

Plastoglobules put nitrogen assimilation in its place

Di Chen,¹ Yongcai Huang,^{1,*} Lulu Gao,¹ and Moyang Liu^{1,2,*}

¹Sichuan Agricultural University, Chengdu 611130, China

²Hainan Research Institute, Shanghai Jiao Tong University, Sanya 572000, China

*Correspondence: lmyunxi@163.com (M.L.); ychuang@scau.edu.cn (Y.H.)

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Nitrogen is indispensable to crop productivity but inefficiently used at field scale. Large fertilizer inputs underpin modern cereal production, yet a substantial fraction of applied nitrogen is not captured by crops, driving production costs and environmental burdens. In maize, where reported nitrogen use efficiency (NUE) can remain below 30%, improving yield per unit nitrogen will require more than stronger nitrate uptake or higher expression of single transporters. It requires an account of how inorganic nitrogen that reaches photosynthetic tissues is organized, detoxified and converted into organic nitrogen with minimal loss.^{1,2}

Chen and colleagues now provide such an account by moving the center of the problem from enzymes themselves to their location.¹ They show that plastoglobules (PGs), lipid droplet-like chloroplast subcompartments associated with thylakoid membranes, function in maize mesophyll cells as nitrogen-responsive hubs for early nitrogen assimilation. The advance is conceptual: the nitrate-to-amino-acid pathway has long been known biochemically, but Chen et al. identify a suborganellar address where nitrite reduction and ammonium assimilation are coordinated (Figure 1).

The first line of evidence is morphological. Across a nitrogen gradient, maize seedlings accumulated biomass and greener leaves, as expected, while mesophyll chloroplasts showed a progressive increase in PG number, accompanied by size remodeling. This response was not simply a by-product of enlarged chloroplasts and was not mirrored as a nitrogen-dependent trend in bundle sheath chloroplasts.¹ The cell-type specificity matters because maize is a C4 plant in which mesophyll and bundle sheath cells divide photosynthetic and nitrogen-metabolic labor. PG dynamics therefore

emerge in the same cellular compartment in which early nitrate assimilation is concentrated.

The response was not confined to maize. Soybean, tobacco, rice and wheat also showed nitrogen-associated increases in PG number, supporting the view that PG remodeling is a broadly conserved response across the tested C3 and C4 lineages.¹ That breadth extends the known functional repertoire of PGs. Earlier work emphasized their roles in lipid metabolism, plastid development, senescence and environmental adaptation.³ Chen et al. now place PGs in primary nitrogen metabolism under growth-relevant nitrogen regimes.

The biochemical evidence is central. Through mesophyll-cell chloroplast fractionation, PG purification and data-independent acquisition proteomics, the authors identified two nitrogen-assimilation enzymes, ZmNIR2 and ZmGLN1 (GS2), among PG-associated proteins.¹ ZmNIR2 reduces nitrite to ammonium, whereas ZmGLN1 (GS2) incorporates ammonium into glutamine. Because these are consecutive steps, their co-localization at PGs provides a plausible channeling logic: reactive and diffusible intermediates can be processed locally rather than allowed to accumulate or disperse through the stroma.

Genetic analysis then converts co-localization into function. Loss of ZmNIR2 or ZmGLN1 (GS2) impaired nitrogen responsiveness and vegetative growth, whereas other tested NIR and GLN/GS paralogues did not show comparable effects.¹ This non-redundancy is important. Many metabolic pathways contain enzyme families with overlapping catalytic potential, but this study indicates that the relevant variable is not simply total nitrite reduc-

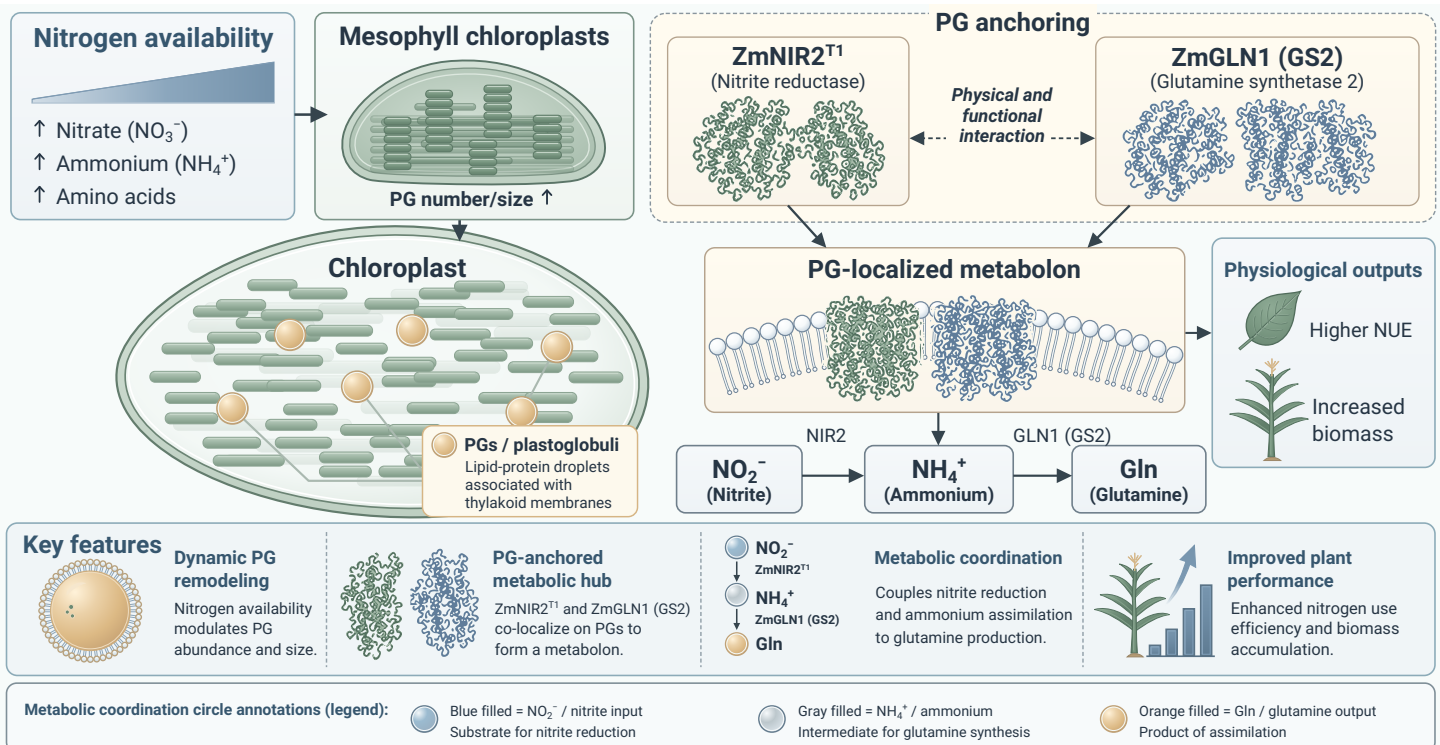


Figure 1. Plastoglobules organize early nitrogen assimilation in maize mesophyll chloroplasts Nitrogen availability promotes PG remodeling in mesophyll chloroplasts, primarily by increasing PG abundance, with accompanying size remodeling. PG-anchored ZmNIR2^{T1} and decameric ZmGLN1 (plastidic GS2) make weak physical contact at the single phospholipid monolayer of PGs, forming a local metabolon that couples nitrite reduction to ammonium assimilation and glutamine synthesis. PGs are shown as yellow droplets. This spatial module is associated with enhanced nitrogen responsiveness and greater vegetative biomass.

tase or glutamine synthetase activity. It is whether the correct isoform is positioned at the correct chloroplast subdomain.

Chen et al. also define a targeting logic. ZmNIR2 and ZmGLN1 (GS2) enter chloroplasts through N-terminal transit peptides, whereas their subsequent association with PGs depends on internal hydrophobic regions.¹ Deleting these regions separates chloroplast import from PG anchoring. This distinction provides a possible engineering code: if hydrophobic-region-mediated targeting can be transferred without disrupting folding, turnover or regulation, chloroplast enzymes may be organized into designed microdomains rather than merely overexpressed as soluble proteins.

The structural and interaction data deepen the model. Cryogenic electron microscopy showed that recombinant ZmGLN1 (GS2) forms a decameric complex, and native gel analysis supported an endogenous oligomeric state that increased with nitrogen supply.¹ Biochemical and biophysical assays further supported a direct but apparently weak association between ZmNIR2 and ZmGLN1 (GS2). In this model, PGs are not passive lipid stores. They are inducible platforms that concentrate enzymes, scale assimilation capacity with nitrogen status and help coordinate conversion of nitrite-derived ammonium into glutamine.

The translational element is notable but should be framed precisely. Natural variation in ZmNIR2 splicing generates isoforms with different localization behavior: the PG-targeted ZmNIR2^{T1} isoform is associated with stronger nitrogen responsiveness, whereas ZmNIR2^{T2} lacks the same PG-anchoring outcome.¹ Overexpression of ZmNIR2^{T1} increased PG abundance, plant height and biomass under multiple nitrogen regimes, and field tests in Harbin showed improvements in plant height and fresh weight.¹ These findings place PG targeting in the breeding landscape, alongside maize genetic work showing that *THP9* and teosinte-derived alleles enhance seed protein, nitrogen assimilation and NUE.^{4,5}

Several mechanistic questions now become central. What senses nitrogen status and triggers PG proliferation in mesophyll chloroplasts? Do nitrogen-dependent PG lipid compositions change in ways that affect redox buffering, thylakoid remodeling or enzyme recruitment? Do bundle sheath PGs execute functions that were not revealed by the nitrogen gradients tested? Because GOGAT activity is generally associated with bundle sheath metabolism in C4 leaves, the next question is not simply whether GOGAT is added to the same mesophyll PG complex, but how the mesophyll ZmNIR2-ZmGLN1 (GS2) module exchanges nitrogenous products with bundle sheath nitrogen metabolism. Is glutamine, glutamate or another metabolite-exchange route the currency that connects the mesophyll PG metabolon with the bundle-sheath GS-GOGAT cycle? Answering these questions will determine whether PGs can be treated as programmable hubs rather than isolated nitrogen-processing droplets.

A second set of questions concerns translation. Increasing the ZmNIR2^{T1} proportion through marker-assisted selection, allele mining or promoter/splicing engineering is attractive. However, maize NUE should be handled as a composite but decomposable trait rather than a single universally standardized readout. For whole-plant growth and silage-oriented maize, nitrogen efficiency may be best captured by vegetative biomass and nitrogen responsiveness; for high-protein maize, by grain or tissue protein content; and for yield-oriented maize, by grain yield, grain quality and fertilizer recovery. A PG-targeted isoform that boosts seedling biomass or vegetative fresh weight must therefore be tested across germplasm, nitrogen-management systems and multi-location field environments, with trait-specific endpoints, grain yield, grain protein, fertilizer recovery and possible trade-offs measured in parallel.

Those trade-offs deserve explicit attention because PGs already participate

in lipid metabolism, plastid development, senescence and stress responses.³ Altering PG abundance or enzyme occupancy could therefore affect photo-synthetic redox balance, prenylquinone metabolism, thylakoid maintenance, stress tolerance or leaf aging. The strength of the Chen et al. study is that it provides concrete molecular handles; the challenge is to evaluate those handles in the integrated physiology of crops in fields.

This work also asks plant metabolism to be drawn differently. Pathways are often represented as linear reaction chains, but cells implement them as spatially organized systems. Enzymes operate in organelles, membranes, contact sites, condensates and microdomains. When a pathway uses reducing power and passes through potentially toxic intermediates, location can become as important as catalytic rate. PGs now join this organizing logic as chloroplast microcompartments that connect nitrogen assimilation with plastid architecture.

Improving crop NUE is usually framed as a sustainability problem, and rightly so. Yet sustainability will not be achieved by agronomic input optimization alone. It will require crops that process nitrogen more efficiently once it enters the plant. By revealing a PG-dependent metabolon that organizes maize nitrogen assimilation, Chen et al. provide a new route into that problem. The lesson is simple: metabolism is not only a question of what enzymes do, but also of where they do it. In maize, plastoglobules have put nitrogen assimilation in its place.

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

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AUTHOR CONTRIBUTIONS

All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.