



Arabidopsis photorespiration is not limited by mitochondrial serine hydroxymethyltransferase 1

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Received: 15 January 2026 / Accepted: 18 March 2026 / Published online: 25 March 2026
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Abstract

Main conclusion Genetic engineering of *Arabidopsis thaliana* reveals that mitochondrial serine hydroxymethyltransferase 1 (SHMT1) protein abundance does not limit the capacity of photorespiration, photosynthesis, or stomatal conductance.

Abstract Photorespiration safeguards photosynthesis from negative metabolic feedback inhibition caused by Rubisco's major oxygenation byproduct, 2-phosphoglycolate, and its downstream metabolites. Previous studies have shown that photosynthetic limitations can be alleviated by enhancing endogenous photorespiratory flux through position-specific enzyme overexpression. Here, we investigated whether overexpression of mitochondrial serine hydroxymethyltransferase 1 (SHMT1) influences this regulatory circuit. However, the 1.3-threelfold increase in SHMT1 protein abundance did not affect the visual phenotype, growth, or photosynthetic gas-exchange parameters, including CO₂ assimilation rates and stomatal conductance, under either standard or photorespiration-promoting conditions. Metabolomic analyses further revealed wild-type-like steady-state accumulation patterns of photorespiratory and other primary metabolites in transgenic lines during both, illumination and darkness, respectively. These results indicate that SHMT1 is already expressed at sufficient levels in *Arabidopsis* wild type, as substantial increases in protein abundance did not enhance photorespiratory flux and growth under laboratory conditions.

Keywords Gas exchange · Metabolomics · Photosynthesis · Rate-limiting step · Stomatal conductance

Introduction

Photorespiration is essential for maintaining efficient oxygenic photosynthesis by preventing metabolic inhibition of the Calvin–Benson–Bassham (CBB) cycle. In addition, it is tightly integrated into primary metabolism through extensive carbon and nitrogen exchange and exerts regulatory control over several biosynthetic pathways, including nitrogen and sulfur assimilation, and the subcellular redox homeostasis (Foyer et al. 2009; Busch 2020). Photorespiration is initiated when ribulose-1,5-bisphosphate (RuBP)

carboxylase/oxygenase (Rubisco) catalyzes the oxygenation of RuBP, producing one molecule each of 3-phosphoglycerate (3-PGA) and 2-phosphoglycolate (2-PG). Due to Rubisco's intrinsic catalytic properties and atmospheric gas composition, oxygenation occurs frequently, leading to substantial 2-PG formation (Busch 2020). As 2-PG is toxic and inhibits several enzymes of the CBB cycle, it must be rapidly recycled through photorespiration, which converts two molecules of 2-PG into one 3-PGA while releasing CO₂ and NH₄⁺ (Bauwe and Fernie 2020).

Despite long-standing efforts to engineer an oxygen-insensitive Rubisco, limited success has shifted attention toward alternative strategies to reduce photorespiratory carbon loss. These include enhanced CO₂ recapture and synthetic bypasses relocating decarboxylation reactions to the chloroplast, which have shown promise in several plant species (South et al. 2018; Xu et al. 2023; Smith et al. 2025). In parallel, optimization of endogenous photorespiratory enzymes has emerged as a powerful approach to improve photosynthesis and growth. While reduced

Communicated by Dorothea Bartels.

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photorespiratory flux impairs CO₂ assimilation, overexpression of distinct enzymes such as 2-PG phosphatase (PGLP1) and glycine decarboxylase (GDC) subunits H and L enhances photosynthesis, growth, and carbon use efficiency (Flügel et al. 2017; Timm et al. 2012, 2015, 2025). These improvements correlate with lower steady-state levels of photorespiratory intermediates, suggesting increased pathway capacity and relief from metabolic inhibition of the CBB cycle.

Although the roles of PGLP1 and GDC are well established, the contribution of other enzymes to photorespiratory flux control remains poorly understood. Therefore, we investigated whether the mitochondrially localized serine hydroxymethyltransferase 1 (SHMT1), which operates in close functional association with GDC, represents an additional limitation for photorespiratory metabolism, photosynthesis, and plant growth. The rationale for investigating SHMT1 abundance stems from the central role of this enzyme in mitochondrial photorespiratory metabolism. Genetic disruption of *SHMT1* causes pronounced photorespiratory phenotypes in both *Arabidopsis* and potato (Schjoerring et al. 2006; Voll et al. 2006), even in the absence of simultaneous manipulations of GDC. These observations, therefore, identify SHMT1 as a plausible candidate for influencing photorespiratory flux. Moreover, enzyme abundance has been shown to affect flux control at several steps of the photorespiratory pathway, as discussed above. In the case of GDC, for example, it was not immediately apparent that increased expression of individual components such as the H- or L-protein would stimulate GDC activity, given that both proteins are already highly abundant in mitochondria (Bauwe 2023) and therefore unlikely to be present at limiting levels.

Although SHMTs constitute a small multigene family in *Arabidopsis*, comprising seven isoforms localized to different cellular compartments including mitochondria, cytosol, chloroplasts, and the nucleus, SHMT1 represents the only mitochondrial isoform directly associated with the photorespiratory glycine-to-serine conversion (Voll et al. 2006). Other SHMT isoforms, including cytosolic and chloroplastic forms, are thought to function primarily in cellular one-carbon metabolism and may contribute to the maintenance of glycine and serine pools in their respective compartments (Nogués et al. 2022). While these pools could potentially influence metabolite exchange between compartments, the mitochondrial SHMT1 isoform is directly linked to the GDC reaction and therefore represents the key SHMT involved in the photorespiratory pathway. Our study, therefore, specifically addressed whether increasing the abundance of this mitochondrial enzyme affects photorespiratory flux *in vivo*.

Materials and methods

Overexpression construct, transformation, and plant growth

To overexpress serine hydroxymethyltransferase 1 (SHMT1), the full-length coding sequence of *Flaveria pringlei* *SHMT1* (FpSHMT1) was PCR-amplified from cDNA using primers FpSHMT1-EcoRI-S (P308) and FpSHMT1-EcoRI-AS (P306) (sequences are listed in Supplemental Table S1). The amplified fragment was cloned into pGEM-T (Invitrogen) for sequence verification and subsequently subcloned into the CaMV polyadenylation cassette of pGreen in sense orientation. The resulting FpSHMT1:CaMV fragment was transferred into the binary vector pGreen0229 (Hellens et al. 2000) carrying the mesophyll-specific, light-inducible ST-LSI promoter (Stockhaus et al. 1989; Timm et al. 2012), generating pG0229:ST-LSI:FpSHMT1:CaMV (Fig. 1A). The construct was introduced into *Agrobacterium tumefaciens* strain GV3101 and transformed into *Arabidopsis thaliana* (*Arabidopsis*) Col-0 plants by floral dip (Clough and Bent 1998). From 20 phosphinotricine-resistant plants, four independent transgenic lines (FpS-L1–L4) with confirmed genomic integration and increased SHMT1 protein abundance (~1.3–threefold relative to wild type) were selected. Homozygous T3 plants were used for all analyses. Plants were grown under standard conditions (10 h light/14 h dark, 20/18 °C day/night, 120–140 µmol m⁻² s⁻¹ photosynthetically active radiation, ~70% relative humidity) on a 4:1 mixture of soil (Type Mini Tray; Einheitserdewerk) and vermiculite and watered with 0.2% Wuxal liquid fertilizer (Aglukon, Düsseldorf, Germany). All experiments were performed with plants at stage 5.1 (Boyes et al. 2001).

Validation of transgenic lines, RT-PCR, and immunoblot analysis

Genomic DNA was isolated from rosette leaves and used to verify transgene integration by PCR. Hence, the *ST-LSI* promoter-*FpSHMT1*_CDS fusion (P280/P306; 2554 bp) was amplified as diagnostic fragment and the ribosomal protein *S16* gen (P444/P445; 432 bp) served as control. Protein abundance was analyzed by SDS-PAGE and immunoblotting according to standard procedure, using specific antibodies raised against recombinant SHMT1 and glycine decarboxylase T-protein (*Solanum tuberosum*).

Measurements of photosynthetic parameters

Gas exchange measurements were performed on fully expanded leaves using an open gas-exchange system as

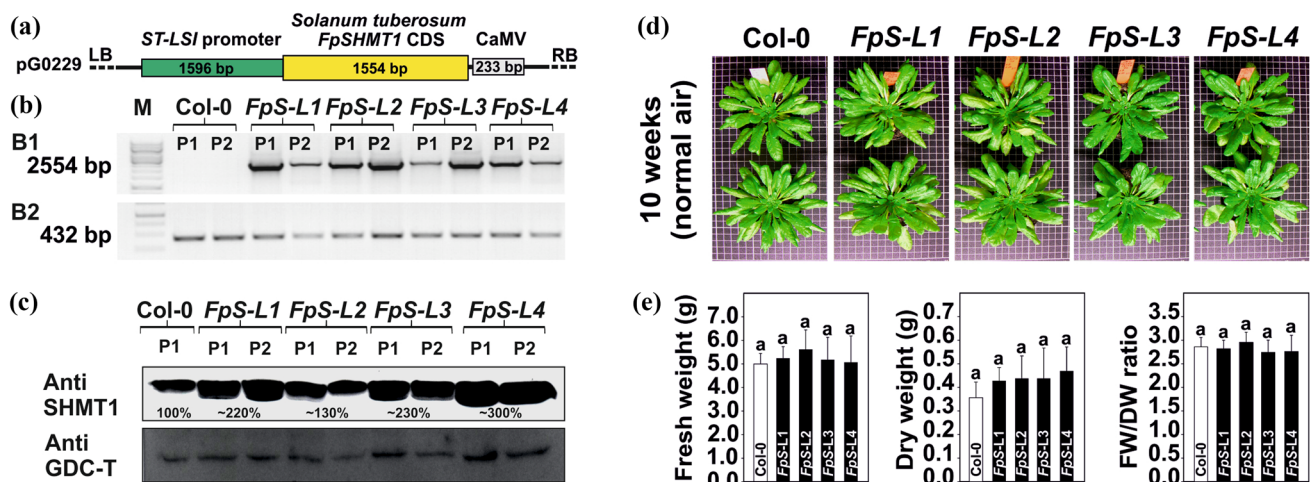


Fig. 1 Isolation, phenotype, and growth of *FpS* overexpression lines. **A** Scheme of the *FpSHMT1* overexpression construct. **B** PCR verification and **C** immunoblots with antibodies against recombinant serine hydroxymethyltransferase 1 (SHMT1) and glycine decarboxylase (GDC) T-protein, using 5 µg total leaf protein per lane of a denaturing polyacrylamide gel and two plant individuals per overexpressor

line *FpS-L1-L4*. **D** Visual phenotype. **E** Selected quantitative growth parameters of the transgenic lines and the wild type after 10 weeks in normal air (400 ppm CO₂). Given are means ± SD of 6 biological individuals. Values that do not share the same letter are significantly different from each other as determined by ANOVA

described previously (Timm et al. 2011). *A/C_i* curves (400, 300, 200, 100, 50, 20, 0, 400 ppm CO₂) were recorded at a photon flux density of 1000 µmol m⁻² s⁻¹, leaf temperature of 25 °C, flow rate of 300 µmol s⁻¹, relative humidity of 60–70%, and three oxygen concentrations (10, 21, and 40% O₂, balanced with N₂). Measurements were conducted during a 6-h window in the middle of the light period.

Metabolite profiling

Primary metabolites were quantified by gas chromatography–mass spectrometry (GC–MS). Leaf material was harvested at the end of the day (9 h light) and night (13 h dark), immediately frozen in liquid nitrogen, and stored at –80 °C. Approximately 30–50 mg of leaf tissue from at least five biological replicates were analyzed. Metabolite extraction, derivatization, and GC–MS analysis were performed as described by Lisec et al. (2006).

Statistical analysis

Statistical significance was assessed by ANOVA or Student's *t* test, with *P* < 0.05 considered as significant.

Results and discussion

Mitochondrial serine hydroxymethyltransferase 1 (SHMT1) functions in close association with the photorespiratory enzyme glycine decarboxylase (GDC), a multi-enzyme system composed of the H-, P-, T-, and L-proteins. Together,

the GDC–SHMT1 reaction cycle catalyzes the conversion of two glycine molecules into one molecule of serine, accompanied by the release of CO₂, ammonia, and NADH (Voll et al. 2006; Bauwe 2023). Previous studies have demonstrated that, under standard growth conditions, GDC activity is constrained by the abundance of the H- and L-proteins, whereas the T-protein does not appear to be limiting (Timm et al. 2012, 2015, 2018). By contrast, the potential flux control exerted by the P-protein remains largely unexplored due to the absence of comparable overexpression studies *in planta*. Notably, increased expression of the H- and L-proteins enhanced overall photorespiratory flux and positively affected photosynthesis and plant growth. Given the central role of the GDC–SHMT1 reaction cycle in photorespiration and its impact on plant performance (Schjoerring et al. 2006; Voll et al. 2006), we sought to determine whether increased SHMT1 abundance could likewise modulate photorespiratory metabolism.

To avoid transcriptional repression caused by RNA interference, the *SHMT1* cDNA from *Flaveria pringlei* was constitutively expressed in *Arabidopsis thaliana* wild-type plants (Col-0). Photorespiration-associated expression characteristics, namely light inducibility and preferential expression in green, chloroplast-containing tissues, were conferred by driving *SHMT1* expression through the *Solanum tuberosum ST-LSI* promoter (Stockhaus et al. 1989), which has previously been used successfully in photorespiratory overexpression studies. Four independent transgenic lines were generated (Fig. 1A; *FpS-L1*–*L4*) and verified by PCR (Fig. 1B). After several rounds of selfing, stable T3-generation lines exhibiting approximately 1.3–threefold increased

SHMT1 protein abundance were selected for detailed analyses (Fig. 1C). The selected lines were examined with respect to growth performance, photosynthetic parameters, and metabolite profiles. To avoid seed-age-related bias, wild-type plants derived from the same seed harvest were grown alongside the transgenic lines in all experiments. Under ambient air conditions, *SHMT1*-overexpressing lines *FpS*-L1-L4 were visually indistinguishable from wild-type controls (Fig. 1D). Consistently, fresh weight, dry weight, and the derived FW/DW ratio did not differ significantly between genotypes. The similar phenotype contrasts with previously described photorespiratory overexpression lines, such as PGLP1 and GDC H- and L-protein overexpressors, which displayed enhanced growth under comparable conditions (Timm et al. 2012, 2015, 2025; Flügel et al. 2017).

Similar to GDC T-protein overexpression lines (Timm et al. 2018), the absence of a growth advantage in *SHMT1*-overexpressing plants suggests that SHMT1 protein abundance does not limit the overall GDC-SHMT1 reaction cycle and, consequently, photorespiratory flux in Arabidopsis under standard growth conditions. This interpretation is consistent with earlier reports describing unaltered growth following *SHMT1* overexpression in both Arabidopsis and rice under non-stress conditions (Liu et al. 2019; Li et al. 2024). Nevertheless, SHMT1 has been implicated in maintaining plant performance under specific environmental conditions, including abiotic and biotic stress (Moreno et al. 2005; Liu et al. 2019), similar to overexpression studies on photorespiratory glycolate oxidase in rice (Cui et al. 2016). However, another study has reported *SHMT1* overexpression to affect biomass accumulation in fast-growing species such as poplar (Zhang et al. 2019), suggesting a more context-dependent role for SHMT1 function. Such growth responses might be explained by the impact of higher SHMT1 activity on C1-carbon metabolism, to which the GDC-SHMT1 reaction cycle contributes (Gashu et al. 2025), but more systematic analysis is pending.

Growth stimulation in previously described plants overexpressing photorespiratory proteins was consistently associated with enhanced photosynthetic CO₂ assimilation (Timm et al. 2012, 2015, 2025; Flügel et al. 2017). In contrast, and in line with the absence of growth stimulation observed in *SHMT1*-overexpressing lines mentioned before, no statistically significant changes were detected in diagnostic photosynthetic gas-exchange parameters. Net CO₂ assimilation rates (A_N), the CO₂ compensation point (Γ), stomatal conductance (g_s), transpiration rates (E), intracellular CO₂ concentration (C_i), and the C_i/C_a ratio remained indistinguishable between transgenic lines and wild-type plants under ambient O₂ levels. Interestingly, although stomatal closure was shown to be partially affected by posttranslational modification of SHMT1 (i.e., protein phosphorylation) in mutant complementation lines (Liu et al. 2019), a general effect of

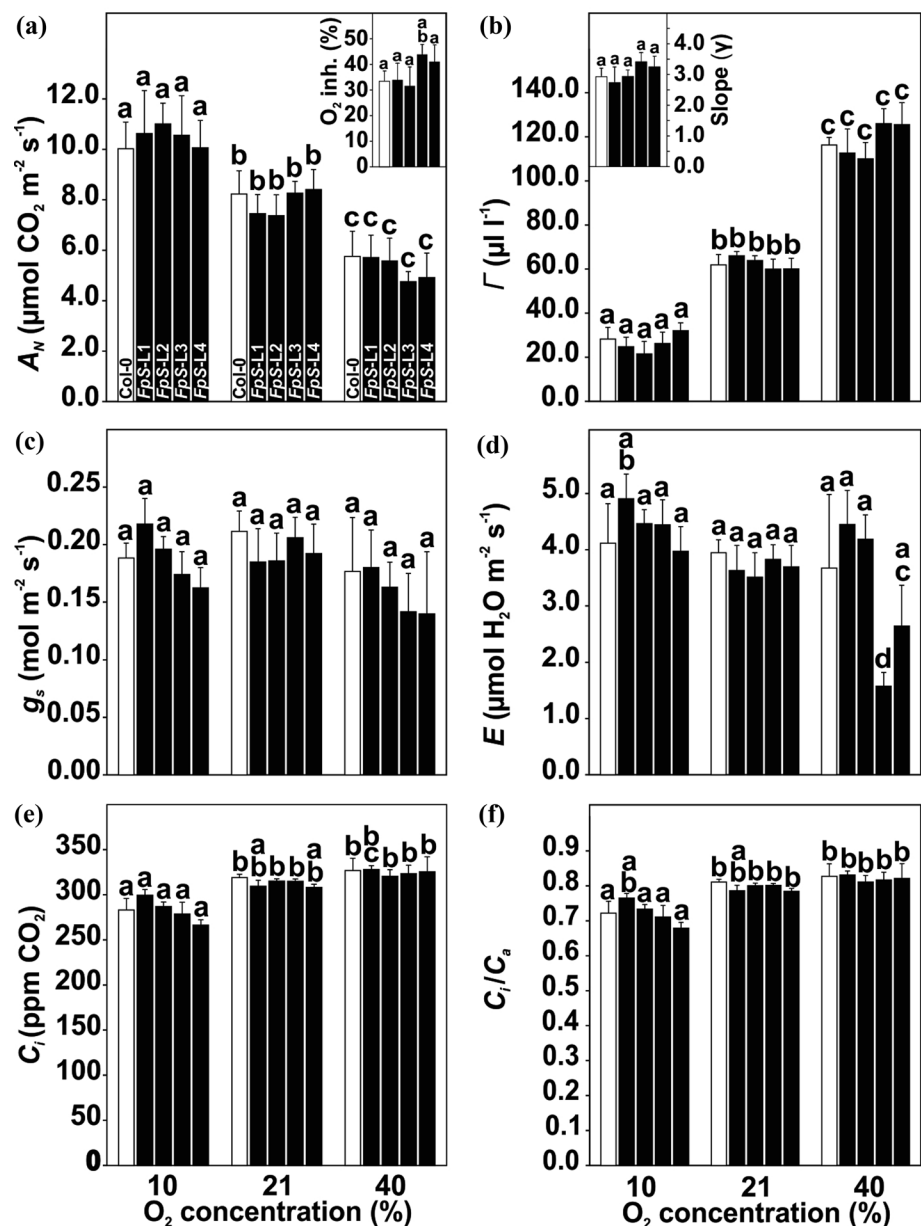
increased SHMT1 protein abundance on g_s can be rather excluded. Nevertheless, guard cell-specific manipulations should be tested in the future, given active photorespiration in these specialized cells seems important for proper stomatal movements (Sun et al. 2025, 2026).

The described gas exchange trends persisted under both reduced (10% O₂) and elevated (40% O₂) oxygen concentrations, which impose decreased and increased photorespiratory pressure, respectively (Fig. 2A–F). Furthermore, oxygen inhibition of A_N and the slope of the O₂-versus- Γ relationship (γ), a parameter reflecting additional CO₂ release via photorespiration (Cousins et al. 2011), were comparable across all genotypes (Fig. 2A, B, insets). Together with the unchanged growth performance described in the preceding section, these gas-exchange data reinforce the conclusion that SHMT1 does not limit the protection of photosynthesis by photorespiration in Arabidopsis under the tested conditions. Further, increasing SHMT1 protein levels alone is insufficient to improve photosynthetic efficiency or plant performance under standard or photorespiration-promoting environments.

Optimizing photorespiratory flux through enzyme overexpression at specific pathway steps, most notably PGLP1 and components of the GDC complex, has previously been shown to reduce steady-state pools of detrimental photorespiratory intermediates. These metabolic adjustments act as a functional metabolic chassis that alleviates negative feedback inhibition on CO₂ fixation, particularly within CBB cycle (Ferne and Bauwe 2020). In light of the absence of growth stimulation and altered photosynthetic gas exchange in *SHMT1*-overexpressing plants, we assessed whether *SHMT1* overexpression affected steady-state metabolite profiles in Arabidopsis under both illuminated and dark conditions.

In contrast to PGLP1- and GDC-overexpression transgenic lines (Timm et al. 2012, 2015, 2025; Flügel et al. 2017), the abundances of selected photorespiratory intermediates remained largely unchanged in *SHMT1*-overexpressing lines compared with wild-type plants (Fig. 3A). Under both illumination and darkness, no consistent differences in steady-state metabolite levels were detected, with the exception of a slight decrease in glycine abundance during the night. Overall, these data indicate that increased SHMT1 protein abundance does not substantially alter photorespiratory metabolite pools under the tested conditions, other than decreased SHMT1 abundances did (Schjoerring et al. 2006). Given that several mutant studies have demonstrated a close metabolic interconnection between photorespiration and mitochondrial respiration, including the tricarboxylic acid (TCA) cycle (Obata et al. 2016), we additionally analyzed representative intermediates of these pathways as well as the associated metabolite γ -aminobutyric acid (GABA). Consistent with the photorespiratory metabolite profiles, no

Fig. 2 Oxygen-dependent gas exchange analysis of *FpS* over-expression lines in comparison with the wild type. Displayed are selected leaf gas exchange parameters at three different O_2 concentrations (3%, 21%, and 40%) determined from all genotypes grown under standard growth conditions to stage 5.1 (Boyes et al. 2001). Given are: **A** net CO_2 assimilation (A_N) and O_2 inhibition of A_N (insert); **B** CO_2 compensation points (Γ) and slopes of O_2 -vs- Γ curves (insert); **C** stomatal conductance (g_s); **D** transpiration rates (E); **E** intracellular CO_2 concentration (C_i); **F** the ratio of the intracellular and extracellular CO_2 concentration (C_i/C_a). Shown are means $\pm$ SD of four to six independent biological replicates. Values that do not share the same letter are significantly different from each other as determined by ANOVA



systematic alterations were observed among these primary metabolites, apart from minor and inconsistent changes in succinate levels (Fig. 3B). Likewise, the largely unchanged abundances of five selected carbohydrates further support the conclusion that *SHMT1* overexpression does not induce broader metabolic shifts (Fig. 3C) under standard laboratory conditions. Previous studies indicate that GDC may operate below substrate saturation in vivo, allowing flexible adjustment of photorespiratory flux to changing environmental conditions (Heineke et al. 2001). In this context, efficient removal of reaction products such as NADH and ammonia has been suggested to play an important role in sustaining high rates of glycine decarboxylation (Bykova et al. 2014). Consistent with this view, enzymes involved

in mitochondrial redox balancing, such as mitochondrial malate dehydrogenase (mMDH), may contribute to maintaining photorespiratory activity (Lindén et al. 2016). These considerations provide a possible explanation for our observation that increasing *SHMT1* abundance alone does not significantly affect photorespiratory flux, suggesting that this enzyme is present already in excess capacity.

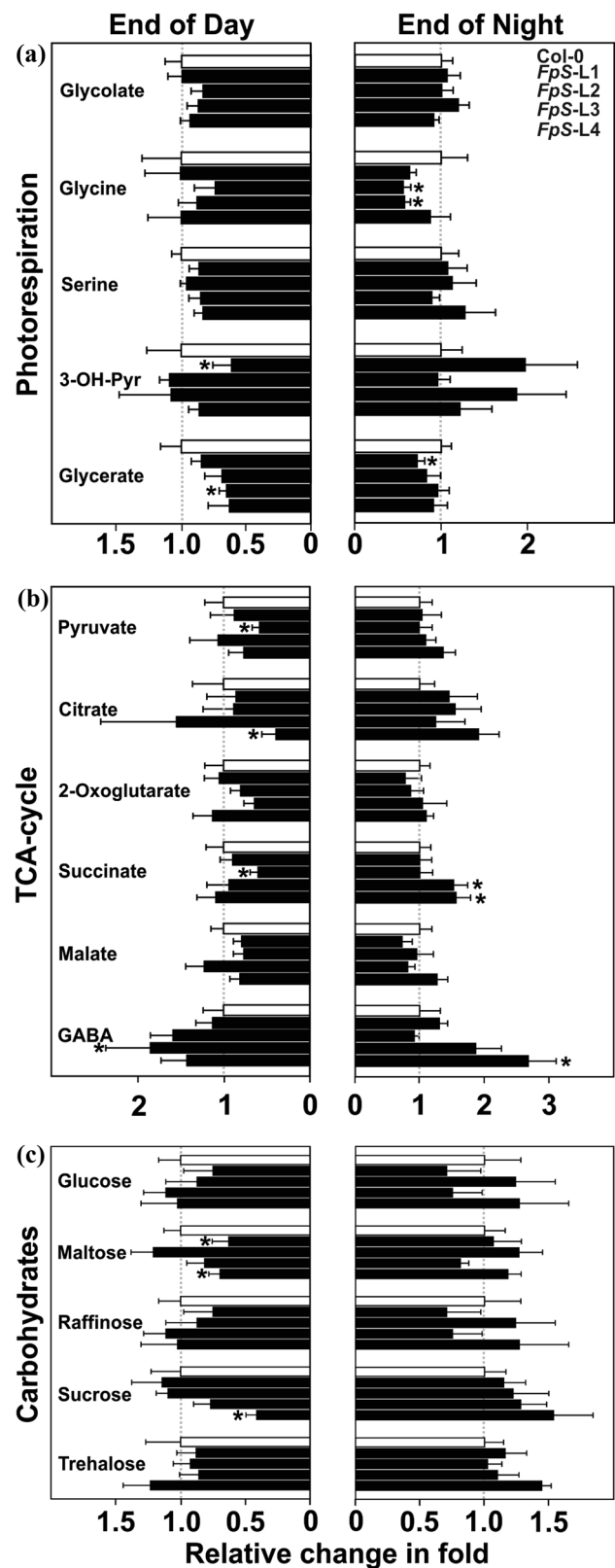
Nevertheless, our metabolomic data demonstrate that additional *SHMT1* supply is metabolically well tolerated in Arabidopsis. The absence of coordinated changes in photorespiratory, respiratory, or carbohydrate metabolism further supports the conclusion that *SHMT1* does not represent a flux-limiting step in photorespiration under standard growth conditions, during either illumination or

Fig. 3 Metabolite accumulation patterns in *FpS* overexpression lines in comparison with the wild type. Metabolite abundances (relative values) were determined by GC–MS analysis at the end of the day and night from all genotypes grown under standard growth conditions to stage 5.1 (Boyes et al. 2001). Given are selected intermediates of: **A** photorespiration; **B** the TCA cycle; **C** carbohydrate metabolism. Shown are means $\pm$ SD of six independent biological replicates. Values marked with an asterisk are significantly different from the wild type at the same harvesting timepoint (the respective value was arbitrarily set to 1) as determined by Student's *t* test ($P < 0.05$)

darkness. However, it remains possible that the importance of SHMT1 may change under environmental stress, including those directly affecting the need for a high photorespiratory capacity. Conditions such as high light, drought, or oxidative stress can challenge photorespiratory activity and alter the subcellular redox balance, potentially increasing the demand for mitochondrial glycine-to-serine conversion and the biosynthesis of one-carbon moieties. In addition, while SHMT1 functions primarily in the mitochondrial photorespiratory pathway of photosynthetic tissues, other SHMTs in other subcellular compartments and tissues, including roots, also participate in one-carbon metabolism and amino acid interconversion (Nogués et al. 2022). Further systematic studies will be required to determine whether modulation of SHMT abundance could influence metabolism under such conditions.

Conclusion

Although photorespiration is energetically costly, it is an essential metabolic repair pathway tightly integrated into oxygenic photosynthesis and plant primary metabolism. Numerous studies demonstrate a strong positive relationship between photorespiratory flux capacity, photosynthetic CO_2 assimilation, and biomass accumulation, with reduced flux impairing and enhanced flux stimulating plant growth. Key enzymes such as PGLP1 and GDC have previously been identified as major control points of this pathway. In contrast, our results indicate that mitochondrial SHMT1, although indispensable for photorespiratory function and closely functional cooperating with GDC, is not limiting for photorespiratory flux under standard growth conditions in Arabidopsis. A moderate (~ 1.3 –threefold) increase in SHMT1 abundance did not improve growth, photosynthesis, and metabolite turnover, suggesting that endogenous SHMT1 levels are sufficient in wild-type plants. However, SHMT1 capacity may become limiting in genetic backgrounds with strongly enhanced photorespiratory flux, such as lines with elevated GDC activity, or environmental stresses, highlighting potential context-dependent control within the pathway.



Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00425-026-04989-x>.

Acknowledgements We wish to thank Kathrin Jahnke for excellent technical assistance and Martin Hagemann (both at University of Rosstock) for critically reading of the manuscript.

Author contributions S.T. and H.B. conceptualized and designed the experiments. S.T. and A.F. performed the experiments and data analysis. A.R.F. provided the metabolite analysis platform. S.T. wrote the manuscript, with revisions made by A.R.F. and H.B. All authors read and approved the final manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. This work was supported by grants from the Deutsche Forschungsgemeinschaft (DFG; Promics Photorespiration Network, FOR 1186) to ARF and HB.

Data availability All data are available in the manuscript. Raw data will be available on request from the corresponding author.

Declarations

Conflict of interest Authors declare that there is no competing financial or personal interest.

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