# Chloroplast sunscreen: Phase separation mitigates midday high-light-triggered photoinhibition in crops

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Midday high-light stress suppresses photosynthetic carbon fixation and causes substantial yield loss in agroecological zones with high photosynthetically active radiation (PAR). Notably, under natural high-PAR midday conditions, light intensity far exceeds crop photosynthetic saturation thresholds. Excess light absorbed by chloroplast photosensitizers continuously induces the accumulation of singlet oxygen ($^1O_2$), a highly cytotoxic reactive oxygen species (ROS) that acts as the central trigger of field-relevant midday photodamage. For over a century, field midday photosynthetic depression has been largely attributed to stomatal closure and post-assimilate metabolic restriction.[1]

To cope with high-light-induced oxidative stress, plants have evolved multiple canonical photoprotective pathways, mainly including non-photochemical quenching (NPQ)-mediated heat dissipation, ROS detoxification, and continuous D1 protein turnover for PSII repair.[2] Nevertheless, these canonical strategies operate exclusively via post-photochemical regulation and suffer from inherent kinetic delays and metabolic costs, making them insufficient to fully alleviate midday photosynthetic inhibition under natural field conditions. Although liquid–liquid phase separation has emerged as a core regulatory mechanism in plant abiotic adaptation,[3] the photoprotective functions of chloroplast-resident phase-transition structures remain poorly defined. Recent evidence pinpoints a distinctive source-buffering photoprotective mechanism involving the singlet oxygen ($^1O_2$)-triggered phase transition of Methylene Blue Sensitivity1 (MBS1), which shifts from dynamic liquid droplets to less-mobile condensates. Under high-light stress, MBS1 conden-

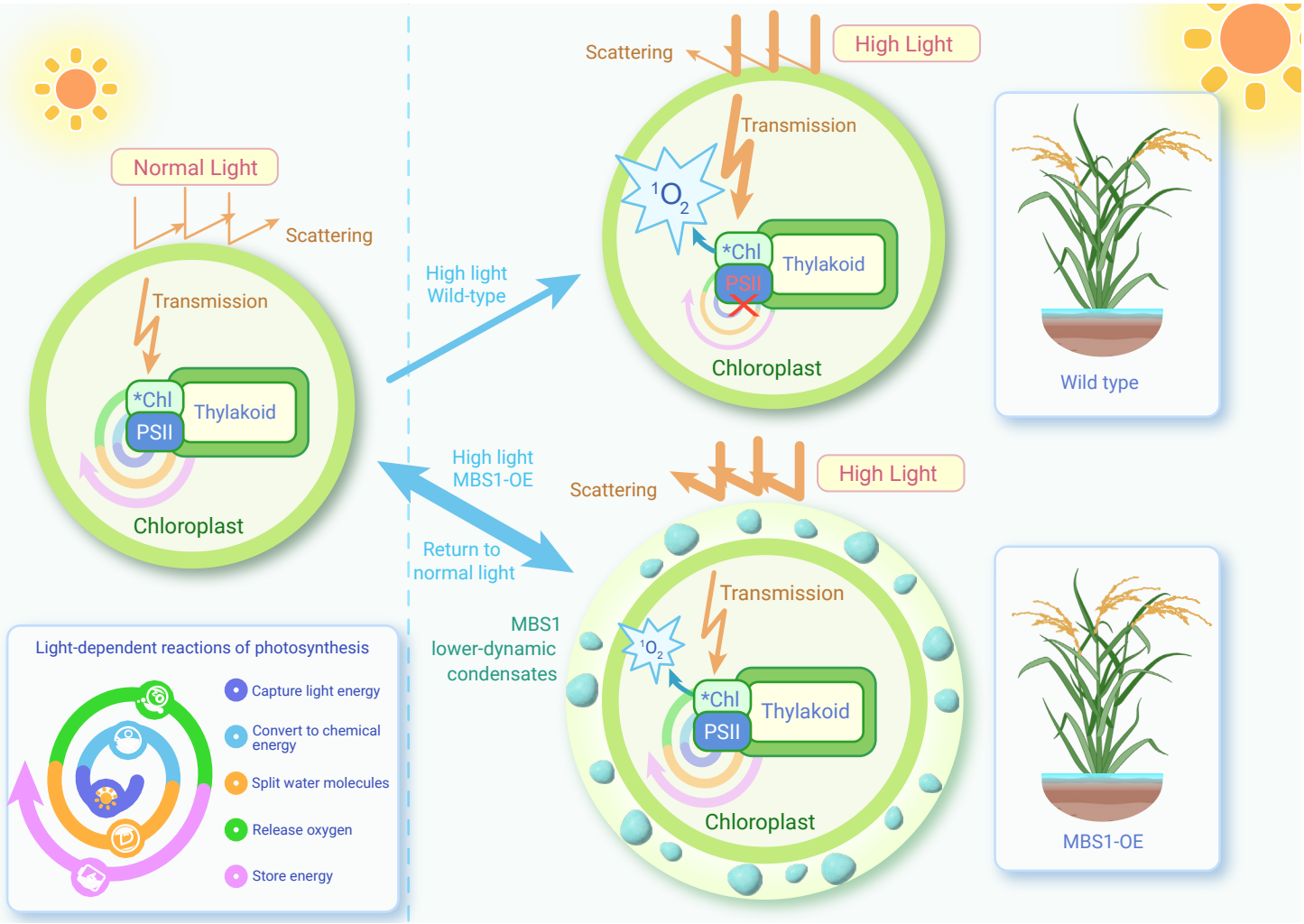


**Figure 1. MBS1-mediated phase separation forms a chloroplast sunscreen that mitigates midday photoinhibition in rice** This schematic illustrates the photoprotective function of MBS1 biomolecular condensates. It compares three physiological scenarios: non-stress normal light, high-light conditions in wild-type rice chloroplasts, and high-light conditions in MBS1-overexpressing (MBS1-OE) chloroplasts. In MBS1-OE plants, high-light-triggered $^1O_2$ drives the transition of dynamic liquid droplets toward low-mobility MBS1 condensates anchored at the chloroplast outer envelope. These condensates function as a passive, broad-spectrum optical shield that scatters excess incident light, curbs cytotoxic $^1O_2$ bursts, and protects PSII against photodamage. By contrast, wild-type chloroplasts lack this pre-thylakoid optical barrier and sustain severe photodamage under high light stress. This reversible regulatory system reconciles the inherent photoprotection-efficiency trade-off.

sates localize to the chloroplast outer envelope in planta, assembling a physical light-scattering barrier (Figure 1). In this Out-of-the-Box article, we put forward a distinct source-buffering photoprotective strategy rooted in $^1O_2$-sensing phase transition, present an unconventional model to revisit midday photosynthetic decline, and highlight the potential of this phase-separation module to guide interdisciplinary breeding for climate-resilient crops.

Under saturating midday irradiance, excess photon flux drives elevated chloroplast $^1O_2$ levels, which serve as a physiological trigger for the MBS1 liquid–liquid phase transition.[4] The intrinsically disordered regions (IDRs) of MBS1 support rapid, reversible condensation to generate nanoscale condensates tethered to the chloroplast outer envelope. Distinct from known post-absorptive biochemical photoprotection, these peripherally anchored assemblies facilitate physical light scattering to establish a previously unrecognized pre-thylakoid defense layer. These phase-separated condensates dynamically buffer excess incident irradiance, limiting photon penetration into thylakoids and curbing runaway $^1O_2$ production as well as photosystem injury. This reversible optical-shielding mechanism carries comparatively low steady-state metabolic overhead relative to constitutively active canonical photoprotective pathways including NPQ and D1-protein turnover. This source-buffering photoprotective layer operates alongside NPQ, antioxidant systems, and PSII repair machinery to mitigate biochemical stress under fluctuating field light conditions. The MBS1-dependent photoprotective module appears functionally conserved across rice, potato, and oilseed sunflower, laying a solid foundation for enhancing field stress tolerance in high-PAR agricultural zones worldwide.

Identifying MBS1 phase-separated sunscreening advances current understanding of midday photosynthetic regulation. When protective structural assembly is insufficient during peak solar irradiation, excessive light is not buffered, leading to unregulated $^1O_2$ accumulation and progressive thylakoid damage. This intrinsic limitation independently drives the midday photosynthetic decline, supplementing known environmental factors. Moderate upregulation or genome editing of MBS1 can optimize light-responsive condensate assembly under midday irradiance stress, stabilizing daily carbon fixation and mitigating photosynthetic depression. Such genetic adjustments hold promise for high-PAR croplands across Northwest China, tropical South America and tropical Africa,[5] and work for both staple and cash crops. Different from conventional stress-resistance genes, which often cause growth trade-offs under favorable conditions, the light-reversible feature of MBS1 structural transition minimizes fitness costs in normal environments. This regulatory module connects fundamental biomolecular mechanisms with agronomic practices, linking subcellular structural control to future germplasm optimization.

Advances in this regulatory paradigm highlight several unresolved mechanistic challenges. Key gaps include the upstream signaling machinery controlling MBS1 expression and $^1O_2$-sensing sensitivity, as well as tissue-specific and environment-dependent dynamics of chloroplast phase-transition assemblies. The physiological crosstalk between MBS1-mediated light scattering and other high-light responses, including stomatal dynamics and downstream $CO_2$-limited metabolic reprogramming, remains largely underexplored. Establishing robust *in vivo* monitoring approaches to quantify energetic dynamics throughout condensate assembly, persistence and disassembly also represents a critical experimental frontier. Deciphering how MBS1 condensates exert early protective action prior to the onset of irreversible oxidative damage further stands as a core mechanistic priority.

Building on these unresolved mechanistic puzzles rooted in the chloroplast-sunscreen paradigm, two concrete conceptual avenues open up for future research. First, biophysical and photophysical quantification is required to dissect the real-time optical behavior of MBS1 condensates inside living plant cells, a goal dependent upon further technical advances in confocal microscopy, which is critical to fully decipher how this phase-separated sunscreen mitigates midday photoinhibition. Second, artificial intelligence (AI)-guided sequence design of MBS1 may re-engineer condensate dynamics and light-scattering performance, enabling precise optimization of this intrinsic photoprotective module for climate-resilient crop breeding. Inspired by this natural chloroplast sunscreen principle, biomimetic nano-coating strategies may also represent a thought-provoking translational prospect, though such material-oriented applications lie beyond the scope of the present plant-focused commentary and will require dedicated follow-up investigations.

In summary, recent research has established a phase separation-centered photoprotective module that is distinct from canonical biochemical pathways. MBS1 dynamic light-scattering nanoassemblies constitute a unique thylakoid-upstream regulatory cascade that alleviates crop midday photosynthetic inhibition. Cross-species conservation of this module endows robust applicability for high-PAR agriculture, offering a low-cost, flexible strategy to stabilize crop yields under variable field light conditions.

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## AUTHOR CONTRIBUTIONS

Ning Shao: Conceptualization, writing draft and editing the final manuscript. Bing Wang and Jiayang Li: Conceptualization and editing. All authors read and approved the final version.

## DECLARATION OF INTERESTS

The authors declare no competing interests.