Bioenergetics of the secondary metabolites production in photosynthetic glandular trichomes

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Abstract

Several commercially important secondary metabolites are produced and accumulated in high amounts by glandular trichomes (GTs), giving the prospect of exploiting trichomes as metabolic cell factories. Due to extremely high metabolic fluxes through GT particular attention was drawn to how they are achieved. The question regarding bioenergetics of these dedicated structures becomes more interesting when one realizes that some cells are photosynthetically active. Despite recent advances, how primary metabolism contributes to GTs high metabolic fluxes is still not fully elucidated. We provide the first reconstruction of specialised metabolism in photosynthetic glandular trichomes of *Solanum lycopersicum*. With increasing light intensities our model shows a shift of carbon partitioning from catabolic to anabolic reactions driven by the energy availability of the cell. Moreover, we show the benefit of using MEV or MEP pathways under different light conditions. Lastly, we can observe the refixation of the CO_2 by RuBisCO in high light conditions. The outcomes of this research close an important gap in knowledge of the role of chloroplast in the synthesis of specialised metabolites in plants' GTs.

Abbreviations: CBB, Calvin-Benson-Bassham cycle; DMAPP, dimethylallyl diphosphate; FBA, flux-balance analysis; F6P, Fructose-6-Phosphate; GEM, genome-scale metabolic models; GT, glandular trichome; IPP, isopentenyl diphosphate; LP, linear programming; MEP, methyl-erythritolphosphate pathwy; MEV, mevalonate pathway; PETC, photosynthetic electron transfer chain; TCA, citric acid cycle.

Keywords: bioenergetics, glandular trichomes, photosynthesis, stoichiometric model, secondary metabolites.

Introduction

Most plant species exhibit cellular outgrowths of their epidermis called trichomes. Due to their often species-specific characteristic, many criteria for classification exist, the most popular one being the division into non-glandular and **glandular trichomes** (GT) [31]. Whilst non-glandular trichomes serve more as a physical and mechanical defence against biotic and abiotic stresses, all GTs are characterised by the ability to synthesize and accumulate vast amounts of valuable specialised (secondary) metabolites. Due to extremely high metabolic fluxes in these organs, production of some metabolites can reach up to 20% of the leaf dry weight, qualifying GTs as true **metabolic cell factories**. Products of GTs include terpenoids, phenylpropanoids, flavonoids, fatty acid derivatives and acyl sugars [12] exhibiting antifungal, insecticide or pesticide properties. Thereby GTs are not only incredibly important to plant fitness, as they contribute to the chemical arsenal of plants, but are also of relevance to multiple industries.

The key carbon source in most GTs of tomatoes is sucrose which is converted into a multitude of organism-specific metabolites in the glands [1]. The massive productivity of hydrocarbon compounds implies however a supply of adequate amounts of not only carbon, energy and reducing power, but also precursors, produced by intermediate pathways. Terpenoids represent the largest and structurally most diverse class of plant metabolites and are major products of GT biosynthesis. Despite their multiplicity, with over 30 000 well-known structures, they are all assemblies of C5 isoprene units built from isopentenyl diphosphate (IPP) and its isomer dimethylallyl diphosphate (DMAPP). There are two identified pathways for IPP and DMAPP production: i) the plastidial 2-C-methyl-D-erythritol 4-phosphate (MEP) pathway from pyruvate and glyceraldehyde-3-phosphate or ii) the cytosolic mevalonate (MVA) pathway from acetyl-CoA [15]. Although the pathways are thought to be largely independent, some exchange of precursors may occur [21], and such (and others [32]) **cross-talk** require further investigation. For instance, is there some cross-talk of plastidial and cytosolic pathways providing the 5-carbon precursors? And if so, what effect does it have on overall productivity? Beyond this, a major issue is the source of energy and its distribution to understand how GTs achieve their high productivity. The question becomes more intriguing when one realises that some of the GTs contain photosynthetically active chloroplasts (as the type VI GT in *S. lycopersicum* [3]). It is still unclear what the advantages and disadvantages of photosynthetic GTs, are in contrast to non-photosynthetic GTs. The separation of cytosolic and chloroplast bound pathways, as well as the utility of photosynthesis, are until now only vaguely understood, and the most recent summary of current advances has been recently provided [5].

To shed light on the advantages of photosynthetic GT for terpenoid synthesis and secondary metabolism, investigations of the systems bioenergetics and reaction flux distributions are needed. Mathematical, computational models provide a coherent framework to study metabolism. Constraint-based stoichiometric models [19] are particularly adequate for exploratory studies of the systemic properties of a metabolic network and investigations of the flux distributions. Such models are static and represent mathematically the network of biochemical reactions of an organism in the form of a matrix [14]. They can focus on various scales, with genome-scale metabolic models (GEMs) aiming at representing the whole biochemical network of an individual organism. GEMs are constructed by assigning biochemical functions to enzymes encoded in the genome, and due to the expansion of the whole genome sequencing, many plant GEMs are currently available, with *Oryza sativa indica* [6], *Arabidopsis thaliana* [22] and *Solanum lycopersicum L.* [33] among many others. Flux Balance Analysis (FBA) [20, 28], a mathematical method that allows calculating the flow of metabolites through the network, is a popular tool to predict the production rate of the compound of interest. FBA requires two assumptions: i) the experimental system is at a steady state, and ii) the network is optimised to maximise or minimise certain biological outcomes, for instance, its biomass. The so-called, cell-specific, objective functions

in GEMs are optimized in a linear programming (LP) approach in which all reaction fluxes are constrained within given boundaries. This constraint-based analysis of GEMs allows the calculation of optimal flux solutions in different conditions, therefore allowing investigations on the metabolic fluxes and bioenergetics of systems.

In this work, we have reconstructed the metabolism in the photosynthetic glandular trichome of a *Solanum lycopersicum* LA4024 using previously published transcriptome and metabolome data [1]. With a general, mathematical framework, we investigated the effect of having photosynthetically active machinery inside of a trichome. In our simulations, we observed the increase in terpenoid production under increasing light intensities. Increased photosynthetic activity shifts the partitioning of uptaken carbons from catabolism to anabolism due to increased energy levels. Bioenergetics and energy levels determine which of the known terpenoid precursor production pathways (MEV, MEP) is more desirable/optimal in different light/stress conditions. Our model can explain the benefits of having chloroplasts in GTs and serves as a groundwork for further investigations of the possible cross-talks between the two pathways of terpenoid precursor synthesis.

1 Methods

1.1 Choice of the model organism

In this study, we have chosen to investigate GT in the tomato genus. *Solanum lycopersicum* serves as an excellent model organism for glandular trichome study due to the availability of i) high-quality complete genome sequence [8], ii) excellent genetic resources [9], iii) comparative multi-omics data [1], iv) several mathematical models available, including whole genome metabolic network reconstruction [33], and v) in contrast to other well studied organisms like peppermint [24, 25], possession of only photosynthetic GT.

1.2 Modelling environment

Our model is implemented in Python, using our in-house developed package `moped`. With `moped` all decision processes and taken steps are well documented in a transparent and repeatable fashion [26]. The annotated script detailing every step we used to construct the model can be found in our GitLab repository at `https://gitlab.com/qtb-hhu/models/glandular-trichomes`.

1.3 Model design and assumptions

Although a genome-scale model of tomato metabolism is available (iHY3410 model [33]), we decided to use the bottom-up approach and perform a reconstruction ourselves, as we were not able to reconstruct the steps of manual curation performed by the authors. We based the model reconstruction on available transcriptomics and metabolomics data [1], the LycoCyc database (tomato metabolic pathway database, version 3.3 [10], available from Solanaceae Genomics Network, http://www.sgn.cornell.edu) and biochemical knowledge in plants from scientific publications. The resulting model consists of 1307 reactions and 1371 metabolites and its behaviour has been ensured to match reported observations [1]. Furthermore, the model quality and consistency have been thoroughly inspected using MEMOTE to ensure the highest quality [18]. There are nine exchange reactions, allowing free exchange of metabolites such as oxygen, as well as light absorption. Light is represented as photosynthetically active photons absorbed by the photosystems. The units of light absorption are represented in $\frac{\mu mol \text{Photons}}{s \cdot m^2}$ and the detailed calculation of our calculations are provided in the Supporting Information. In this model, we decided not to include a free carbon dioxide influx as it has been reported that carbon dioxide exchange is 100 times lower in photosynthetic GTs than in leaves [1].

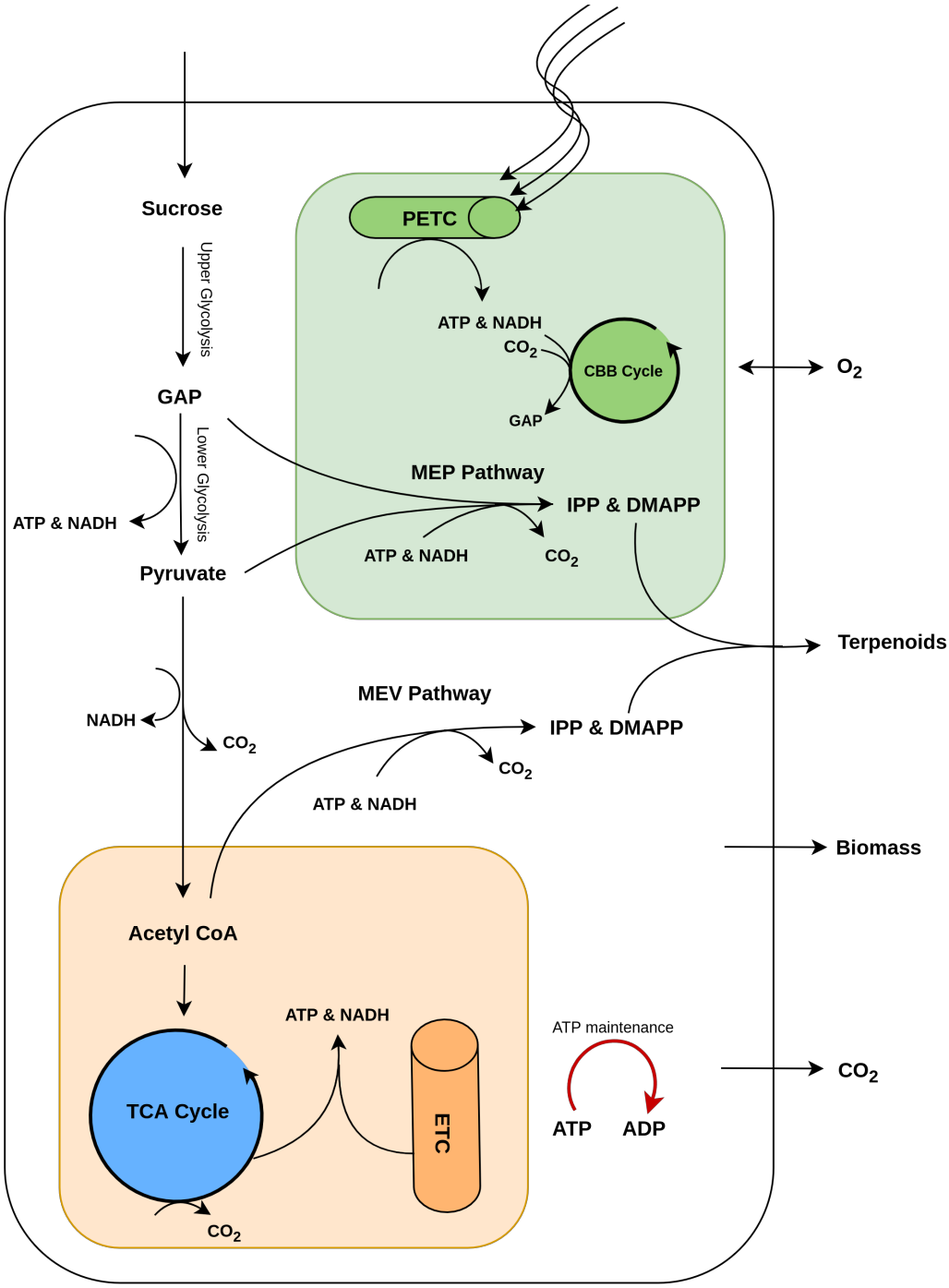

Figure 1. Schematic overview of the key processes included in a constraint-based model of photosynthetic glandular trichome metabolism. While the model is built using transcriptome and metabolome data and includes a large number of reactions, only pathways and metabolites of importance to the results are highlighted in the presented model scheme.

In most constraint-based models and their analyses, the maximization objective is the production of biomass [13]. While this may be applicable for prokaryotic organisms, we doubt

that photosynthetic glandular trichome cells are maximising the increase of their replication rate, and rather maximise terpenoid synthesis while also having a mandatory production rate of macromolecules to keep cells intact. For this, our model includes an objective function to produce terpenoids while requiring a fixed flux through a function of biomass synthesis, consuming typical components like amino acids, sugars, nucleotides and fatty acid precursors. For this, we used an *E. coli* biomass function, as our main concern was to capture the necessity for growth and self-repair, while the primary objective function of a glandular trichome is terpenoid production. To describe additional energy required for the maintenance of cells, we implemented a representative reaction for ATP maintenance, as it is common practice in metabolic modelling [7]. After subsequent gap-filling using Meneco, a tool for metabolic network completion [23], our model can simulate the synthesis of all compounds found within the metabolomics data [1], all terpenoids found in photosynthetic GTs of tomato [4] as well as all compounds within biomass from sucrose, light, orthophosphate, ammonia, sulfate, protons and water. The resulting model is a data-driven, yet simplified, constraint-based model which is tested against infeasible energy and mass generating cycles. Within our model simplifications, we found that a model consisting of three essential compartments (cytosol, intermembrane space and extracellular space) sufficiently represents photosynthetic GT metabolic profiles (Fig. 1). While detailed compartmental separation is common practice in large genome-scale metabolic models, it would not make any difference to the results of our model simulations due to the fact that there are several intercompartmental transporters between the chloroplast and the cytosol for energy equivalents like ATP and other key metabolites [11]. Adding over-detailed compartmentalisation to the model would therefore not alter any of our results and is left out for the sake of model simplicity and preventing unfavourable model modifications. All details and information about the exact construction process of the model, as well as all investigations and analyses, can be found in our provided scripts at `https://gitlab.com/qtb-hhu/models/glandular-trichomes`.

2 Results

We used our model to perform a general analysis in which we simulate the rate of terpenoid synthesis over systematically increasing light intensities via parsimonious Flux Balance Analysis (pFBA). Fig. 2 displays that with increasing light absorptions, the rate of terpenoid synthesis in photosynthetic glandular trichomes increases up until approximately 10 $\frac{\mu\text{mol Photons}}{s \cdot m^2}$. This increase in terpenoid synthesis rate with increasing absorbed light is particularly interesting due to the fact that the model can not utilize atmospheric carbon dioxide, and sucrose being the only carbon source. This means that there is a change in metabolic fluxes which enables this increase in terpenoid synthesis rate. To further investigate what changes in the metabolism of photosynthetic glandular trichomes in increasing light intensities, we inspect the respective changes in the exchange fluxes of the model. Fig 2 shows the exchange fluxes of carbon dioxide and oxygen in our pFBA model simulations over increasing light absorptions. Noticeably, the excretion of carbon dioxide systematically decreases up until approximately 10 $\frac{\mu\text{mol Photons}}{s \cdot m^2}$. Interestingly, the consumption of oxygen decreases to zero at approximately 7 $\frac{\mu\text{mol Photons}}{s \cdot m^2}$. From this light intensity on, oxygen excretion begins and increases until 10 $\frac{\mu\text{mol Photons}}{s \cdot m^2}$. These observations are crucial for a general understanding of the model behaviour. An increase in absorbed light causes higher photosynthetic activity, resulting in oxygen production. This explains the decreasing oxygen uptake and the switch to oxygen excretion at 7 $\frac{\mu\text{mol Photons}}{s \cdot m^2}$ absorbed light. However, the steady decrease in carbon dioxide excretion is especially noteworthy. Most carbon dioxide is produced within catabolism, therefore the model behaviour hints at a decrease in catabolic activity in higher light intensities.

To investigate how the catabolic activity in our model simulations changes over increasing

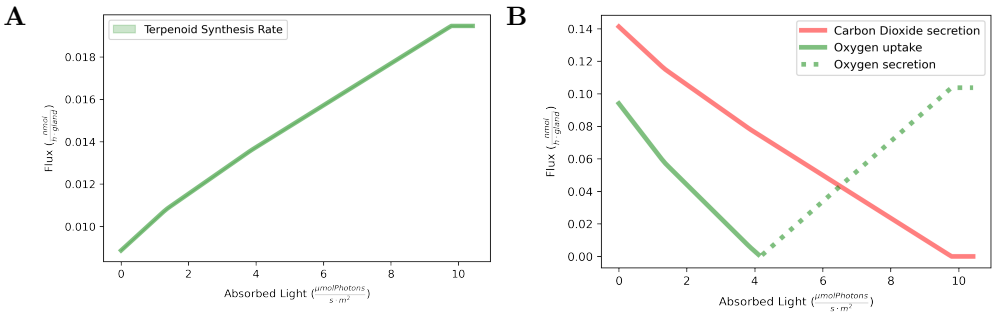

Figure 2. Impact of light influx on the predicted fluxes through the photosynthetic glandular trichome. **a** Terpenoid synthesis flux over different rates of absorbed light. **b** Oxygen and carbon dioxide exchange fluxes over different rates of absorbed light.

light intensities, we further inspect representative reactions for relevant catabolic pathways in our model. As sucrose, a disaccharide is the only carbon source in our model, we inspect representatives of the upper glycolysis, the lower glycolysis and the TCA cycle. Fig. 3 displays the fluxes of these reactions over different light intensities (shown on the x-axis as fractions of saturating light intensities) relative to their fluxes in the dark. The sucrose synthase and saccharase represent upper glycolysis activity. The 6-phosphofructokinase, GAP dehydrogenase and pyruvate kinase represent lower glycolysis activity and the pyruvate dehydrogenase and the citrate synthase represent TCA cycle activity. Furthermore, the RuBisCO rate is displayed to monitor the rate of carbon refixation. The results show that fluxes of upper glycolysis remain completely unchanged in increasing light intensities, however, the fluxes in lower glycolysis decrease in higher light conditions. An even higher impact can be observed for the TCA cycle activity. The pyruvate dehydrogenase activity steadily decreases, and the citrate synthase activity abruptly decreases in increasing light conditions. These observations show that catabolic pathways which are not responsible for energy and redox equivalent production (like upper glycolysis) are unaffected by increasing light intensities. However, the lower glycolysis and the TCA cycle, both catabolic pathways that produce energy and redox equivalents, display a strong flux decrease in higher light conditions. The increase in terpenoid synthesis flux observed in Fig 2, and the decrease in catabolic fluxes in Fig 3 strongly suggest that increasing light conditions shift the carbon partitioning from catabolic to anabolic pathways. This shift is enabled due to the energy and redox equivalent production of the photosynthetic electron transport chain in photosynthetic glandular trichomes. The metabolic network is not dependent on the energy from oxidising carbon bodies in high light conditions, and can therefore use more of those carbon bodies in terpenoid synthesis pathways. Interestingly, RuBisCO activity increases in higher light intensities, displaying that higher energy levels allow the refixation of carbon that is lost as carbon dioxide in anabolic processes (like Terpenoid synthesis). GAP, pyruvate and acetyl-CoA are carbon bodies which can be used to produce either energy and redox equivalents or terpenoid precursors. Acetyl-CoA is the initial substrate of the TCA cycle in which it is oxidised to gain energy and redox equivalents but is also the initial substrate of the MEV pathway.GAP and pyruvate are metabolites within the lower glycolysis pathway and also initial substrates of the MEP which is a terpenoid synthesis pathway present in photosynthetic GTs.

To further analyse how the consumption of these metabolites depends on the illumination, we simulated the relative consumption rate of GAP/pyruvate and Acetyl-CoA by the aforementioned pathways over increasing light intensities. Fig 4 displays the proportions of the consumption of these compounds by the TCA, MEV and MEP pathways. In low light intensities, more than half of the substrates are consumed by the MEV pathway, and the remainder is consumed by the TCA cycle, in both cases in the form of acetyl-CoA. In

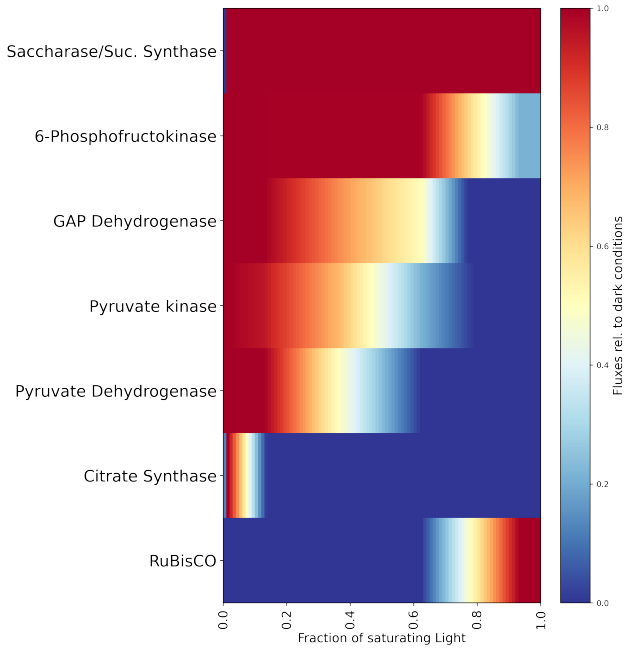

Figure 3. The relative fluxes of six selected catabolic reactionsand one carbon fixation reaction calculated for increasing fractions of saturating light. The fluxes are normalised to the respective fluxes under completely dark conditions.

higher light intensities, the fraction of substrates consumed by the TCA cycle is decreasing until it does not consume any more substrates. At this point, the relative flux of lower glycolysis starts decreasing, and the MEP pathway is beginning to consume proportions of the substrates, gradually taking over. This is a very important observation that shows that increasing light intensities, leading to higher energy levels due to photosynthetic activity, shift the carbon partitioning from catabolic to anabolic pathways by reducing the TCA cycle and lower glycolytic flux and increasing terpenoid synthesis. Furthermore, it shows that the two terpenoid synthesis pathways, MEP and MEV, are more advantageous at different energetic levels. In lower light intensities, and therefore lower energetic levels, the MEV pathway seems to be more advantageous because the conversion of GAP and pyruvate to acetyl-CoA produces energy and redox equivalents, and the resulting acetyl-CoA can directly be used in the TCA cycle to generate additional energy and redox equivalents. In higher light intensities, and therefore higher energetic levels, the MEP pathway is more advantageous because the high energy levels provided by photosynthetic activity remove the necessity of providing energy and redox equivalents via lower glycolysis and the TCA cycle.

Instead, GAP and pyruvate can directly be used as substrates with higher energy contents (than acetyl-CoA) in the MEP pathway, and therefore further increase the fraction of carbon used in anabolism, enabling more efficient terpenoid synthesis. This phenomenon can also be observed in Fig 5, in which we used model simulations to calculate the fluxes of the final MEV and MEP reactions in systematically changing light conditions and ATP maintenance costs.

In this analysis, higher ATP maintenance costs reflect increased energy requirements of cells in e.g. stress conditions. At low light conditions and low ATP maintenance costs, the MEV pathway is the main terpenoid synthesis pathway, with very little MEP pathway activity. In low light conditions and high ATP maintenance costs, the MEV pathway is the only active pathway. However, the overall terpenoid synthesis flux is relatively low due to the increased demand for catabolic flux in such conditions. At high light conditions and high ATP maintenance costs, the MEP pathway is carrying the majority of terpenoid

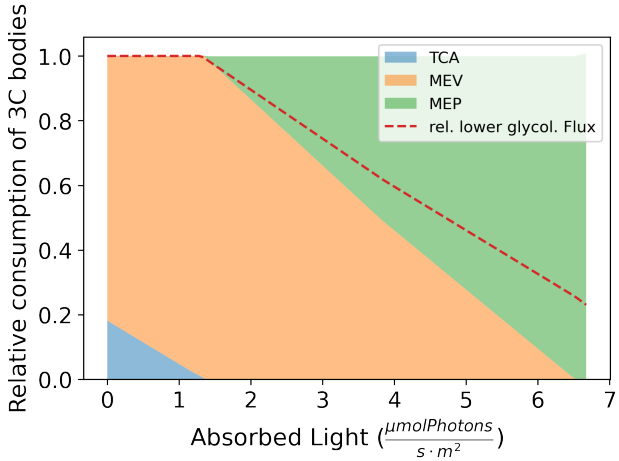

Figure 4. Relative consumption of GAP, pyruvate and acetyl-CoA (here described as 3C bodies) by different pathways over increasing fractions of saturating light. The fraction of the lower glycolysis flux relative to dark conditions is displayed as a dotted line.

synthesis flux. In high light conditions and low ATP maintenance costs, the MEP pathway is the only active terpenoid synthesis pathway, providing the highest terpenoid synthesis flux. It appears as if the distribution of terpenoid synthesis between the MEV and the MEP pathways is highly dependent on the light conditions and resulting energy levels of the photosynthetic GTs.

The high rate of terpenoid synthesis in high light conditions is also resulting from increased rates of carbon refixation. It remains unknown how active the CBB cycle is in photosynthetic GTs. To quantify the impact of different carbon refixation fluxes, we performed a systematic analysis in which we calculated the terpenoid synthesis rate over different amounts of absorbed light and systematically changed the activities of RuBisCO. Fig. 6 displays that in higher light conditions, increased carbon refixation fluxes can increase the rate of terpenoid synthesis by almost 20%. However, interestingly, the overall rate of carbon refixation is not very high. This is because the rate of carbon refixation is purely dependent on the available carbon dioxide produced by anabolic processes, which is limited.

3 Discussion

In photosynthetic glandular trichomes, synthetic pathways of terpenoids and other secondary metabolites are not only found in the cytosol of the cells, but also the chloroplasts. The additional terpenoid synthesis pathways in photosynthetic glandular trichomes have been subject to many speculations. One speculation for example is that terpenoid production in chloroplasts is specialized for the production of particular secondary metabolites. Another speculation is that the pH in chloroplasts may be more beneficial for terpenoid synthesis [17].In our work, we introduce a simplified, yet a data-driven constraint-based model of photosynthetic glandular trichome metabolism which shows that one of the two different synthesis pathways is more advantageous for terpenoid production than the other in different energy availabilities. We show that with lower energy availability, the cytosolic MEV pathway is more advantageous for terpenoid synthesis because the catabolic pathways, producing the key initial substrate acetyl-CoA from sucrose, provide additional energy and redox equivalents needed for all cellular activities, including terpenoid synthesis. However, higher energy availability (coming from photosynthetic activity in higher light conditions) removes the need for the additional energy and redox equivalents gained from the conversion of sucrose to acetyl-CoA. Therefore substrates with higher energy levels (GAP and pyruvate)

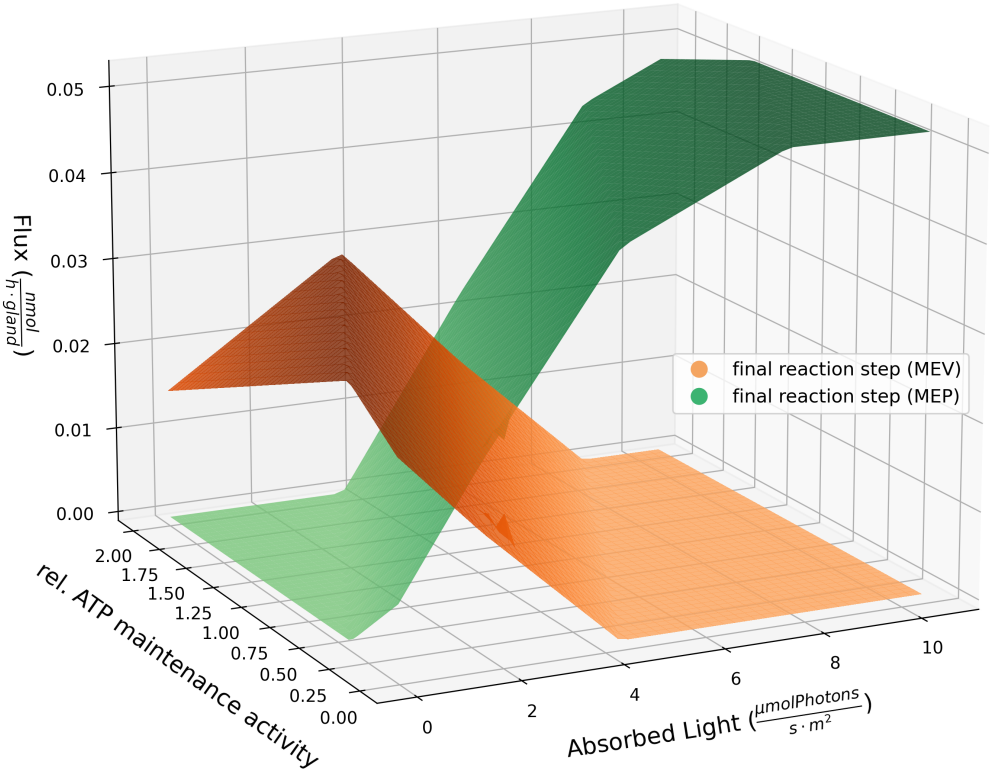

Figure 5. Fluxes of the final reaction steps of the MEV and MEP pathway over increasing relative ATP maintenance activities, as well as increasing rates of light absorption.

can be directly used for terpenoid synthesis. This basic shortcut of catabolic reactions reduces the loss of carbon as carbon dioxide and increases the flux of carbon through anabolic processes with the help of energy equivalents gathered through photosynthesis.

We show that in higher light conditions, energy levels of the photosynthetic GTs are so advantageous, that the energy can be spent to perform carbon refixation using the CBB cycle. In the supplementary material, we calculated that in order to maintain the same rate of terpenoid synthesis in low light, only half of the sucrose is required in high light conditions. This displays again that the benefit of including chloroplasts in glandular trichomes is not only the ability to shift carbon partitioning from catabolic to anabolic processes but also to further maximize carbon use efficiency. It is important to note that the increase in terpenoid synthesis from carbon refixation is not nearly as high as the increase from the shift in carbon partitioning, as seen in Fig. 6.

Interestingly our model showed that even without CBB cycle activity and without special constraints, the TCA cycle may be reversed in high energy availability and function as a reductive TCA cycle. A reductive TCA cycle could be able to replace the function of the CBB cycle, using energy to fix carbon dioxide which was produced in catabolic and anabolic reactions, increasing carbon use efficiency. This is a very interesting observation, as, from a

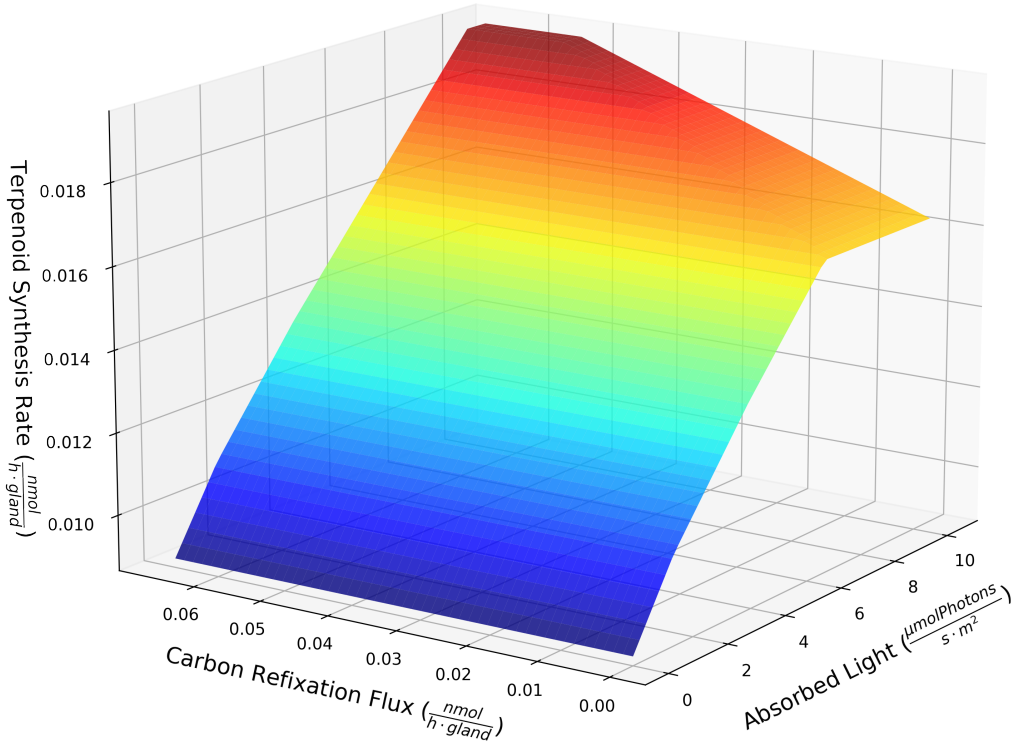

Figure 6. Predicted flux of the terpenoid synthesis under changing carbon refixation rates, as well as increasing rates of light absorption.

bioenergetic point of view, such a scenario is possible. However, we decided to adjust the key reactions of the TCA cycle for this scenario as irreversible reactions to prevent this phenomenon to be included in our results for now. The reason for this decision is that the reductive TCA cycle is usually found in green sulfur bacteria and different thermophilic prokaryotes and archaea [2, 30]. This indicates that from a phylogenetic perspective, the presence of a reductive TCA cycle in photosynthetic GTs is rather unlikely. However, we think that this model suggestion is worth investigating the fluxes of the TCA cycle in light conditions in photosynthetic GTs, as it has been suggested that carbon dioxide may be recovered [27]. Generally, instead of showing that chloroplastic terpenoid synthesis pathways provide improved production of particular terpenoids, our work shows that the chloroplast in photosynthetic GTs functions as an energy battery in light conditions, which can be used to shift carbon from catabolic to anabolic fluxes and even enable carbon dioxide refixation and therefore improve carbon use efficiency. To support our findings, experiments are needed which can keep track of the rate of terpenoid synthesis in similar sucrose availability but different light absorptions.

The photosynthetic carbon refixation indicates that there may be photorespiration present in photosynthetic GTs. Although photorespiratory genes were very low expressed in the transcriptom data [1], and photorespiration is not included in our model, we show

that in high light there is oxygen evolution in photosynthetic GTs. Therefore, further data obtained in high light intensities and gas exchange rates is required to investigate putative photorespiratory activities. Furthermore, it remains unclear if and how high evolution of reactive oxygen species and photodamage is present in photosynthetic GTs. For this, quantitative metabolic data for the components of the electron transport chain is needed, as well as measurements of the photosynthetic efficiency in photosynthetic GTs. Finally, more questions regarding the dynamics, and not only bioenergetics of trichomes arise. E.g., what is the composition of terpenoids under different light intensities, or how can we improve the production of a terpenoid of interest? As these processes are heavily dependent on enzyme kinetics and saturation, constraint-based models like ours are not the optimal method for answering these questions. However, mechanistic models based on ordinary differential equations can include such information (if available) and may be helpful to give further insights into terpenoid synthesis in photosynthetic GTs. New experimental data is therefore required to advance further our understanding of the biosynthesis of these **metabolic cell factories**.

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Conflict of interest

The authors declare that they have no conflict of interest.

Supporting Information

The computational model presented here, together with the code to reproduce the computational analysis are openly available on the GitLab repository https://gitlab.com/qtb-hhu/models/glandular-trichomes or can be requested from the authors.

Calculation of flux units and light intensity units

A suggested terpenoid production rate of glandular trichomes has been provided by Turner *et al.* [29] at 0.017 $\frac{nmol}{h \cdot gland}$. Assuming that this rate can be applied to the maximal terpenoid production rate of photosynthetic glandular trichomes of tomatoes, we transform our calculated fluxes to the corresponding units by $\text{Flux} \cdot \frac{0.017 \frac{nmol}{h \cdot gland}}{\text{max. Terp flux}}$.
In order to convert the Fluxes of Photons into units of light intensities, we first have to calculate the surface of the glandular trichome on which light can be absorbed. Measured values of the diameters of glandular trichomes from [16] providing an estimate of 50 μm diameter of circular surface of a glandular trichome. Assuming that the glandular trichomes surface is a circle, the surface area can be calculated as:
$A = \pi(\frac{50\mu m}{2})^2 = 2000\mu m^2 = 2 \cdot 10^{-9} m^2$
To calculate the conversion factor for the photon absorption of glandular trichomes, we first calculate the units of photons absorbed by the gland at saturated light flux and maximal terpenoid production predicted by our model as:
$0.017 * \frac{\text{Max. Light Flux}}{\text{Max. Terp. Flux}} = 0.017 * \frac{300}{7.3} = 0.7 \frac{nmol \text{Photons}}{h \cdot gland}$.
To convert this unit into $\frac{\mu mol}{s \cdot m^2}$, we first calculate the corresponding unit for $\frac{nmol \text{Photons}}{h \cdot gland}$ by:
$\frac{1 nmol \text{Photons}}{h \cdot gland} = \frac{1}{7200} \frac{mol \text{Photons}}{s \cdot m^2} = 14 \frac{\mu mol \text{Photons}}{s \cdot m^2}$

for our maximal Light flux, this corresponds to $0.7 \cdot 14 \frac{\mu mol \text{Photons}}{s \cdot m^2} = 9.8 \frac{\mu mol \text{Photons}}{s \cdot m^2}$ as the saturating light intensity, providing the light flux conversion factor of $\text{Light Flux} \cdot \frac{9.8 \frac{\mu mol \text{Photons}}{s \cdot m^2}}{\text{sat. Light flux}}$.

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