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Review

Photosynthetic Adaptation in Poplar Under Abiotic and Biotic Stress: Integrating Molecular, Physiological, and Biotechnological Perspectives

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Abstract: In the context of global climate change, the carbon storage and sequestration capacity of terrestrial ecosystems is of increasing concern. Poplars are widely planted because of their fast growth and environmental adaptability. We reviewed the effects of abiotic and biotic stresses on photosynthesis in poplar, focusing on the damage caused by adversity conditions to photosynthetic apparatus, which leads to decreased carbon dioxide (CO_2) assimilation and an increase in reactive oxygen species (ROS)-induced oxidative damage. The mechanisms of photosynthesis response to stress in poplar are reviewed, especially the role of genes regulation in regulating photosynthetic efficiency. These findings are particularly important for improving the resilience of poplar under changing environmental conditions. In addition, we discussed a range of strategies to enhance photosynthesis in poplar under stress, such as genetic engineering and synthetic biology. These approaches provide theoretical guidance for improving the resilience of poplar and insights for improving other crops facing similar challenges.

Keywords: poplar; photosynthesis; stress; ecosystem; synthetic biology

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1. Introduction

Climate change is an important cause of current carbon storage and fixation impacts [1]. Forests are one of the most important terrestrial ecosystems, actively removing carbon dioxide from the atmosphere through carbon sequestration, which accounts for about 45% of terrestrial carbon stocks and is an important carbon sink [2,3]. Therefore, they are crucial in balancing and offsetting anthropogenic carbon emissions [3].Trees account for about 82% of terrestrial ecosystems and are an important vital renewable resource for biofuels and biomaterials [4,5], providing oxygen and generating economic benefits [6]. Thus, afforestation has been promoted to enhance carbon sequestration [7].

Poplars are the most widely planted economic trees in the world due to their fast growth rate and their important role in timber production and ecological restoration [8]. The cultivated poplar area in China has exceeded 700 million hectares [9], ranking first in the world [10]. Studies have shown that poplars have a high capacity for carbon sequestration and adaptation to environmental conditions [11,12]. In addition, poplars also contributes to conserving biodiversity and ecosystem water conservation [13].

Photosynthesis is highly sensitive to environmental stresses such as drought, high salinity and temperature anomalies, which severely impair plant productivity [14]. Under natural growing conditions, especially in terrestrial ecosystems, plant photosynthesis has been under non-steady-state conditions due to changing environmental conditions [15]. For example, plants are inevitably subjected to biotic and abiotic stresses in non-cultivated environments such as forests, grasslands, and wetlands [16]. Abiotic stresses such as drought, temperature anomalies, salinity, and heavy metals significantly affect plant growth and yield [17,18]. For example, drought stress reduces leaf chlorophyll content and photosynthetic capacity by triggering the expression of transcription factors associated with abscisic acid (ABA) biosynthesis and the regulation of photosynthesis-related genes in *Trollius chinensis* [19]. Under drought and low temperature stress, chlorophyll content, stomatal conductance, and thus the net photosynthetic rate of cotton were reduced [20]. Low temperatures have been demonstrated to cause genes associated with photosynthesis in maize plants to be downregulated [21]. High-temperature stress caused a decrease in photosynthetic efficiency, supercomplexes of thylakoid membranes, and content of photosystem reaction center proteins in *Pisum sativum* [22]. The vital photosynthetic enzymes Rubisco and PEPCase activities were inhibited in rice seedling leaves under saline stress [23]. Heavy metal stress reduces chlorophyll biosynthesis genes levels and interrupts the photosynthetic apparatus in pepper seedlings [24].

In the current context of climate change, ecosystems and agricultural activities face new challenges due to environmental stresses [25]. The effects of abiotic stresses on crop photosynthesis were briefly described earlier, and the study of poplar, one of the trees with high value in woody biomass production, on its tolerance to abiotic stresses has also received extensive attention. However, the key issue is the lack of systematic research or summaries in related fields. This paper provides an overview of recent developments in our understanding of how poplar regulates its photosynthetic capacity to respond to environmental stresses at the physiological and molecular levels. Additionally, we also briefly summarize the impact of biotic stresses on poplar photosynthesis. The goal is to enhance our understanding of how poplar balances growth while coping with environmental stresses, especially in climate change.

2. Poplar Photosynthesis Under Abiotic Stress

2.1. Drought Stress

Water-use efficiency (WUE) reflects a critical balance between carbon assimilation and water loss in plants, making it a key determinant of plant fitness under changing environmental conditions [26]. Plants with higher WUE will have a competitive advantage in natural ecosystems and be economically significant for agricultural production. The efficiency of carbon assimilation, particularly through Rubisco activity and the regeneration of RuBP, plays a significant role in determining WUE [27].

The photosynthetic capacity of *Populus cathayana* is highly vulnerable under drought conditions, with key physiological indicators such as photochemical quenching (qP) and the maximum quantum yield of photosystem II (ΦPSII) significantly reduced [28]. This reduction in photosynthesis is primarily attributed to stomatal closure, which limits the entry of CO_2 from the atmosphere into the leaf, thereby diminishing canopy photosynthesis and increasing the risk of carbon starvation [29]. Several studies have shown that stomatal regulation is critical for optimizing plant responses to water stress and maintaining photosynthetic efficiency [30–32] (Figure 1).

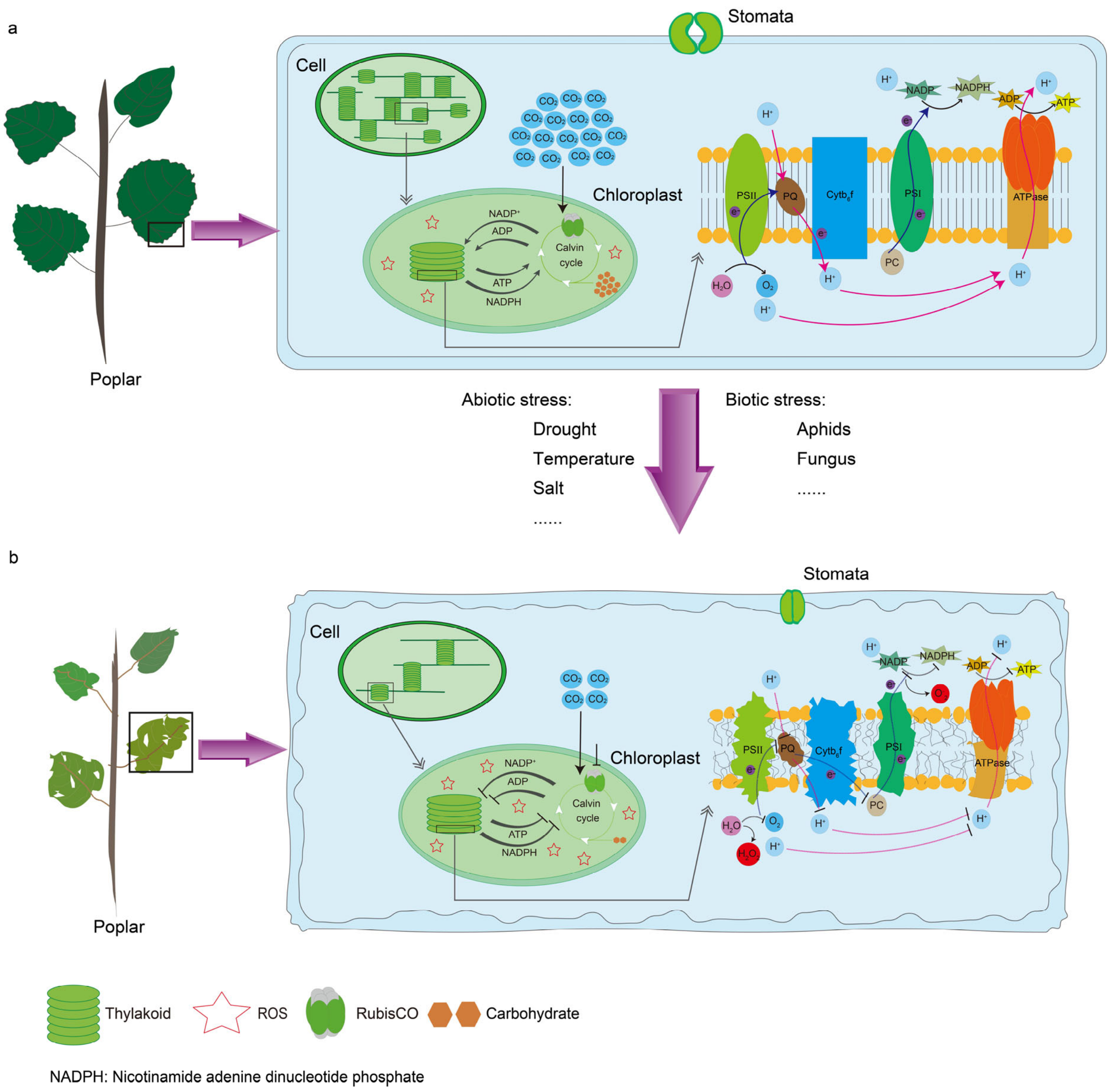

Figure 1. Effect of biotic and abiotic stresses on photosynthesis in poplar. (**a**) Photosynthesis in leaves under normal conditions. Under suitable growth conditions, the cell morphology is stable, the chloroplasts structure and the grana lamella in the chloroplasts are normal; the stomata are open, and more CO_2 enters into the leaves and reaches the active site of Rubisco carboxylation. The electron transfer that occurs in the thylakoid membrane carries on normally, and the ATP and NADPH produced are used for carbon fixation and the formation of carbohydrates, which are used in the normal conduct of life activities of poplar. (**b**) After experiencing abiotic stress (e.g., drought, abnormal temperature, salt stress, etc.) and biotic stress (e.g., aphid infestation, fungal infection, etc.), the cellular environment changes, and the grana lamella in the chloroplasts decreases; stomata are closed, leading to a decrease in CO_2 reaching the carboxylation active site of Rubisco. After the stress, the electron transport chain and the activity of Rubisco are inhibited, and an increase in ROS leads to oxidative stress, impairing the photosynthetic apparatus and inhibiting the normal conduct of photosynthesis. Carbon fixation is restricted, and the carbohydrates delivered to the plant are reduced, which is unfavorable to the conduct of life activities.

A multi-omics approach identified *DUF538*, *TAR2*, and *AbFH2* (Table 1) in *Populus tomentosa* linked to stomatal morphology, suggesting their roles in stomatal development and drought tolerance [21]. Overexpressing *PdERECTA* (Table 1) in triploid white poplar reduced stomatal density and increased size, improving water use efficiency and photosynthesis under drought stress [33]. ABA, a key regulator of stomatal movement, controls CO_2 absorption during photosynthesis under water stress. An ABA-insensitive hybrid poplar showed reduced stomatal conductance and lower photosynthesis under drought, emphasizing the role of ABA in photosynthetic regulation [34]. In mature leaves of poplar, overexpression of *Pu-miR172d* (Table 1) has been shown to negatively regulate stomatal density by inhibiting *PuGTL1* expression. This regulation reduces photosynthesis rates and stomatal conductance, ultimately compromising drought tolerance [35].

Additionally, ectopic expression of a pine cytoplasmic glutamine synthetase gene (*GS1a*) in hybrid poplar increased the expression of key chloroplast enzymes (Table 1), such as superoxide dismutases (SOD). It reduced oxidative damage, thereby maintaining photosynthetic activity under drought stress [36]. Transcription factors such as NAC, DREB, MYB, and bZIP regulate plant responses to environmental stresses, influencing photosynthesis [37]. In *Populus trichocarpa*, *NAC029* knockout preserved higher photosynthetic capacity and photosystem efficiency under drought, while the miR6445-*NAC029-GSTU23* module modulated photosynthesis through ROS homeostasis [38].

Moreover, changes in internal leaf CO_2 concentration (C_i) are linked to fluctuations in the maximum photosynthetic rate (A_{max}), which is the lowest due to carboxylation limitations [39]. Overexpression of *ZXzF* from the drought-tolerant C_4 plant *Zygophyllum xanthoxylon* in Euro-american poplar increased chlorophyll content and intercellular C_i and alleviated drought-induced damage to PSII and photosystem I (PSI) proteins, mitigating carbon assimilation inhibition under drought [8]. These findings highlight complex mechanisms in optimizing photosynthesis and drought tolerance in poplar.

2.2. Temperature Stresses

Tree growth and physiological metabolism are influenced by temperature fluctuations and soil moisture changes [40]. Photosynthesis is inhibited just above optimal temperatures, resulting in decreased productivity and enzyme deactivation [41]. High temperatures cause physical, biochemical, and molecular changes in trees, reducing photosynthesis and productivity. Overexpression of *PagGRF15* in poplar lacking miR396a targets resulted in higher chlorophyll content and photosynthetic efficiency under heat stress (Table 1). This effect was mediated by miR396a through its regulation of genes related to photosynthesis [42]. Similarly, overexpression of *PttEXPA8* from *Populus tomentosa* increased chlorophyll content under high temperatures (Table 1) [1]. Sex-specific differences in *Populus cathayana* response to heat were observed, with females exhibiting greater heat resistance due to better stomatal regulation and water use [40]. Meanwhile, males showed higher sensitivity to temperature effects on carbon assimilation and water balance. Short heat periods reduce photosynthesis in hybrid aspen, with irreversible inhibition under prolonged heat stress [40,43,44].

Heat stress decreases the net photosynthetic rate by inhibiting electron transport and inactivating Rubisco (Figure 1). Studies show that heat stress affects PSII more than PSI in *Populus simonii*, leading to the negative regulation of the carboxylation, reduction, and regeneration processes of the Calvin cycle. Heat stress inhibits carboxylation and reduces Rubisco activity, which leads to a significant decline in photosynthetic efficiency at higher temperatures [45]. The temperature sensitivities of Rubisco and photosynthetic electron transport differ. As plants adapt to higher temperatures, net assimilation per unit leaf area decreases. This reduction is primarily due to decreased Rubisco carboxylase activity and decreased CO_2-saturated net absorption rate [46]. This may be linked to genetic variation in Rubisco activase heat sensitivity (Table 1), as shown in differences between *Populus balsamifera* and *Populus deltoides* [41].

In addition, low temperatures also negatively affect the growth and development of poplar, causing damage to chloroplast structure and reducing photosynthetic rates in

Populus cathayana [47]. However, poplar transformed with *Cryptomeria fortunei CfICE1* showed improved chloroplast integrity, higher chlorophyll content, and increased antioxidant enzyme activity, which helped maintain photosynthesis. *CfICE1* exerted its role by promoting the expression of stress-responsive genes, thereby enhancing heat tolerance through the upregulation of *CBF1* and *CBF3* while repressing *CBF2* (Table 1), which supported photosynthesis [48]. Low temperatures also produce ROS, leading to chloroplast oxidative damage [49]. Low temperatures disrupt chloroplast function by altering membrane lipids and enzyme activity, reducing photosynthetic efficiency and excessive ROS production. This oxidative stress contributes to visible chilling injury, including chlorosis, stunted growth, and cell death [50,51]. Overexpressing *Populus euphratica PeSTZ1* in 84k poplar enhanced ROS scavenging by activating *PeAPX2* (Table 1). This resulted in higher photosynthetic activity than the wild type [52].

2.3. Salt Stress

Salt stress reduces photosynthesis, plant biomass, and crop production [53,54]. Under abiotic stress, chloroplasts shape and structure change affect cytosolic CO_2 diffusion [55]. Salt stress significantly lowers intercellular CO_2 concentration in mature leaves of *Populus balsamifera*, reducing carbon assimilation [56]. In female *Populus cathayana*, salt stress increases mesophyll spongy cell density, decreases chloroplast density and surface area, and reduces CO_2 diffusion to chloroplasts, inhibiting photosynthesis [57].

Salt stress damages photosystems and disrupts the PSII electron transport chain (Figure 1). AMF can enhance plant tolerance to high salt and alkali levels [58,59]. For example, AMF enhances plant resistance to salt stress by improving osmotic protection, boosting antioxidant capacity, and regulating ion balance. Mycorrhizal halophytes exhibit lower sodium and soluble sugar concentrations than non-mycorrhizal plants, indicating better salt regulation. AMF also increases root H^+ efflux and K^+ influx, promoting fatty acid metabolism and improving salt tolerance [60,61]. In *Populus cathayana*, salt exposure decreased the maximal photosynthetic efficiency of PSII (Fv/Fm) and ΦPSII values, reducing plant biomass, but inoculation with *Rhizophagus intraradices* improved these parameters [62]. *Funneliformis mosseae* inoculation reduced Na^+ toxicity in salt-stressed poplar by stabilizing the photosynthetic electron transport chain and enhancing photosynthesis [63]. In 84k poplar, salt stress decreased photosynthetic rate and chlorophyll fluorescence parameters, which were improved by inoculation with *Rhizophagus irregularis* [64]. In *Populus euphratica*, AMF inoculation increased PSII efficiency and improved Fv/Fm and non-photochemical quenching (NPQ) in male and female plants under salt stress [65].

Autophagy plays a role in plant photosynthesis under salt stress [66]. PagATG18a, involved in autophagy, interacts with PagAPX2/PagLHCB1 to maintain photosynthetic efficiency in *Populus trichocarpa* under salt stress (Table 1), increasing antioxidant enzyme activity and reducing ROS accumulation [67]. In *Populus euphratica*, overexpression of *PeNAC045* reduced stomatal conductance and photosynthesis under salt stress (Table 1), suggesting it may act as a stress response regulator with a negative function [37]. Overexpressing transcription factors such as *PeSTZ1* boosts *PeZAT12* expression and activates *PeAPX2* (Table 1), enhancing antioxidant accumulation, ROS detoxification, chlorophyll retention, and photosynthesis, improving salt tolerance [68]. Using new technologies such as RNA affinity purification sequencing (RAP), PeGRP2 was found to interact with the mRNA of PetC and RbcMT (Table 1), negatively affecting photosynthesis under salt stress [69].

2.4. Other Stress

Cadmium (Cd) negatively impacts thylakoid membranes and reduces enzyme activity, particularly by inhibiting Rubisco (Figure 1), a key enzyme in photosynthesis [70,71]. Cd can also disrupt the structure of Rubisco by replacing magnesium (Mg), leading to the irreversible separation of its subunits [72,73]. *Populus yunnanensis* shows an imbalance in its photosynthetic system under Cd stress [72]. Genotypic differences in poplar, such as in *Populus nigra* genotypes Poli and 58-861, showed varied Cd stress responses, with genotype 58-861 experiencing more damage to carbon assimilation and electron transport [74]. Hybrid poplar A4A (*Populus nigra* × *Populus americana*) was less affected by Cd than other genotypes [71]. Transcriptome analysis of *Populus tomentosa* under Cd stress identified photosynthesis as the main pathway impacted, with two Cd-responsive lncRNA gene pairs (*MSTRG.22608.1-PtoMYB73* and *MSTRG.5634.1-PtoMYB27*) suggesting MYB transcription factors modulate photosynthesis through ROS production (Table 1) [75].

Ambient ozone (O_3) levels reduce photosynthesis in trees and crops by decreasing chloroplast size, impairing mesophyll conductance, and limiting CO_2 transport to the chloroplast carboxylation site in poplar [76]. The oxidative effect of O_3 damages mesophyll cells and inhibits photosynthetic enzymes [77]. Furthermore, plant density stress leads to competition for light and affects microhabitat conditions such as temperature, water, and nutrients [78]. High-density stress activates poplar carbonic anhydrase (CA) genes, which increase CO_2 fixation by facilitating inorganic carbon movement to the carboxylase site, improving carbon sequestration. Adjusting planting density can optimize gene expression and enhance the carbon sequestration capacity of poplar [13,79].

In addition, the interaction of multiple abiotic stressors, such as drought combined with high temperature or heavy metal contamination, exerts non-additive and often synergistic effects on poplar physiology, critically impairing photosynthetic capacity, ROS homeostasis, and resource allocation [80]. For instance, in *Populus yunnanensis*, concurrent drought and heat stress sharply reduce photosynthetic efficiency, evidenced by Fv/Fm and ETR declines while triggering ROS overproduction and lipid peroxidation (elevated MDA and proline). The antioxidant system becomes overwhelmed, as seen in suppressed enzyme activities and disrupted ROS scavenging, further exacerbating oxidative damage. Protective mechanisms such as ABA and dehydrin synthesis may fail under severe stress combinations, leading to cellular dysfunction [81]. Drought and heavy metals jointly reduce biomass, PSII efficiency, and long-term WUE, with *Populus cathayana* females exhibiting greater sensitivity than males [82].

3. Poplar Photosynthesis Under Biotic Stress

In addition to abiotic stresses, poplars are threatened by various biotic stresses during its growth (Figure 1) [83]. *Pemphigus spirothecae* infests poplar woodlands, producing galls on petioles [84]. The net photosynthetic rate per area decreased with increasing infestation severity [85]. Aphid eating further diminishes the quantity of carbon exported from the leaf [86]. It has been suggested that reduced mesophyll diffusion conductance, decreased amounts or activities of photosynthetic rate-limiting proteins, and inhibition of photosynthetic electron transport are the main factors contributing to the gall-triggered reduction in leaf photosynthesis. These factors collectively led to a decrease in photosynthetic efficiency [87]. Fungal infections can likewise lead to reduced photosynthesis [88]. The trees were found to be infected with a fungal pathogen called *Melampsora larici-populina*, which causes a disease known as *Populus balsamifera* leaf rust. This illness decreases both the total biomass of the leaves and their photosynthetically active portion. A contributing factor to this decrease is the spread of chlorosis and necrosis [89].

EDS1 is a crucial regulator of salicylic acid (SA)-dependent defense responses against biotic stress [90]. Hybrid aspen *EDS1* influences the expression of genes encoding proteins involved in photosynthesis and hormone homeostasis regulation (Table 1) [91]. The genes responsible for encoding photosystem subunits, pigment-binding proteins, ATP synthase, and cytochromes have been observed to be downregulated in *EDS1*-silenced lines. However, the transgenic lines had higher CO_2 assimilation rates and photosynthetic performance than wild-type plants. The authors speculate that the increase in photosynthesis in *EDS1*-silenced poplar may be related to reduced SA levels [91].

Table 1. Related genes regulating photosynthesis in poplar under stress.

Stress	Gene	Species
Drought	*DUF538, TAR2, AbFH2*	*Populus tomentosa* [21]
	PdERECTA	*Populus nigra* × *(Populus deltoides* × *Populus nigra)* [33]
	Pu-miR172d, PuGTL1	*Populus ussuriensis* [35]
	GS1a	*Populus tremula* × *Populus alba* [36]
Temperature	*PagGRF15*	*Populus alba* × *Populus glandulosa* [42]
	PttEXPA8	*Populus tomentosa* [1]
	Rubisco activase	*Populus deltoides* [41]
	CBF1, CBF2, CBF3	*Populus davidiana* × *Populus bolleana)* [48]
	PeSTZ1, PeAPX2	*Populus euphratica* [52]
Salt	*PagATG18a, PagAPX2, PagLHCB1*	*Populus trichocarpa* [67]
	PeNAC045	*Populus euphratica* [37]
	PeSTZ1, PeZAT12, PeAPX2	*Populus alba* × *Populus glandulosa* [68]
	PeGRP2	*Populus euphratica* [69]
Heavy metal	*PtoMYB73, PtoMYB27*	*Populus tomentosa* [75]
Biotic Stress	*EDS1*	*Populus tremula* × *P. tremuloides* [91]

This table shows genes that respond to drought, temperature, salt, heavy metal, oxidization, and biotic stress in poplar.

4. Improvement Strategy

Gene editing technology, particularly CRISPR-based systems, offers new opportunities to enhance photosynthesis in poplar under stress (Figure 2). CRISPR/Cas9 provides high precision and cost-effectiveness for modifying plant traits, but its efficiency and off-target rates still need improvement [92,93]. Multiple factors and genes regulate photosynthesis in poplar, so it is often difficult to comprehensively improve photosynthetic capacity by editing only a single gene. Although simultaneous editing of multiple genes has great potential, it presents technical challenges and complexity. Advances in CRISPR systems, such as CRISPR-Cas12a, CRISPR-Combo, and CRISPR-CasF offer new possibilities for expanding gene editing [94,95]. These technologies exploit a powerful approach to poplar trait improvement by enabling the modification of the genome, which would be difficult to achieve with traditional breeding techniques [96]. However, challenges remain in optimizing the expression and coordination of multiple sgRNAs, managing editing efficiency, and understanding the complex gene networks that control plant traits [97]. The MISSA 2.0 toolkit offers a promising solution to these challenges, enabling the efficient assembly of multiple CRISPR systems for multiplex genome editing [98]. Nevertheless, regulatory gene network dynamics are important for fully realizing the potential of multiplex genome editing for plant improvement. In addition, the ability of multiplexed CRISPR to precisely modify multiple gene family members offers the possibility of addressing the complexity of polygenic regulation [99].

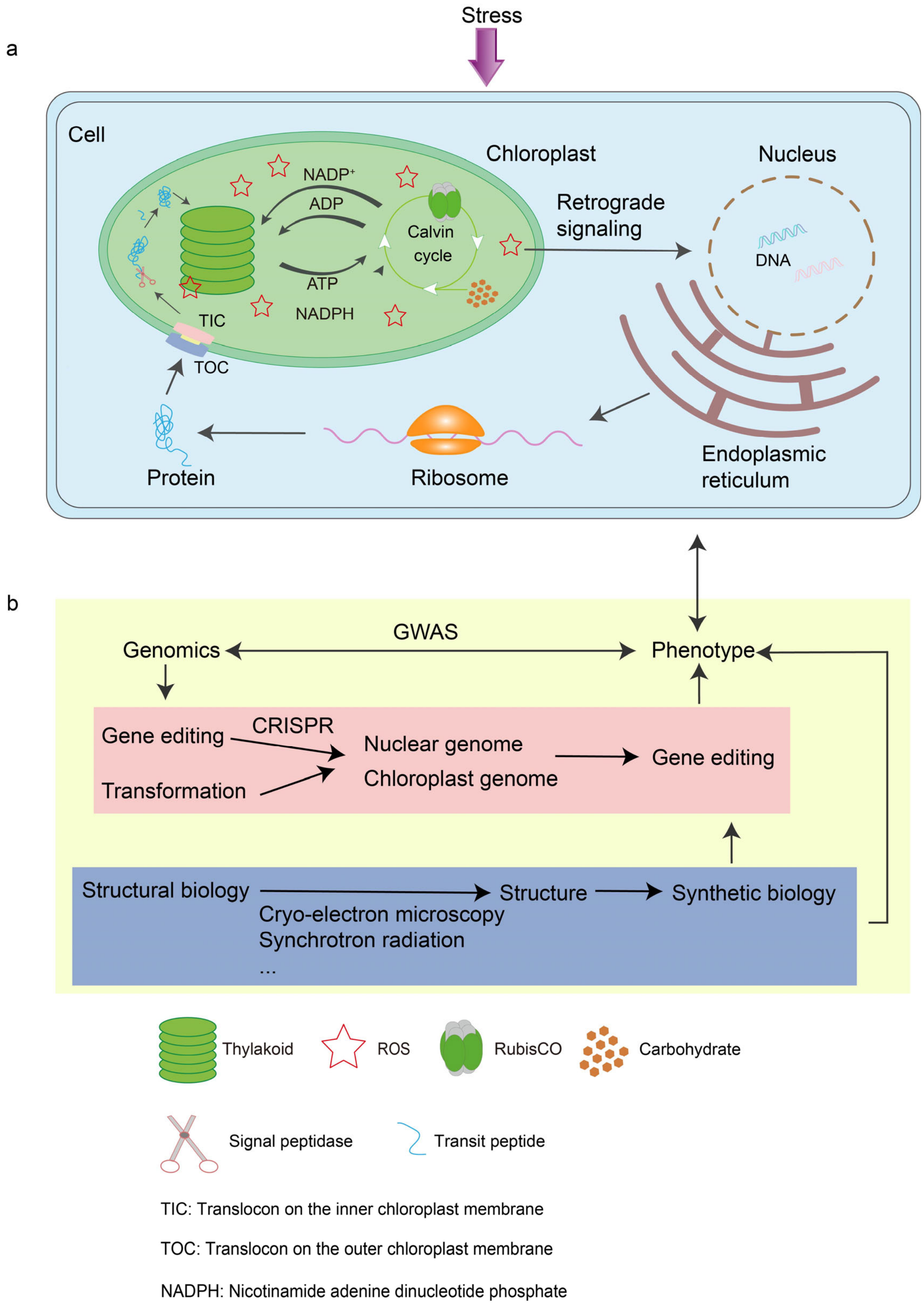

Figure 2. Strategies to improve photosynthesis in poplar under stress. (**a**) Proteins in chloroplasts are encoded by the nuclear and chloroplast genomes, respectively. Proteins with chloroplast transit peptides encoded by the nuclear genome are transported to chloroplasts via the TIC/TOC transporter, where the transit peptides are excised, and the mature proteins function in the chloroplasts. Stress can cause a surge in ROS, which may damage chloroplasts. However, small amounts of ROS also act as signaling molecules, regulating nuclear genes expression through retrograde signaling pathways to maintain cellular homeostasis. (**b**) The application of new technologies is conducive to the analysis

of regulatory mechanisms. GWAS reveals the relationship between genes and phenotypes through a comprehensive study of the genome and can further edit the nuclear genome and the chloroplast genome by means of gene editing and genetic transformation, i.e., analyze and create phenotypes by means of genetic engineering; and the analysis of the three-dimensional (3D) structure of components by means of technologies related to structural biology is conducive to the increase in the understanding of the functions of components, thus providing a theoretical basis for synthetic biology. The analysis of the 3D structure of components by structural biology-related technologies is conducive to increasing the understanding of the functions of components, thus providing a theoretical basis for synthetic biology; structural biology and synthetic biology are conducive to the development and application of genetic engineering, thus promoting the generation of beneficial traits.

Genetic modification can be a valuable strategy for tree improvement. It is especially useful for creating poplar hybrids with enhanced stress resistance and improved photosynthesis under stress conditions (Figure 2). Chloroplasts, essential for photosynthesis, rely on the coordinated expression of both plastid and nuclear genomes [100]. While chloroplast transformation offers a promising platform for creating transgenic plants, progress has been slow due to challenges such as polyploidy and limited transformation techniques [101]. Nanotechnology advances chloroplast transformation, using nanomaterials to transfer DNA and enhance stress resistance [102,103]. For example, single-walled carbon nanotubes have been coated with single-stranded DNA to effectively deliver it to chloroplasts. Additionally, polyethylenimine has been used to promote the binding and release of plasmid DNA into the nuclei of mature land plants [104,105]. Moreover, selenium-chitosan nanoparticles regulate photosynthesis and antioxidant activity in *Dracocephalum moldavica* under Cd stress [106]. However, exogenous genes may cause genetic contamination, affecting wild poplar genetics and ecosystem stability. A minichromosome-based approach could enable stable chloroplast transformation without introducing foreign genes [107].

Synthetic biology offers novel ways to enhance photosynthesis (Figure 2). Combining photosynthetic improvements in poplar under stress with synthetic biology can design more efficient photosynthetic and carbon fixation pathways [108]. Studies have been conducted to transfer several enzyme genes into rice through genetic engineering techniques, resulting in new photorespiratory pathways that regulate photosynthesis and increase yield [109]. Stomatal engineering strategies have also expanded recently, aiming to increase water use efficiency while improving plant carbon assimilation efficiency [110]. Structural biology helps determine protein 3D structures. This information allows synthetic biology to design new biological systems and enable specific biosynthetic reactions or biotransformation processes (Figure 2). For example, PSI-LHCI structures in *Arabidopsis* were studied using cryo-electron microscopy [111]. Future research using advanced structural biology and spectroscopy techniques could reveal how photosynthetic protein complexes in forest trees respond to stress, providing insights to enhance photosynthesis under adverse conditions.

In addition, the poplar genome and transcriptome can be further explored. Methods such as genome-wide association studies (GWAS), co-expression analysis, metabolomics, proteomics, and other multi-omics analyses can be integrated to better understand the regulatory mechanisms of photosynthesis in poplar under stress conditions (Figure 2). GWAS is one of the most important methods for discovering genetic variations controlling important agronomic traits. Recently, GWAS has been used to identify genetic determinants of metabolic diversity in plants and has been widely used to address the genetic architecture of important metabolic traits in different species. [112–114]. In addition, integrated metabolic GWAS (mGWAS), expression quantitative trait nucleotides (eQTNs), and weighted gene co-expression network analysis (WGCNA) provide a powerful framework for studying gene interactions [115]. These research tools have been instrumental in increasing our understanding of the genetic basis of resistance and have provided insights to improve breeding programs for poplar under adverse environmental conditions.

5. Conclusions and Future Perspectives

In recent years, there has been increasing attention on poplar photosynthesis under stress, due to its vital role in ecosystem functioning. We reviewed the effects of abiotic stress and biological stress on the photosynthesis of poplar and prospected the strategies to improve the photosynthetic capacity of poplar. Poplar photosynthesis under stress involves multi-gene regulatory networks, and the expression of chloroplast nuclear genes also involves chloroplast retrograde signaling pathways.

However, the following challenges still exist in the current research on the mechanism of photosynthesis in poplar under adversity. The deep-seated molecular mechanisms regulating photosynthesis, the complexity of genetic variation among poplar species, and the specific mechanisms of synergistic or antagonistic effects between adversities are still unclear. In addition, there are fewer studies on the links between photosynthesis and other metabolic pathways. In future studies, emphasis should be placed on multidisciplinary cross-fertilization and integration of genomics, transcriptomics, and metabolomics to gain a deeper understanding of the genetic and biochemical pathways involved in photosynthesis. Further research on these mechanisms will provide new ideas for poplar resistance breeding. At the same time, it promotes the carbon cycle of terrestrial ecosystems and improves the carbon sequestration capacity. These are of great significance in addressing the ecological challenges in the context of current climate change.

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Abbreviations

The following abbreviations are used in this manuscript:

CO_2	Carbon dioxide
ROS	Reactive oxygen species
AMF	Arbuscular mycorrhizal fungi
qP	Photochemical quenching
PSII	Photosystem II
ΦPSII	The maximum quantum yield of photosystem II
ABA	Abscisic acid
SOD	Superoxide dismutases
C_i	CO_2 concentration
A_{max}	The maximum photosynthetic rate
PSI	Photosystem I

Fv/Fm	The maximal photosynthetic efficiency of PSII
NPQ	The nonphotochemical quenching
RAP	RNA affinity purification sequencing
Cd	Cadmium
Mg	Magnesium
O_3	Ambient ozone
SA	Salicylic acid
GWAS	Genome-wide association study
3D	Three-dimensional

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