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The best of both worlds: photosynthesis and Solanaceae biodiversity seeking a sustainable food and cosmetic industry

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1 Introduction

The global food supply crisis is one of humanity's most significant risks (World Economic Forum, 2023). Climate change is causing the loss of natural resources, which is closely related to this crisis (Mirzabaev et al., 2023). Therefore, it is crucial to implement sustainable food systems that ensure food security for both present and future generations. Thus, food should be available, accessible, and nutritious (Peng and Berry, 2018). Delaying the implementation of these goals will contribute to food insecurity and lead to a more polarized world.

Improving photosynthetic efficiency is critical to ensure food security because it generates 90% of plant biomass (van Bel et al., 2003) and increases crop yield (Brestic et al., 2021). However, photosynthesis is affected by high temperatures (Mathur et al., 2014), irregular rains (León-Sánchez et al., 2016), and drought (Wang et al., 2018), among others. The persistence and severity of these phenomena reduce the photosynthetic rate, exerting selection pressure mainly in C3 plants (Sello et al., 2019), affecting their adaptation biodiversity and could lead to an irreversible loss of genetic diversity (Demír, 2021), which is relevant to implement sustainable food production systems through genetic improvement (Salgotra and Chauhan, 2023).

The Solanaceae family is a prime example of climate change vulnerability because their centers of origin are in countries highly vulnerable to climate change (Samuels, 2015). In this regard, Solanaceae is among the 12 most diverse plant families, and more than 1,500 native species can be found in South America alone, and Peru standing out for its diversity (Palchetti et al., 2020). This richness translates into genetic and metabolic diversity that can be useful to improve the crop photosynthetic rate. Therefore, it is essential to identify the critical genes for light and dark phases.

2 The underlying genetic architecture related to photosynthetic efficiency:

Regarding the light phase (Figure 1), Leister (2023) proposes a list of genes, including the D1 gene of the photosystem II reaction center (PSII), that improve photosynthetic performance and plant growth when overexpressed. Thus, Chen et al. (2020) showed that Arabidopsis transgenic lines that overexpress D1 doubled their biomass under thermal stress (42°C). The D1 biosynthesis is mediated by genes that ensure psbA correct translation (Zhang et al., 2000). Thus, LPE1 binds to the 5' end of psbA to facilitate association with HCF173 (Jin et al., 2018), which prevents exonucleotide degradation of psbA mRNA, ensuring its binding to the ribosome (Bollenbach, 2003). In addition, HCF244 is coexpressed with HCF173, which encodes a gene necessary for the translational initiation of psbA and stabilization of this messenger RNA (Link et al., 2012). These genes are relevant for plant development, in Arabidopsis lpe1-3 mutant showed a 70% reduction in the rosette size, and a drastic reduction in the ratio of variable fluorescence to maximum fluorescence (Fv/Fm) (Jin et al., 2018). For hcf173, Link et al. (2012) also had a similar reduction in rosette size in Arabidopsis than lpe1-3. RNA is highly unstable in hcf173, leading to a drastically impaired accumulation of PSII polypeptides (Schult et al., 2007). On the other hand, the hcf244 mutant cannot grow under autotrophic conditions due to a drastically impaired accumulation of PSII proteins (CP47, CP43, D1, and D2); reaching only about 10% to 20% of wild-type levels (Link et al., 2012). Both, HCF173 and HCF244 were identified by Bhattacharya et al. (2023) in tomato stromal proteome as part of the 29 orthologous proteins involved in the assembly, stability and repair of the PSII complex.

Another critical component of the electron transport chain is the cytochrome b6/f complex (Rochaix, 2011). Mutants in tomatoes of the petM subunit of this complex showed lower electron transport rate, CO2 assimilation, and carotenoid content than the wild type. In addition, mutants of the petM-4 line showed late autotrophic growth (Bulut et al., 2023). In tobacco, petA, B, and D mutants showed a lower content of thylakoid membranes (Monde et al., 2000). Considering that the cytochrome b6f complex regulates the acclimation of photosynthetic organisms to changing light conditions (Malone et al., 2021) and that algae have an exceptional ability to adapt to such conditions (Sukenik et al., 1987), Yadav et al. (2020) identified that tobacco specimens transformed with cytochrome b6 gene from Kappaphycus alvarezii have a net photosynthetic rate higher than the wild type by approximately 60%. This improved performance was also evident in the growth and starch accumulation of the transgenic lines. Yadav et al. (2018) reported similar results with transforming tobacco specimens with the UfCytb6 gene from Ulva fasciata. These findings show that photosynthetic and growth enhancement of tobacco specimens through manipulation of cytochrome b6f subunits is a potential way to improve their performance in lightchanging environments.

In addition to the structural genes of PSII, the NADPH dehydrogenase or NDH complex is also relevant for the light phase since it participates in the cyclic transport of electrons to maintain the balance of the redox system to mitigate oxidative stress in the photosynthetic apparatus (Ma et al., 2021). The *CRR23*, *NDH48*, and *NDH45* subunits guarantee the accumulation and stabilization of this complex in *Arabidopsis*. Thus, the *crr23* mutant showed a 12.5% reduction in the accumulation of the NDH complex (Shimizu et al., 2008), while *ndh48* and *ndh45* revealed

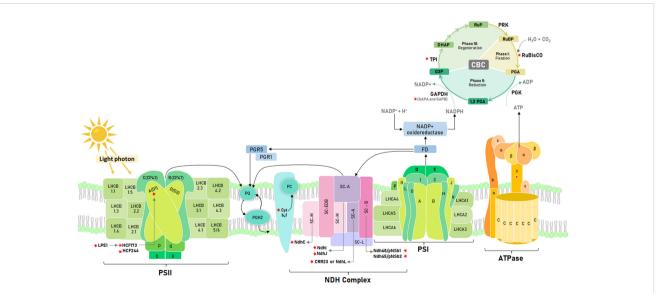


FIGURE 1

Schematic representation of the photosynthetic electron transport chain and the Calvin Benson cycle. Key photosynthetic genes identified with red stars. Light phase: Low photosynthetic effciency 1 (LPE1), High Chlorophyll fluorescence phenotype 173 (HCF173), High Chlorophyll fluorescence phenotype 244 (HCF244), D1 reaction center (D1), Cytochrome b6f complex (Cyt b_6 f), NAD(P)H dehydrogenase-like (NDH) complex subunits (NdhC, NdhJ, NdhJ, NdhJ or CRR23, Ndh48 and Ndh45), ATP sintase gamma subunit (γ Subunit). Dark phase: Ribulose bisphosphate carboxylase oxygenase (RuBisCO), Glyceraldehyde-3-phosphate dehydrogenase subunits (GAPA and GAPB) and Triosephosphate isomerase (TPI). Electron flow represented with black lines.

functional deficiencies of this complex (Sirpiö et al., 2009). On the other hand, in tobacco, a 25% reduction in the photochemical efficiency of PSII was identified in mutants for the C, J, and K subunits due to the increase in ROS at -4°C and 42°C (Wang et al., 2006). It is crucial to study subunits that cause a decrease in photosynthetic efficiency because of temperature stress. Mutations in these subunits can negatively impact the plant's ability to withstand frost. Therefore, it is essential to investigate these subunits in potato wild relatives as a potential solution to this problem (Nicolao et al., 2023).

On the other hand, ATPC1, the γ subunit of ATP synthase, induces conformational changes in the catalytic region of this enzyme that are necessary for ATP synthesis (Cheuk and Meier, 2021). It possesses two cysteine residues that regulate ATP synthase activity in response to fluctuating intracellular redox conditions due to the unstable activity of the photosynthetic electron transfer chain associated with changing light intensity (Akiyama et al., 2023). In *tobacco*, Rott et al. (2011) identified that atpc1 mutants showed a reduction of more than 50% in growth after 14 weeks and also a reduction in the chlorophyll a/b ratio; this change suggests a rearrangement of the photosynthetic apparatus. Furthermore (Kohzuma et al., 2013), identified that the knockout of *atpc1* in *Arabidopsis* cannot perform autotrophic growth.

On the other hand, overexpression of enzymes in the dark phase (Figure 1) does not necessarily result in improved photosynthetic efficiency. According to Zhao et al. (2021), balancing the catalytic activity of the different enzymes in the Calvin Benson Cycle (CBC) is crucial. RuBisCO is one of the most essential enzymes studied for enhancing photosynthetic efficiency, biomass accumulation, and crop yield (Lin et al., 2021). An evaluated strategy to make the catalytic activity of RuBisCO more efficient is to increase the concentration of CO₂ around this enzyme through synthetic engineering, as this could increase the photosynthetic efficiency of C3 plants by 25% (Zhu et al., 2010). In nature, a greater availability of foliar CO2 was observed in Solanum pennellii, a wild relative of tomato, where the distribution of its stomata limits the diffusion of CO₂ by photorespiration, facilitating its fixation and a consequent higher photosynthetic rate (Muir et al., 2014). However, despite the greater availability of CO₂, a limiting factor is the catalytic inefficiency of RuBisCO compared to CO2 and O2 as substrates. The short subunit of RuBisCO controls the affinity regulation of these molecules (Genkov et al., 2010). In tobacco, mutations in this subunit have been found to reduce the total content of RuBisCO by 93% and biomass accumulation by 90% compared to the wild-type.

Despite the recent improvements, Lin et al. (2021) suggest that the most effective way to enhance the RuBisCO efficiency is to modify the long subunit; the active site of the enzyme is located there, making it vulnerable to changes in temperature and humidity. In this context, previous studies have identified that high temperatures and dry environments can reduce RuBisCO efficiency by up to 40% (Parto and Lartillot, 2018). This scenario is common for many crops, which may experience a loss of productivity ranging from 3 to 13% for each one-degree increase in temperature (Zhao et al., 2017). Indeed, Lin et al. (2022) conducted a study to address a problem related to RuBisCO efficiency in hot and dry environments. They explored the potential of thermostable RuBisCO ancestors in Solanaceae and found that they have superior catalytic efficiency, suggesting that by utilizing the genetic diversity of their ancestors, it is possible to improve the enzymatic efficiency of RuBisCO.

Glyceraldehyde 3-phosphate dehydrogenase (GAPDH) is a crucial enzyme in the reduction stage of the CBC. According to Petersen et al. (2003), GAPDH plays a significant role in this process. Rius et al. (2006) has reported that if GAPDH is deficient, it can hinder glycolysis and reduce CO₂ fixation by approximately 25%. The GAPDH is used to create photosynthates and regenerate Ribulose 1,5 bisphosphate. GAPA and GAPB are the two subunits that make up the GAPDH enzyme. Deleting either GAPA or GAPB can significantly reduce carbon assimilation in Arabidopsis. Simkin et al. (2020) have reported that carbon assimilation decreases by 73% by GAPA deletion, while the deletion of GAPB leads to a 34% reduction. In rice, GAPB overexpression increases CO₂ assimilation and chlorophyll content even under low light conditions (Liu et al., 2020). In contrast, in *Arabidopsis*, carbon assimilation is higher for *gapb* than *gapa*.

Triose phosphate isomerase (TPI) is another essential enzyme in the CBC, playing a pivotal role in the first reaction of the regeneration stage (Johnson, 2016). TPI has a critical C-terminal region, vital for its catalytic, regulatory, or folding function. This region is essential for efficiently converting glyceraldehyde 3phosphate molecules into dihydroxyacetone phosphate and vice versa (Castro-Torres et al., 2018). Mutations in TPI's plastid form in Arabidopsis result in chlorotic leaves and almost no growth after ten weeks of evaluation because of the accumulation of methylglyoxal, which is twice that of the wild type. As a result, the transition from heterotrophic to autotrophic growth is delayed (Chen & Thelen, 2010). Moreover, TPI has cysteine residues similar to the GAPB subunit of the GAPDH enzyme. In Arabidopsis and photosynthetic microorganisms such as Synechocystis and Chlamydomonas, these residues facilitate its stability and activity by being close to the catalytic site (Dumont et al., 2016; Castro-Torres et al., 2018). In tomato, the mutation of its TPI genes only showed visible phenotype changes in double mutant lines tpi1tpi2. In these individuals, Chen et al. (2023) found reduced TPI activity, chlorotic variegation, and reduced carbon-assimilation efficiency in contrast to the wild type. However, assessing the thermostability of TPI1 and TPI2 proteins in tomatoes, the author found that TPI2 may be more stable than TPI1 under heat stress at 42°C.

3 The cosmetic and personal care industry: the role of photosynthesis in lycopene production

In addition to ensuring food production, photosynthesis supports plant secondary metabolism since its products are precursors (Qaderi et al., 2023) of over 50 thousand secondary metabolites (Teoh, 2016). Because of their properties, there is growing interest in identifying new secondary metabolites as industry inputs to enhance agricultural sustainability and improve their production (Ozyigit et al., 2023). Thus, plant and food waste are processed as a promise source to obtain secondary metabolite for the cosmetic industry (Faria-Silva et al., 2020). The cosmetic and personal care industry uses plant-derived secondary metabolites to formulate products (Ribeiro et al., 2015). This market has seen significant growth from 2016 to 2022 (Liyanaarachchi et al., 2018) as consumers prefer natural products (Nadeeshani Dilhara Gamage et al., 2022). Products containing lycopene for skin care are trendy (Choi et al., 2022) due to their antioxidant capacity, improving skin elasticity and hydration (Franco et al., 2021). Thus, lycopene price is over \$6000 per kg (Zia-Ul-Haq et al., 2021). Unfortunately, competition with the food industry affects lycopene supplies (Khan et al., 2021). Although lycopene chemical synthesis can be an alternative, the chemical residues in this process affect its overall quality (Li et al., 2022). Therefore, it is relevant to increase its concentration (Costa et al., 2021) to generate a circular production system.

The biosynthesis of lycopene and other carotenoids begins with the 2-C-methyl-D erythritol 4-phosphate pathway that uses glyceraldehyde 3-phosphate (GAP) and pyruvate (Sathasivam et al., 2021) to form 1deoxy-D-xylulose 5-phosphate (DXP) via 1-deoxy-D-xylulose-5phosphate synthase (DXS) (Simpson et al., 2016). The manipulation of DXS increases lycopene production (Kang et al., 2005), and its overexpression results in a twofold increase in the carotenoid content (Morris, 2006). The activity of DXS depends on the availability of GAP, GAPDH being the photosynthetic enzyme that generates this molecule (Petersen et al., 2003). GAPDH has predominant activity in photosynthetically active tissues (Kelly and Gibbs, 1973), favoring the biosynthesis of carotenoids such as lutein, beta-carotene, violaxanthin, and neoxanthin (Sun et al., 2018) that protect the photosynthetic apparatus from oxidative photodamage (Kim et al., 2018). In green tissues of plants, the regulation of carotenoid biosynthesis must occur in a coordinated manner with the assembly of the photosynthesis apparatus (Lu and Li, 2008). On the other hand, phytoene synthase (PSY) knock-out, a critical enzyme for carotenoid biosynthesis, completely suppresses photosynthesis (Sun et al., 2018).

4 Conclusion

The cosmetic and personal care industry uses plant-derived secondary metabolites, like lycopene, to avert skin photodamage

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and aging. Therefore, it is necessary to link diversity in plant secondary metabolism with the underlying genetic architecture related to photosynthetic gene diversity (LPE1, HCF173, HCF244, D1, Cytochrome b6f complex and NDH complex subunits, APTase γ subunit, RuBisCO, GAPA, GAPB and TPI) to add value to the Solanaceae biodiversity to develop new crops and thus prevent competition with the food industry.

Author contributions

CA-B: Writing – original draft, Writing – review & editing. GZ: Conceptualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

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