring variation in source–sink regulation and carbon translocation efficiency. Although optimizing these components is critical for sustained yield improvement, substantial knowledge gaps remain in understanding the underlying genetic and physiological variation.

Natural variation also occurs in thermal acclimation capacity, which determines how plants maintain photosynthetic efficiency and homeostasis under long-term environmental fluctuations. In tropical and temperate forest plants, the optimum temperature for CO_2 assimilation tends to shift upward with increasing mean daily temperature (Wu et al., 2025). Similar patterns are observed in crops: Cold-tolerant species shift their photosynthetic optimum downward under low temperatures, whereas cold-sensitive species show limited regulatory capacity and lower plasticity (Yamori et al., 2010; Fang et al., 2023). Mechanistic analyses further reveal that RuBP carboxylation limits photosynthesis in cold-tolerant species, while RuBP regeneration constrains performance in cold-sensitive species (Yamori et al., 2010).

These findings collectively demonstrate that natural variation in photosynthetic acclimation, resource allocation, and physiological plasticity is a key determinant of ecological and agronomic resilience. Such variation represents an important adaptive mechanism for maintaining photosynthetic performance under dynamic environmental conditions.

MOLECULAR AND GENETIC BASIS OF PHOTOSYNTHETIC NATURAL VARIATION

Photosynthesis relies on the coordinated function of numerous molecular components, many of which show extensive natural variation in their structure, abundance, or regulation. Such molecular variation gives rise to phenotypic differences described above, and shapes how individual genotypes cope with various environmental stressors. Understanding the molecular and genetic basis of these variations is therefore essential for improving photosynthetic efficiency and crop productivity.

Variation in chlorophyll retention and senescence regulation

Natural variation within chlorophyll metabolism, including synthesis, degradation, and age-dependent retention, represents one of the most well-studied forms of photosynthetic natural variation. Shin et al. (2020) reported that promoter polymorphisms at the *Stay-Green* gene (*OsSGR*) accelerate chlorophyll degradation in *indica* cultivars compared to *japonica* cultivars in rice, shortening the former's photosynthetically active period. Conversely, allelic variation at *TaGGR*-6A significantly increases chlorophyll stability and carbon assimilation capacity in wheat (Chen et al., 2025a). More recently, Yuan et al. (2026) demonstrated that leaf stay-green and early senescence are also influenced by the source–sink dynamics, which can disrupt chloroplast ultrastructure and trigger early senescence. Whether mediated by specific genes or systemic feedback, these variations ultimately determine the shift in the timing of chlorophyll degradation and leaf senescence.

While “stay-green” phenotypes have traditionally received the most attention, natural variation in the “stay-yellow” genotype is also physiologically meaningful. In some yellow-leaf variants, key photosynthetic traits like RuBisCO carboxylation capacity (V_{cmax}), maximum electron transport rate (J_{max}), and photosynthetic nitrogen use efficiency (PNUE) are enhanced (Zhou et al., 2023b, 2023c). This phenomenon occurs likely due to reduced excess light absorption and strategic reallocation of reserved nitrogen toward core photosynthetic proteins to maintain photosynthetic efficiency (Zhou et al., 2023b). This phenomenon highlights that no single chlorophyll phenotype is universally optimal; rather, the adaptive value of stay-green or stay-yellow traits depends on the genomic background and the broader coordination of photosynthetic and nitrogen use processes.

Variation in excitation balance and regulation of non-photochemical quenching

Natural variation also occurs throughout the photosynthetic electron transport chain. While substantial natural variation has been reported for linear electron transport (LET) components, the current mechanistic understanding focuses more on elucidating how genotypes adjust excitation balance and photoprotection under dynamic light environments. Because PSI and PSII have distinct light absorption properties and antenna structures, plants must continually rebalance excitation between the two photosystems. Photosynthetic state transitions mediated by reversible phosphorylation of light-harvesting complex II (LHCII) represent a key acclimation mechanism that reallocates antenna complexes toward either PSII (state 1) or PSI (state 2) depending on which photosystem is preferentially excited (Minagawa, 2011, 2025). Natural allelic variation in the kinases STN7 and STN8, which regulate LHCII and PSII core proteins (e.g., D1 and D2) phosphorylation, respectively, contributes to genotype-specific differences in acclimation capacity and high-light tolerance (Tikkanen et al., 2010; Tikkanen and Aro, 2026).

Moreover, when light energy exceeds photosynthetic capacity, plants must shift toward energy dissipation mechanisms. Under excess light, NPQ plays a central role in dissipating surplus excitation energy (van Amerongen and Croce, 2025). NPQ consists of several components with distinct regulatory controls, including the relatively rapid energy-dependent qE and the slower zeaxanthin-dependent qZ. Notably, both components are mechanistically interconnected and mutually dependent. Natural variation in the slower qZ component is primarily associated with zeaxanthin accumulation and xanthophyll-cycle enzyme activity (Glowacka, 2025). Natural variation in the qE and qZ responses—regulated by PsbS, VDE, and ZEP—produces pronounced genotypic differences in NPQ amplitude and relaxation kinetics (Wang et al., 2017; Glowacka, 2025; Zuo, 2025). Previous studies have confirmed substantial natural diversity in NPQ patterns among genotypes and species under various environmental conditions (Shomali et al., 2023; Sahay et al., 2024; Gotarkar et al., 2025; Zuo, 2025). Recently, Vath et al. (2026) conducted high-throughput phenotyping of photoprotection in sorghum (*Sorghum bicolor*) and revealed a polygenic architecture underlying NPQ variation, involving numerous small-effect loci. Together, these findings highlight NPQ as a promising but underutilized trait for breeding: Faster NPQ relaxation can increase photosynthetic efficiency under fluctuating light, whereas stronger sustained NPQ may enhance tolerance to chronic high light or drought. However, NPQ traits remain difficult to use in practice because they are highly environment-sensitive, challenging to phenotype, and the optimal balance among NPQ components for yield improvement is still unclear.

Building on insights from natural variation, several engineering strategies have aimed to accelerate NPQ dynamics (Figure 2). Co-overexpression of Arabidopsis VDE, PsbS, and ZEP (the VPZ construct) in tobacco and soybean accelerated NPQ relaxation during fluctuating light conditions, thereby improving photosynthetic efficiency, biomass accumulation, and final yield (Kromdijk et al., 2016; De Souza et al., 2022). Yet, species-specific outcomes—such as growth inhibition in Arabidopsis (Garcia-Molina and Leister, 2020) and no observed yield benefit in potato (Lehretz et al., 2022)—underscore that engineered pathways interact with endogenous variation and must be tailored to crop-specific photosynthetic contexts. Collectively, these findings demonstrate that integrating natural allelic diversity with targeted genetic engineering offers a promising route to optimize excitation balance and photoprotection in crops.

Variation in cyclic electron transport (CET)

Cyclic electron transport (CET) represents another major axis of natural variation influencing photosynthetic performance, especially under fluctuating or stressful environments (Figure 1). CET runs around PSI and supplements ATP production without generating NADPH, thereby shifting inter-photosystem energy demands and supporting photoprotection. Across vascular plants and algae, two CET routes have been identified: the antimycin A-sensitive PGR5/PGR5-LIKE PHOTOSYNTHETIC PHENOTYPE 1 (PGRL1)-dependent pathway and the antimycin A-insensitive NADH dehydrogenase-like (NDH)-dependent pathway (Shikanai, 2014; Yamori and Shikanai, 2016; Zhang et al., 2023b).

Natural variation in PGR5 and its associated regulators plays a central role in shaping CET capacity. Comparative studies reported considerable natural variation in PGR5 across taxa, reflecting its functional plasticity and adaptation to different light environments. In *Chlamydomonas*, PGR5 is indispensable for photoprotection under high or fluctuating light (Jokel et al., 2018), while functional divergence may arise from differences in redox properties within PGRL1 and PGR5 across species (Hertle et al., 2013; Buchert et al., 2020; Chaturvedi et al., 2024). The recent identification of

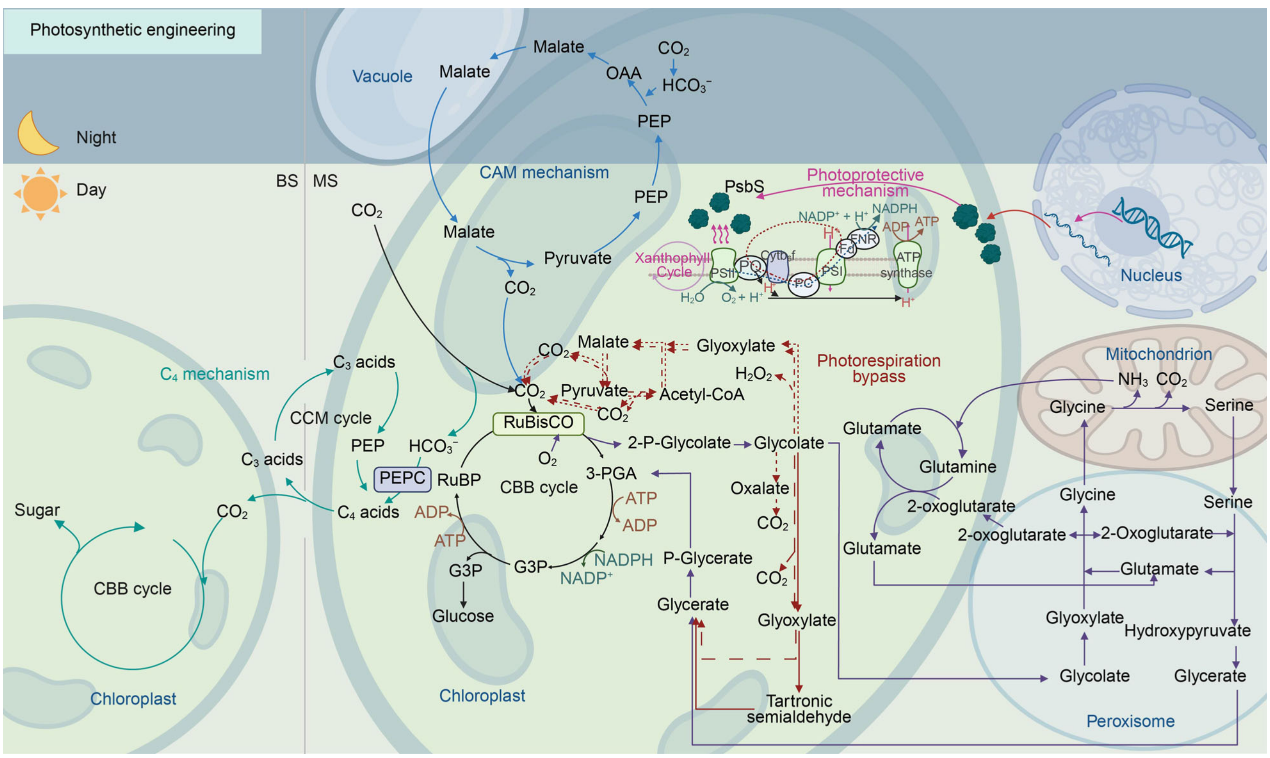

Figure 2. Blueprint for engineering major photosynthetic pathways

Four major engineering strategies are proposed for improving photosynthetic efficiency: (1) Modification of the native photorespiratory pathway (purple)—to implement representative optimized photorespiratory bypass routes (red) to minimize carbon and energy losses (where different line types represent several bypasses discussed in the main text); (2) Integrating C_4 photosynthetic traits by coordinating biochemical and anatomical features of both mesophyll (MS) and bundle sheath (BS) cells (green); (3) Introducing CAM mechanisms to improve water use efficiency and enhance photosynthetic activity during drought or heat stress (blue); and (4) Regulation of photoprotective mechanisms—optimizing NPQ dynamics to enhance energy use efficiency under fluctuating light (pink). Together, these strategies form a blueprint for future photosynthetic improvement.

PGR5-like 2 (PGRL2) adds further complexity to CET regulation (Ruhle et al., 2021).

Under stress conditions, such as drought, high light, or fluctuating irradiance, photorespiration increases and plants require additional ATP. Constituting a critical regulatory node in photosynthetic energy metabolism, natural variants of PGR5, PGRL1, and PGRL2 represent promising genetic targets for optimizing photoprotection, balancing the ATP/NADPH ratio, and enhancing photosynthetic adaption under dynamic environments. Together, these findings illustrate how CET-related variation contributes to the diversity of photosynthetic strategies in nature and offers opportunities for improving crop performance through allele mining and precision engineering.

Variation in carbon assimilation and photorespiration

At the carbon fixation stage, especially for C_3 plants, natural variation in RuBisCO remains a major determinant of photosynthetic efficiency. Although the large subunit (RbcL) is highly conserved, the small subunit (RbcS) displays extensive polymorphism affecting holoenzyme stability and kinetics (Spreitzer, 2003; Kapralov and Filatov, 2007). Evolutionary divergence among RuBisCO types (I–IV) across taxa further reflects adaptation to different CO_2/O_2 environments and resource conditions (Tabita et al., 2007; Taylor-Kearney et al., 2024). In C_3 plants, RuBisCO remains the major rate-limiting step of the Calvin–Benson–Bassham (CBB) cycle, and natural variation in its sequence, regulation, and kinetic properties contributes to interspecific differences in carbon assimilation efficiency and photorespiration intensity, alongside additional constraints such as CO_2 diffusion and RuBP regeneration (Kapralov and Filatov, 2007; Galmes et al., 2014; Orr et al., 2016; Prywes et al., 2025).

Harnessing natural variation at the molecular level for RuBisCO improvement represents another important research direction. To this end, RuBisCO activase (RCA) is worth mentioning; it is a molecular chaperone and restores RuBisCO activity by removing inhibitory phosphorylated sugars from its active site. Early studies of Arabidopsis mutants revealed that RuBisCO requires RCA for light-dependent activation (Somerville et al., 1982; Salvucci et al., 1987). Genetic variation analysis indicates that *RCA* genes show extensive allelic diversity, alternative splicing, and expression variation across species, contributing to differences in RuBisCO activation efficiency. For example, in maize, *ZmRCAβ* expression strongly correlates with grain yield, and yet, its promoter is weaker than the rice *RCA* promoter, suggesting that promoter engineering or allele mining of *RCA* could further enhance photosynthetic efficiency and yield potential (Zhang et al., 2019b).

Apart from its carboxylation activity, RuBisCO also catalyzes an oxygenation reaction that initiates photorespiration, leading to substantial carbon loss. The relative magnitude of carboxylation versus oxygenation reactions depends on the specificity of RuBisCO for CO_2 relative to O_2. As this specificity is conserved within a species, instead of aiming at manipulating the specificity *per se*, focus has been placed on developing photorespiratory bypasses to mitigate the photorespiratory loss (Figure 2). Based on previous work, South et al. (2019) reported three engineered photorespiratory pathways into tobacco, by combining enzymes from *Escherichia coli* (*E. coli*) and plants. Each pathway was designed to metabolize 2-phosphoglycolate and recycle its products back into the CBB-cycle intermediates for utilization, resulting in increased photosynthetic rates and biomass accumulation. Similarly, in rice, a glycolate shunt was engineered by overexpressing three endogenous genes—*OsGLO3*, *OsOXO3*, and *OsCATC*—which improved photosynthetic efficiency by ~27% and enhanced both biomass and nitrogen content (Shen et al., 2019). Further chloroplast-targeted engineering of glycolate metabolism—including rice glycolate oxidase, *E. coli* catalase, glyoxylate carboligase, and tartronic semialdehyde reductase—enabled a localized CO_2 release and improved carbon fixation efficiency (Wang et al., 2020). These advances highlight how natural and synthetic variation can be leveraged to optimize carbon fixation and energy use efficiency in C_3 crops (South et al., 2019; Wang et al., 2020; Chen et al., 2026).

Variation in hydraulic–photosynthetic coordination

Natural variation in water transport also shapes photosynthetic performance. For example, aquaporins (AQPs), particularly plasma-membrane intrinsic proteins (PIPs), facilitate the transport of water and small molecules across membranes, with some isoforms also mediating CO_2 diffusion (Moshelion et al., 2015; Pawlowicz and Masajada, 2019). This dual role links AQPs directly to carbon assimilation and WUE. PIPs participate in diurnal regulation of hydraulic conductivity while influencing both stomatal conductance (g_s) and leaf hydraulic conductance, creating genotype-specific strategies for coordinating water and carbon fluxes (Sharipova et al., 2022).

Functional studies illustrate this natural diversity. In Arabidopsis, *AtPIP1;2* influences mesophyll conductance (g_m) and WUE, thereby impacting the efficiency of CO_2 assimilation and photosynthetic water use (Heckwolf et al., 2011). However, inconsistent results have been reported in knockout studies: *pip1;2*, *pip1;3*, and *pip2;6* mutants showed no significant differences in g_m, highlighting redundancy within the AQP family (Kromdijk et al., 2020). Moreover, in barley, salt stress suppresses *HvPIP2;2* expression, reducing hydraulic conductivity and inducing stomatal closure (Sharipova et al., 2022). These examples indicate how natural regulatory variation in AQPs determines plant water adaptation strategies.

Collectively, photosynthesis is driven by synchronized processes that regulate cellular and genetic variation in pigments, photosystems, and enzymes, shaping light use efficiency, stress tolerance, and developmental outcomes. These natural variations not only provide valuable resources as genetic resources but also serve as important references for future photosynthetic engineering.

REGULATORY MECHANISMS WITHIN PHOTOSYNTHETIC NATURAL VARIATION

Photosynthesis is governed not only by the structural and enzymatic components of the light reactions and the CBB cycle but also by multi-layered regulatory networks that generate substantial natural variation in photosynthetic efficiency. These networks include transcription factors (TFs), microRNAs (miRNAs), and epigenetic modifications, all of which shape how plants modulate photosynthetic activity across developmental stages and environmental fluctuations (Ali and Taylor, 2001; Berry et al., 2013; Imam et al., 2014; Wang et al., 2018; Zhou et al., 2023a; Hankofer et al., 2026).

Variation in these regulatory layers—particularly in promoters and other *cis*-regulatory regions—plays a central role in determining genotype-specific photosynthetic performance and offers valuable targets for breeding and engineering (Ali and Taylor, 2001; Berry et al., 2013).

Transcriptional regulation

Transcriptional regulation represents a major source of natural variation in photosynthetic performance. Multiple TF families—including DNA-binding one zinc finger (DOF), GOLDEN2-LIKE (GLK), basic leucine zipper (bZIP), myeloblastosis (MYB), GATA (a transcription factor family defined by their type IV zinc finger domain), basic helix–loop–helix (bHLH), and dehydration-responsive element-binding (DREB)—coordinate chloroplast development, light signaling, and metabolic allocation (Toledo-Ortiz et al., 2014; An et al., 2020; Nam et al., 2021; Tu et al., 2022; Wei et al., 2022, 2023; Frangedakis et al., 2024; Ye et al., 2025). Across species and cultivars, these TFs show extensive variation in gene copy number, DNA-binding specificity, and expression patterns, often driven by polymorphisms in *cis*-regulatory regions. For instance, studies of the GLK family demonstrated that although their core roles in chloroplast biogenesis and chlorophyll biosynthesis remain highly conserved, their binding sites and transcriptional profiles have diverged extensively across lineages, reflecting adaptive regulatory evolution (Tu et al., 2022). This diversification often correlates with promoter region variation, highlighting the central role of *cis*-regulatory diversity in shaping photosynthetic capacity. In C_4 plants, natural variation in DOF transcription factors and *cis*-regulatory elements enables bundle-sheath-specific gene expression, demonstrating how ancestral regulatory codes can be harnessed to improve photosynthetic efficiency and providing targets for introducing C_4 traits into C_3 crops (Swift et al., 2024).

Natural variation also arises from interactions between TFs and miRNAs, forming regulatory modules that fine-tune photosynthetic gene expression. A well-characterized example is the OsNF-YB7–miR5810–OsMRLP6 module in rice: OsNF-YB7 activates miR5810 transcription, while promoter polymorphisms in miR5810 lead to genotype-specific differences in miR5810 levels (Gao et al., 2023). Moreover, miR5810 further regulates the downstream target, OsMRLP6. Overexpressed miR5810 or repressed OsMRLP6 impaired chloroplast development and photosynthetic performance. This example shows how *cis*-regulatory variation in non-coding regions can propagate through TF–miRNA networks to shape photosynthetic performance. Additional miRNAs families regulate genes involved in chloroplast development, redox balance, and light responses, and displayed remarkable expression variation among species and cultivars (Islam et al., 2023; Nazari et al., 2024).

These examples illustrate how natural regulatory diversity in TFs and miRNAs contributes to heritable differences in photosynthetic efficiency and has been subject to selection during domestication. Such regulatory modules therefore represent valuable targets for breeding and for engineering enhanced photosynthetic capacity.

Epigenetic regulation

Epigenetic modification—including DNA methylation, histone modifications, and chromatin remodeling—constitutes an additional layer of natural variation affecting photosynthesis. It is usually heritable when plants are exposed to certain environmental conditions over several consecutive generations. These mechanisms enable rapid and reversible responses to environmental signals without altering DNA sequences, contributing to phenotypic diversity and adaptive plasticity.

Comparative studies reveal pronounced species- and genotype-specific epigenetic modifications in light and stress responses. For instance, in *Arabidopsis thaliana*, the *PIF7–REF6* module regulates shade acclimation responses via *H3K27me3* demethylation and enhances hypocotyl elongation after repeated shade exposure (Cheng et al., 2024). Shade-responsive genes are induced in the wild type but are suppressed in *pif7* and *ref6* mutants, demonstrating that *PIF7–REF6* binding and demethylation are essential for transcriptional reprogramming. A similar result has also been observed in soybean (*Glycine max*), where particularly lower CHH at the *GmGLK10* promoter enhances its expression under fluctuating environments (Xun et al., 2024). Together, these studies underscore how natural epigenetic polymorphism fine-tunes downstream gene expression and contributes to photosynthetic acclimation across species.

Importantly, certain epigenetic states can be stably inherited across generations under recurring environmental stress, forming a kind of "molecular memory" that preserves adaptive photosynthetic responses (Duarte-Aké et al., 2019; Cheng et al., 2024). In addition, such heritable epigenetic variation represents a long-term evolutionary resource that complements genetic variation in shaping plant resilience and productivity.

LINKING VARIATION IN PHOTOSYNTHESIS TO VARIATION IN CROP YIELD

Crop yield ultimately depends on the acquisition and distribution of photosynthates at the canopy level, which in turn depend on leaf-level photosynthesis (Yin et al., 2022). Natural genetic variation has long been a major driver of yield improvement; for example, sustained yield gains in global wheat production largely reflect selection on photosynthetic traits embedded in elite germplasm (Ding et al., 2025). This highlights the importance of continued exploration of natural diversity in photosynthetic traits, particularly as modern high-throughput phenotyping and genomics now enable more precise dissection of these quantitative traits.

As climate change intensifies, development of crops with a resilient photosynthetic machinery capable of maintaining efficiency under heat, drought, and fluctuating CO_2 conditions is becoming increasingly urgent (McAusland and Murchie, 2020; Kromdijk and McCormick, 2022). Elevated CO_2 may alleviate photorespiratory losses in C_3 plants, and yet, concurrent heat and water stress often compromise photosynthetic stability (Rezaei et al., 2023; Li et al., 2025a). Harnessing natural variation in thermotolerance, water use efficiency, nitrogen use efficiency, and canopy architecture offers valuable genetic resources for developing climate-resilient crops.

Moreover, natural variation in photosynthetic plasticity across ecotypes also reveals how multiple photosynthetic components operate in a coordinated manner under varying environmental conditions. For example, variation in NPQ capacity shapes energy dissipation under high light, influencing electron transport available for CO_2 fixation. Similarly, differences in RuBisCO substrate affinity reflect intrinsic trade-offs between carbon fixation and photorespiration. At the whole-plant level, variation in canopy structure, source–flow–sink balance, and timely physiological responses to environmental fluctuations determines the overall canopy photosynthetic efficiency in a coordinated manner, ultimately contributing to crop yield.

Importantly, many historical yield improvements have only indirectly influenced photosynthesis, revealing a gap between mechanistic understanding and breeding practice. Closing this gap will require integrative approaches that connect natural genetic variation in photosynthetic traits with agronomic performance in field environments (Yin et al., 2022). Future research should leverage advanced technologies to explore multi-scale natural variations, identify optimal combinations of superior alleles, and deploy them through breeding or precision engineering, thereby translating natural diversity into effective strategies for enhancing crop yield potential.

APPLICATIONS OF PHOTOSYNTHETIC NATURAL VARIATION IN CROP IMPROVEMENT

Natural variation provides the most direct and powerful genetic resource for improving photosynthetic performance in crops. Liang et al. (2021) summarized current strategies for mining such variations in crops, which facilitate the identification of key genes governing complex traits and offer a theoretical foundation for molecular breeding.

Gene identification and functional validation

In photosynthesis research, genome-wide association studies (GWAS) and bi-parental quantitative trait locus (QTL) mapping remain central tools (Gu et al., 2012; Qu et al., 2017). These approaches have identified numerous gene loci associated with key photosynthetic traits. For instance, in rice and wheat, several QTLs linked to flag leaf photosynthetic capacity and grain weight show stable effects across diverse genetic backgrounds, demonstrating the existence of robust allelic variation within natural populations, providing valuable targets for molecular design breeding.

To improve both mapping resolution and detection power, nested association mapping (NAM) and multi-parent advanced generation intercross (MAGIC) populations have been developed. Both population types incorporate multiple parental lines. NAM populations enable fine localization of genetic loci for complex traits while maximizing allelic diversity (Ladejobi et al., 2016). MAGIC populations, created through multi-generational recombination, yield highly diverse and recombined genomes ideal for dissecting polygenic traits and accelerating breeding progress (Arrones et al., 2020; Ferguson et al., 2025). Coupled with high-throughput phenotyping platforms, these populations have greatly accelerated the discovery of candidate genes.

A growing number of genes associated with leaf- and canopy-level photosynthetic traits have now been identified and validated (Table 1), including both candidate genes and functionally characterized alleles showing haplotype-level variation. However, most studies remain at the QTL-mapping stage, with relatively few proceeding to functional characterization, mechanistic elucidation, or demonstrable contributions to yield improvement, showing that future work needs to move beyond just locating genetic loci and focus on how to use diverse haplotypes in molecular breeding. This gap underscores the challenges of reliably phenotyping photosynthesis at scale and highlights the importance of integrative approaches that link natural variation to physiological function.

Optimizing existing regulators

In addition to identifying new photosynthetic genes, natural variation is also highly valuable for optimizing already characterized regulators through superior haplotypes or coding variants. For example, high-photosynthesis alleles from *indica* rice cultivars Habataki (Chr 5) and Takanari (Chr 10) improved the photosynthetic rate, biomass, and grain yield when introgressed into the *japonica* cultivar Koshihikari (Yamashita et al., 2022). Similarly, *NARROW LEAF1* (*NAL1*) is a vital gene regulating photosynthesis, and its superior haplotypes have been identified and functionally validated. Ouyang et al. (2024) demonstrated that combining two

Table 1. Summary of genes associated with natural variation in leaf- and canopy-level photosynthesis

Plants	Gene names	Traits	References
Rice	*OsbHLH153*	Leaf angle	Dong et al. (2018)
	OsbHLH173		
	OsbHLH174		
	OsNHX1	Stomatal closure response during high to low light transition	Qu et al. (2020)
	SD1	Plant height	Wang et al. (2025a)
	NAL1	Flag leaf width	
	LEAF1	Plant height, flag leaf length, and leaf width	
	NAL22	Leaf width	Xu et al. (2023)
	ACP2	Photosynthetic P use efficiency (PPUE)	Liu et al. (2024)
		Net photosynthetic rates under saturated light under Pi-starvation condition ($A_{sat}Pi^{-}$)	
	OsSGR	Chlorophyll content, stay-green duration	Shin et al. (2020)
Soybean	*GmFtsH25*	Photosynthetic efficiency	Wang et al. (2023)
Maize	*ZmbZIP27*	Leaf angle	Chen et al. (2024)
	ZmIRX15A	Stomata density	Zhang et al. (2023a)
	lac1	Smart canopy, leaf angle	Tian et al. (2024)
	RAVL1-brd1	Ideal plant architecture, leaf angle	Tian et al. (2019)
Wheat	*TaHXK3-2A*	Stomata index	Li et al. (2022)
	TaARF15-A1	Leaf senescence	Li et al. (2023a)
	TaTRNH1-3B	Leaf senescence	Jin et al. (2025)
	TaNAM	Green leaf duration (GLD) after anthesis	Zhou et al. (2024)
	TaGGR-6A	Leaf chlorophyll content	Chen et al. (2025a)
Tomato	*GPA1*	Leaf width	Wang et al. (2025b)
Arabidopsis	*GVS1*	Leaf senescence	Lyu et al. (2019)
	PHT4;4 and bZIP58	Stay-green phenotype under iron–phosphorus deficiency	Nam et al. (2021)
Foxtail millet	*SiCHLI*	Leaf color	Liang et al. (2023)

Genes were identified through forward-genetic or haplotype-based analyses. All listed genes have been functionally validated.

elite *NAL1* alleles resulted in improved canopy photosynthesis, plant architecture, and grain yield compared with the homozygous allele genotype, illustrating that integrating different natural variations is a practical way to optimize both leaf shape and photosynthetic rate simultaneously.

Despite these advances, conventional breeding approaches remain time-consuming and present several limitations in the introgression of target loci. The rapid development of genome editing technologies now enables precise modification of specific bases or regulatory segments, offering a way to directly harness elite natural variation while dramatically shortening breeding cycles. So far, applications in the field of photosynthesis are still limited, but emerging cases illustrate the potential. For example, *OsDREB1C* is the central node of photosynthesis, nitrogen utilization, and flowering. Enhancing its expression could improve overall plant development and grain yield (Wei et al., 2022). Luo et al. (2025) further reported repositioning *OsDREB1C* under a strong promoter by CRISPR-Cas9-mediated inversion, thereby boosting the final yield, demonstrating the potential of targeted regulatory editing.

Collectively, natural variation in photosynthesis provides valuable guidance for future breeding. Taking these variations as theoretical bases and integrating multiple strategies to exploit them may further improve whole plant-level photosynthesis, thereby contributing to yield improvement.

CHALLENGES AND FUTURE PERSPECTIVES

Persistent global hunger underscores the urgent need to systematically explore natural photosynthetic variations for sustainable yield improvement. As the fundamental process driving plant growth, photosynthesis directly governs source–sink relationships, biomass accumulation, and yield potential. Although remarkable progress has been made—from physiological characterization to molecular and genomic elucidation—many components of the photosynthetic machinery remain underexplored, leaving significant knowledge gaps (Figure 3).

A central challenge arises from the pronounced genotype × environment (G × E) interactions observed in photosynthetic traits. Variants that perform well under controlled conditions often fail to maintain consistent responses across diverse environments. Since photosynthetic traits are highly sensitive to environmental conditions, reliable

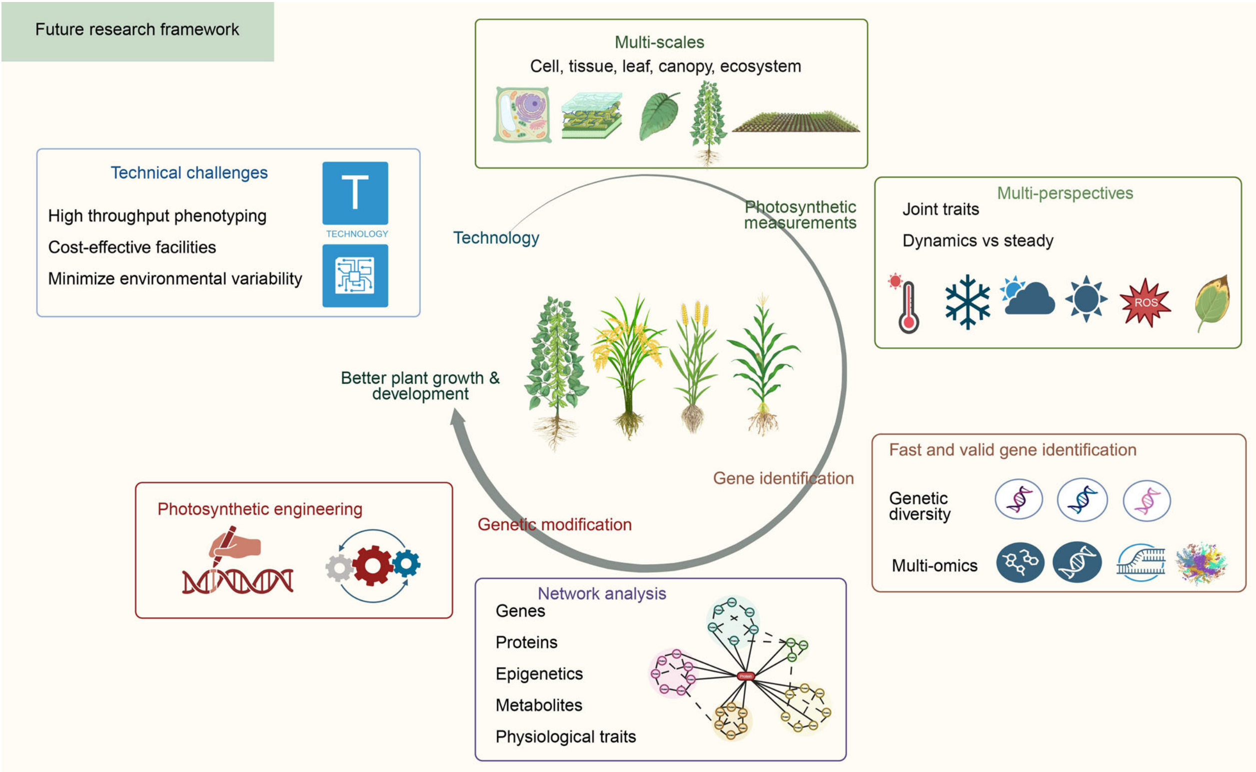

Figure 3. Framework for future photosynthesis research

For future photosynthesis research strategies, high-throughput, field-relevant photosynthetic phenotyping must first be developed to minimize environmental noise, therefore ensuring that measurements more accurately reflect underlying genetic effects. In addition, photosynthetic measurements should be conducted across multiple scales—including the cell, tissue, leaf, canopy, and ecosystem levels—and integrated with other physiological traits for comparative analyses. By leveraging various approaches, candidate genes can be identified more rapidly and accurately. Network analyses should incorporate information across genomic, transcriptomic, proteomic, metabolic, and physiological levels, providing a solid foundation for photosynthetic gene engineering to improve plant growth and productivity.

evaluation requires multi-year, multi-site, and dynamic measurements. However, even in large-scale data sets, stable QTL intervals are rarely observed, highlighting the complexity of quantitative traits. Additionally, many photosynthetic traits in natural populations show subtle phenotypic differences, complicating forward-genetic screening and functional validation (Li et al., 2023b). Importantly, even minor allelic variations may exert substantial effects on plant electron transport, stress response, and overall photosynthetic performance; yet, they often escape detection in large-scale analyses. Therefore, advancing our understanding of photosynthetic variation depends on long-term, multi-environment, and multi-scale approaches, supported by precise high-throughput phenotyping technologies.

Despite decades of continued progress, several key scientific questions remain unsolved. Can existing natural variation be exploited to break the theoretical limits of photosynthetic capacity? Which variants truly determine efficiency and yield stability across environments? How can RuBisCO's catalytic properties be optimized without compromising protein stability? Can photorespiratory and CO_2-concentrating pathways be re-engineered to achieve sustained carbon assimilation under stress? Addressing these questions will require sustained and interdisciplinary collaborations across molecular biology, physiology, genomics, bioinformatics, and breeding.

Looking forward, several strategic priorities emerge. First, the development of high-resolution, field-relevant phenotyping tools—including hyperspectral imaging, chlorophyll fluorescence kinetics, and drone-based canopy monitoring—will enable dynamic tracking of photosynthetic traits under realistic environmental conditions. Second, integrative multi-omics data—genomics, transcriptomics, proteomics, metabolomics, and epigenomics—will accelerate the discovery and pyramiding of beneficial natural variants. Third, regulatory network analyses should expand beyond gene–gene interactions to incorporate coordinated variation among genes, proteins, metabolites, epigenetic features, and physiological traits, providing a systems-level understanding of photosynthetic performance. Finally, designing climate-resilient, high-efficiency ideotypes will require predictive models capable of identifying allele combinations that maximize carbon gain while maintaining stability across diverse agroecosystems.

Ultimately, deepening our mechanistic understanding of natural photosynthetic diversity will catalyze the next transformative leap in agricultural productivity. By translating natural variation into actionable breeding and engineering strategies, we can develop crops with higher photosynthetic efficiency, enhanced resilience, and more stable yields, providing a fundamental basis for sustainable agriculture and global food security in the face of accelerating environmental change.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

W.Z. conceptualized the manuscript. Y.Z. and L.X. performed the literature search, drafted the manuscript, and prepared all figures. S.W., S.S., P.C., X.Y., and W.Z. contributed to manuscript revision and provided critical feedback. All authors have read and approved the contents of this paper.

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