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PRIMARY AND SECONDARY METABOLISM, PHOTOSYNTHESIS, AND OXIDATIVE STRESS: FUNDAMENTAL AND APPLIED ASPECTS

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ABSTRACT

Reactive oxygen species (ROS) generated in the photosynthetic apparatus play a dual role as both toxic by-products and essential signalling molecules under abiotic stress. This review analyses the interconnections between primary metabolism, secondary metabolism, photosynthesis, and oxidative stress mechanisms. Recent evidence shows that metabolic flux is redirected from primary to secondary pathways during stress, increasing the production of phenolics, terpenoids, and alkaloids [1–3]. The balance between PSII photoinhibition and repair is governed by ROS signalling and antioxidant enzymes (SOD, CAT, APX, GR) [4]. Key research gaps include quantitative modelling of metabolic flux, differentiation of ROS signals under combined stresses, and translation of laboratory findings to field conditions. Biotechnological tools such as CRISPR/Cas9 offer promising routes to improve stress tolerance and secondary metabolite yield [5].

Keywords: primary metabolism, secondary metabolism, photosynthesis, oxidative stress, reactive oxygen species, antioxidant defence, photoinhibition

INTRODUCTION

Global climate change and population growth threaten crop productivity, with abiotic stresses (drought, salinity, extreme temperatures, high light) causing more than 50% yield losses worldwide [6]. Photosynthesis sets the upper limit of productivity, but its efficiency declines under stress due to ROS overproduction and photoinhibition. Plants respond by reprogramming primary and secondary metabolism. Primary metabolites (sugars, proline, glycine betaine) serve as osmoprotectants, while secondary metabolites (phenolics, terpenoids, alkaloids) function in defense and signaling [7,8].

This article systematically analyses the interplay among photosynthesis, ROS dynamics, and metabolic reprogramming, identifies research gaps, and discusses biotechnological interventions for improving stress tolerance.





LITERATURE REVIEW

Primary and secondary metabolism

Primary metabolism provides energy and carbon skeletons for growth. Under stress, flux is shifted towards secondary metabolism via the shikimate, MEP, and MVA pathways [2,9]. Secondary metabolites are induced by signalling molecules (H_2O_2 , NO, MeJA) and transcription factors (MYB, WRKY, NAC) [3].

Photosynthesis and photoinhibition

Abiotic stresses reduce stomatal conductance, Rubisco activity, and PSII efficiency (Fv/Fm). Photoinhibition occurs when PSII photodamage exceeds its repair, mainly due to ROS attacking the D1 protein [4,10]. Non-photochemical quenching (NPQ) and the xanthophyll cycle provide photoprotection but at the cost of reduced quantum yield [11].

Oxidative stress and antioxidant defence

Major ROS sources are chloroplasts, mitochondria, and NADPH oxidases (RBOHs). At low concentrations, ROS (H_2O_2 , 1O_2 , $O_2^{\bullet-}$) act as signals for acclimation; at high concentrations they cause lipid peroxidation (MDA), protein oxidation, and DNA damage [12]. Antioxidant systems include enzymes (SOD, CAT, APX, GR, GPX) and non-enzymatic compounds (ascorbate, glutathione, tocopherol, flavonoids) [13,14]. Overexpression of SOD, APX, or CAT enhances stress tolerance but may interfere with ROS signalling if too high [15].

Crosstalk

Chloroplastic ROS trigger retrograde signalling that coordinates nuclear gene expression for both primary and secondary pathways. Reduced glutathione (GSH) acts as a metabolic cue of OPDA signalling, co-regulating photosynthesis and defence [16]. ROS also induce secondary metabolite synthesis by activating PAL, CHS, and other key enzymes [17].

Research gaps

Quantitative modelling of metabolic flux between primary and secondary metabolism under multiple stresses is lacking. Specific ROS signatures (spatial, temporal, concentration) that distinguish signalling from damage remain poorly defined. Few studies integrate controlled environment experiments with field validation and computational modelling.

Research Questions and Hypotheses

RQ1: How is metabolic flux redistributed between primary and secondary metabolism under drought, salinity, heat, and high light?

RQ2: Which ROS species and concentrations act as switches between photoprotection, repair, and secondary metabolite induction?

RQ3: Can combined overexpression of SOD, APX, and CAT via CRISPR/Cas9 improve PSII phototolerance and yield more effectively than single gene overexpression?





H1: Under stress, the shift from primary to secondary metabolism is quantitatively measurable and regulated by MYB/WRKY transcription factors.

H2: H_2O_2 and $^1\text{O}_2$ are the primary signalling ROS; their ratio determines metabolic reprogramming.

H3: Combined overexpression of multiple antioxidant genes produces synergistic protection without compromising ROS signalling.

METHODOLOGY

Model plants: *Arabidopsis thaliana* and *Oryza sativa* (or *Nicotiana tabacum* for rapid testing).

Stress treatments: drought (PEG 6000, -0.5 MPa), salinity (100–200 mM NaCl), heat (35 – 40°C , 48 h), high light (1500 – $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Photosynthetic parameters: Chlorophyll fluorescence (Fv/Fm, ΦPSII , NPQ) using PAM, gas exchange (Pn, gs) with IRGA.

ROS and oxidative damage: H_2O_2 (Ti(IV) method), $\text{O}_2^{\bullet-}$ (NBT reduction), MDA (TBA assay).

Antioxidant enzymes: SOD, CAT, APX, GR (spectrophotometric).

Metabolites: Primary (sugars, proline) by colorimetry; secondary (phenolics, flavonoids) by Folin-Ciocalteu and AlCl_3 .

Gene expression: RT-qPCR for SOD, CAT, APX, GR, PAL, CHS, MYB, WRKY.

Genome editing: CRISPR/Cas9 for multiplex overexpression of SOD+CAT+APX.

EXPECTED RESULTS

Under single stresses, Fv/Fm declines from 0.83 (control) to 0.50–0.65, while H_2O_2 increases 2.5–4.0-fold and MDA increases 2.0–3.0-fold [4,10]. Antioxidant enzyme activities rise 1.5–2.5-fold, with the highest induction under high light [14]. Secondary metabolites (phenolics, flavonoids, anthocyanins) accumulate 2–3-fold above control [2,7]. In CRISPR/Cas9 lines overexpressing SOD/CAT/APX, H_2O_2 and MDA are reduced by $\sim 50\%$ compared to wild-type under stress, Fv/Fm improves from 0.45 to 0.65, and yield increases from 12.5 g/plant to 17.8 g/plant (projected) [5,15].

DISCUSSION

The redistribution of metabolic carbon from primary to secondary pathways is an adaptive strategy that prioritises defence over growth. However, the quantitative thresholds that trigger this switch remain unknown. Our analysis supports the idea that H_2O_2 and $^1\text{O}_2$ act as dose-dependent signals: low pulses induce acclimation, while chronic excess causes photoinhibition and cell death [12,18].





The role of GSH as an OPDA-signalling cue [16] highlights a direct link between redox status and jasmonate-dependent secondary metabolism. Similarly, ROS-activated MAPK cascades and transcription factors (MYB, WRKY) coordinate the expression of both antioxidant genes and secondary biosynthetic genes [17]. CRISPR/Cas9-mediated multiplex engineering of antioxidant enzymes shows promise, but careful tuning is required to avoid quenching beneficial ROS signals [15,19]. Field validation remains a major gap; most studies are conducted under controlled conditions that do not mimic diurnal fluctuations or combined stresses. Future research should integrate metabolomic flux analysis, single-cell ROS imaging, and multi-stress field trials. Translational efforts must consider that enhancing secondary metabolism may divert resources from yield; thus, inducible or tissue-specific promoters are preferable.

CONCLUSION

Primary and secondary metabolism are not separate but dynamically linked via ROS-driven signalling networks. Photosynthesis serves as both the source of ROS and the target of oxidative damage. Antioxidant defence systems are essential for maintaining redox balance, but their overexpression must be fine-tuned. Key research gaps include quantitative modelling of metabolic flux, spatiotemporal ROS signatures, and integrated field validation. CRISPR/Cas9 offers powerful tools for engineering stress tolerance and secondary metabolite production, provided that tissue-specific and stress-inducible expression strategies are adopted.





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