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Research article

Suppressing photorespiration for the improvement in photosynthesis and crop yields: A review on the role of S-allantoin as a nitrogen source

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ABSTRACT

Environmental variations resulting in biotic and abiotic stresses demand adaptive changes in the photosynthetic machinery. To cope with these challenges, plant scientists are constantly striving to enhance photosynthetic activity. The photorespiration pathway, which fixes O_2 and releases CO_2 in C_3 plants, competes with photosynthesis. One method to increase yield would be to enhance photosynthesis by engineering the photorespiratory pathway. To date, three engineered photorespiratory pathways have been produced, of which two have been proven experimentally in the model plant, *Arabidopsis thaliana*. These approaches might be helpful in enhancing crop resilience to future environmental challenges. In partially photorespiratory suppressed plants, it is hypothesized that a gene cluster may have formed between bacterial glycolate dehydrogenase (*GDH*), glyoxylate carboligase (*GCL*), and tartronic semi aldehyde (*TSR*) genes with *Arabidopsis* allantoin degradation genes like *Arabidopsis allantoinase* (*AtALN*) to utilize S-allantoin as a source of nitrogen. Observations of the use of allantoin as an exclusive source of nitrogen or energy by *Arabidopsis* and *Escherichia coli* led us to propose a genetic switch control model between nitrogen assimilation and energy producing pathways in partially photorespiratory suppressed plants.

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1. Introduction

The increasing food demands of the expanding global population necessitate global efforts to increase the crop production to ensure food security and protect environment and natural resources. It has been estimated that the world population will reach 9.1 billion in 2050 (Fahad et al., 2016a, b, c, d), while food production will need to be increased by 70% (FAO, 2009). This must be achieved in the face of increasingly unfavorable environmental conditions (Fahad and Bano, 2012; Fahad et al., 2013; Fahad et al., 2014a, b; Fahad et al., 2015a, b) The green revolution of the 1960s brought about an exponential increase in the production of cereal crops (Cerdà et al., 2016; Keesstra et al., 2016). Such an increase in agricultural food production worldwide was mainly associated with higher (almost 7-fold) use of N fertilizers (Hirel et al., 2007). As a result, both the recent and future intensification of the use of N fertilizers in the agriculture sector already has and will continue to have major detrimental impacts on the diversity and functioning of ecosystems. N nutrition plays a critical role in plant dry matter accumulation through the control of both the leaf area index and specific leaf N (amount of N per unit of leaf area). Therefore, there is a tight relationship between N supply, leaf N distribution, and leaf photosynthesis (Gastal and Lemaire, 2002). Moreover, the photosynthetic N use efficiency (PNUE), dependent on the level of CO_2 saturation of Ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco), is another factor that needs to be taken into consideration when C_3 or C_4 crop species are discussed. At suboptimal N availability, C_3 plants have a greater N use efficiency (NUE) than C_4 plants, whereas at higher N levels, the reverse is true (Sage and Coleman, 2001; Sage et al., 2012). Consequently, identifying the regulatory factors that control the balance between N allocation to maintain photosynthesis and the reallocation of the remobilized N to sink organs (such as young developing leaves and seeds) in C_3 and C_4 species are of great importance, particularly under limited N conditions (Sage and Coleman, 2001; Sage et al., 2012).

Generally, the photosynthetic capacity of C_3 plants is restricted by multiple environmental factors. Under a high CO_2 supply and enough illumination, the activity of Rubisco often limits carbon fixation. Rubisco works very slowly; thus, it catalyzes only a few reactions per second. Another major limitation on the efficiency of CO_2 fixation is the ability of oxygen to bind to the active site of the enzyme in a non-productive reaction in which ribulose bisphosphate is broken down and CO_2 is released; this process is known as photorespiration (Wingler et al., 2000). Photorespiration is believed to cause 25% of yield losses to net photosynthetic productivity (Sharkey, 1988; Raines, 2011). Rubisco catalyzes two competing reactions, carboxylation and oxygenation, the rates of which depend upon the relative concentrations of CO_2 and O_2, as well as on temperature. Carboxylation leads to net CO_2 fixation, whereas oxygenation generates glycolate that can only be metabolized outside chloroplasts by photorespiratory processes in peroxisomes and mitochondria (Ogren, 1984; Medrano et al., 1995). Therefore, plant growth and yield can be improved by increased photosynthesis and/or reduced photorespiration.

Attempts to reduce photorespiration by the overexpression of C_4 enzymes in C_3 plants without spatial separation into two tissues have been made, which have shown limited success so far. In recent decades, the knowledge of glycolate metabolism in *Escherichia coli* was used by Peterhansel's group to establish a novel pathway that can metabolize glycolate in the chloroplasts of *Arabidopsis*, which produced 30% more biomass under controlled conditions (Keibeish et al., 2007). A second engineered glycolate metabolism pathway was established in the peroxisome of tobacco plants (*Nicotiana tabacum* L), where glycolate was converted to tartronate semialdehyde, which was returned to the photorespiratory cycle by an isomerase reaction that forms hydroxypyruvate. This was further converted to glycerate and transported into the chloroplast where it formed 3-phosphoglyceric acid (3PGA) (Carvalho et al., 2011).

A number of researchers (Fahnenstich et al., 2008; Maurino and Peterhansel, 2010; Maier et al., 2012) have shown that it is possible to completely oxidize glycolate to CO_2 in chloroplasts by combining endogenous enzymes of the chloroplast with introduced enzymes. This could convert glycolate completely to CO_2 and overcome the problem of hydrogen peroxide (H_2O_2) production during glycolate oxidation using catalase (CAT), an enzyme from the peroxisome that detoxifies H_2O_2. Glyoxylate is further converted to malate by the combined action of acetyl-S-CoA and malate synthase.

The discovery of the allantoin transporter, (AtUPS1) in *Arabidopsis* has paved the way regarding the use of allantoin as a backup source for N, particularly under limited N conditions (Desimone et al., 2002). The two functional allantoinase genes responsible for the degradation of allantoin, *AtALN* and *RpALN*, were reported to be overexpressed in the absence of other N sources, hence providing evidence for allantoin as an alternative nitrogen source (Yang and Han, 2004). Nitrogen is a very important resource for sustainable yield; hence, it can be hypothesized that allantoin could be used as a source of N by *Arabidopsis* plants with partially suppressed photorespiration. These observations allowed us to suspect that the sustainable biomass production in partially photorespiratory suppressed *Arabidopsis* plants might be caused by the formation of a favorable gene cluster to use allantoin as a nitrogen source. In the present article, we summarize recent data on suppressing photorespiration in plants with the ultimate objective of enhancing photosynthesis and crop yields. Furthermore, allantoin, as a N source under N-limited conditions in partially photorespiratory suppressed plants is also discussed.

2. Biochemistry of photorespiratory pathways

2.1. Natural photorespiratory pathway

Ribulose 1, 5-bisphosphate (Rubisco) can perform two competing processes viz., carboxylation and oxygenation. Carboxylation results in 3-phosphoglycolate (3PGA), which can enter in the Calvin cycle (Calvin et al., 1950), while oxygenation produces 2-phosphoglycolate (2PGA), which is metabolized through the photorespiratory pathway, as described by Tolbert et al. (1997). 2-PGA is dephosphorylated to glycolate in the chloroplast, and subsequently transported into the peroxisome, where it is oxygenated to produce glyoxylate; H_2O_2 is also produced during this process. Glycine, produced from glyoxylate in the peroxisome by the process of transamination, is then transported into the mitochondria, where it is decarboxylated to serine (Dalton and Burris, 1962); this releases CO_2 and NH_3 and produces reducing power in the form of NADH. Serine from mitochondria travels to the peroxisome, where the deamination of serine produces hydroxypyruvate, which is reacted with NADH to produce glycerate. Glycerate is subsequently carried to the chloroplast, where ATP is consumed to produce 3PGA as a three-carbon compound that can enter the Calvin cycle (Calvin et al., 1950; Leegood, 2007; Russell, 2010).

2.2. Introducing the bacterial glycerate pathway in the chloroplasts of *Arabidopsis*

Glycolate is metabolized through the photorespiratory pathway, which consumes energy in the form of ATP and causes the loss of 25% of fixed CO_2. To overcome this loss, Kebeish et al. (2007) transferred the whole glycerate metabolic pathway from *Escherichia coli* into the chloroplasts of *Arabidopsis thaliana*, which resulted in 30% and 65% increases in shoot and root dry weight, respectively. This method is based on the principle of increasing the CO_2 concentration in proximity to Rubisco. This pathway requires three enzymatic activities: glycolate dehydrogenase (GDH), controlled by a gene having three subunits; glyoxylate carboligase (GCL); and tartronic semi aldehyde (TSR). Bari et al. (2006) identified the open reading frame for GDH (*AtGDH*) in *Arabidopsis*. Kebeish et al. (2007) also used *AtGDH* and showed that

AtGDH not only enhanced biomass, but also improved the plant growth and photosynthesis.

2.3. A glycolate metabolizing pathway engineered in tobacco

A second engineered glycolate metabolism pathway was established in the peroxisome. In the engineered pathway, glycolate is metabolized to TSR, which is returned to the photorespiratory cycle by an isomerase reaction to form hydroxypyruvate. Hydroxypyruvate is then converted to glycerate and transported into the chloroplasts, where it forms 3PGA (Carvalho et al., 2011).

Nölke et al. (2014) also reported an engineered glycolate metabolism in chloroplasts, using a combination of introduced and endogenous enzymes. The glycolate oxidase enzyme from the peroxisome was relocated into the chloroplasts along with CAT to detoxify the effects of H_2O_2 production by glycolate oxidase (GO). Malate synthase reacts with acetyl-S-CoA to produce malate, a C4 compound, during storage lipid mobilization in the glyoxysomes of young plants (Cornah et al., 2004). Both malic enzyme and pyruvate dehydrogenase, already present in chloroplasts, oxidize glycolate to CO_2 completely via the activity of Rubisco oxygenase in the chloroplasts. The CO_2 produced is then available for refixation and should inhibit further oxygenation of Rubisco. This pathway activation in chloroplasts resulted in increased biomass accumulation and improved photosynthetic efficiency. As a result of the overall reaction, glycolate and O_2 is converted to CO_2 and H_2O, along with reducing equivalents (Fahnenstich et al., 2008; Maurino and Peterhansel, 2010; Maier et al., 2012). It is worth mentioning that this pathway bypasses the Calvin cycle by not producing 3PGA (Peterhansel et al., 2012). In short, the efficient regulation of Rubisco could be helpful in improving the crop yield (Parry et al., 2013).

2.4. The photorespiratory pathway and its engineered bypasses

The enzymes required at different stages of the photorespiratory pathway were reviewed and compared by Peterhansel and his colleagues (Peterhansel et al., 2010, 2011, 2012), who clearly elaborated the differences among the three bypasses and between naturally occurring photorespiration at the enzymatic level (Table 1). Peterhansel et al. (2012) reported two potential benefits of the bypasses: first, increased chloroplastic CO_2 concentration in the vicinity of Rubisco, which could reduce the oxygenation of Rubisco in bypass 1 and bypass 3; and second, the avoidance of transamination reactions and thus reduction in energy costs that occur in fixation, as the release of CO_2 in the mitochondria or peroxisome using bypass 2 strongly depends on the ability of chloroplasts to fix CO_2 outside of the chloroplasts, which requires an active channeling system (Fig. 1).

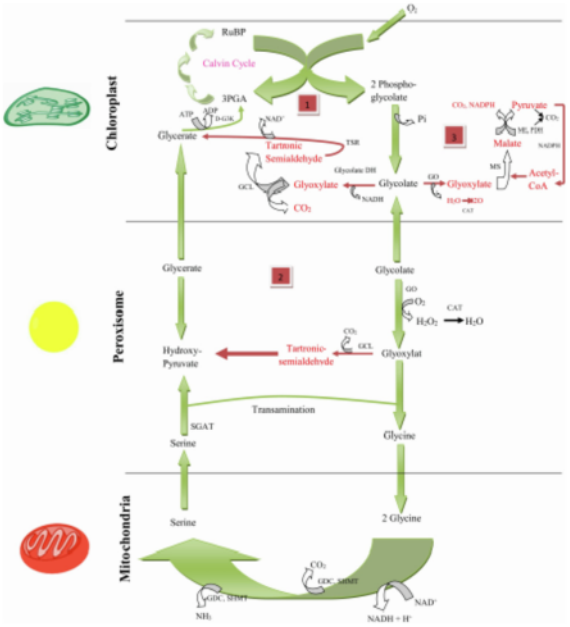

Fig. 1. The photorespiratory pathway and its bypasses.

2.5. Energy balance of the engineered pathways vs. naturally occurring photorespiration

Subsequently, Peterhansel et al. (2012) compared the energy balance of the three bypasses with each other, as well as with naturally occurring photorespiration. The energy conversion data in Fig. 2 shows that the total ATP required for natural photorespiration is 12.25, which is reduced to 9.25 and 11.75 by bypass 1 and 2, respectively, whereas in bypass 3 this number was increased to 17.5. The higher demand of bypass 3 compared to that of natural photorespiration challenges its applicability in plant systems because it will require other parameters, such as the ability to reduce the oxygenation of Rubisco in chloroplasts and/or improve CO_2 refixation (Peterhansel et al., 2011, 2012).

The proven role of photorespiration in dissipating excess photochemical energy (Igamberdiev, 2001) is an argument against the photorespiratory bypasses. As photorespiratory bypasses may eliminate the excess energy sink during stress conditions, this could have a detrimental effect on plant growth and yield. This hypothesis is supported by the observation that during photorespiration, strong electron sinks and reactive oxygen species (ROS) are produced, which maintain a sophisticated balance in photosynthetic yield by working as an extra energy sink. Careful observation of the process indicated that peroxisomal glycolate oxidases produce ROS, which effectively functions in

Table 1
Comparison of the enzymatic reactions of photorespiration, three bypasses, and the mutant response survival plasticity.

Reaction	Photorespiration	Bypass 1	Bypass 2	Bypass 3	Photorespiratory mutants	Mutant survival
Phosphoglycolate dephosrylation	PGLP	PGLP	PGLP	PGLP	*pglp1*	Responds poorly to low CO_2, shows link to TCA cycle
Glycolate oxidation	GO	GlycolateDH	GO	GO		
H_2O_2 Detoxification	CAT	–	CAT	CAT		
Transamination	GGAT	–	–	–		
Decarboxylation	GDC, SHMT	GCL	GCL	ME, PDH		
NH_3 release	GDC, SHMT	–	–	–	*shm1*	Can grow if initially grown under high CO_2
Transamination	SGAT	–	–	–		
Reduction	HPR	TSR	HPR	–	*hpr1*	Mildly affected growth
Glycerate Phosphorylation		GK	GK	–	*glyk1*	Can survive only better than *pglp1*
Other				MS		

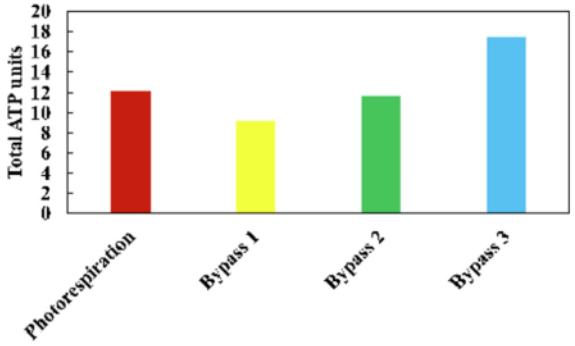

Fig. 2. Energy balance of three bypass pathways in relation to original photorespiration pathway (Reproduced from Peterhansel et al., 2012).

detoxification of the photosynthetic apparatus. Evolutionary studies of glycolate dehydrogenase and glycolate oxygenase in cyanobacteria and early eukaryotes suggested that higher plants prefer glycolate oxygenase instead of glycolate dehydrogenase, which burns excess reducing power (Kern et al., 2011). Some researchers argued that the excess production of glyoxylate in the peroxisome may leak into the cytoplasm, where cytosolic glycolate oxidase or hydroxypyruvate could convert it back to glycolate, thus producing a biochemical cycle that can oxidize the excess reducing power (Givan and Kleczkowskiin, 1992; Timm et al., 2008). Another approach that could be adopted is modifying plants to effectively switch the engineered photorespiratory pathways on/off according to the needs of the plant. Such a mechanism requires further experiments on the factors that control the onset of photorespiration. Such genetic switches have been revealed; for example, the ethylene genetic on/off switch (Qiao et al., 2012).

3. Advantages of photorespiration

3.1. Reactive oxygen species and signaling processes in plants

It is widely accepted that plant metabolism is minimized by certain types of stress, e.g., drought triggers the production of ROS, and the reaction 44 uirements of the cell are maintained by an antioxidant system (Noctor and Foyer, 1998; Zheng et al., 2016; Hussain et al., 2018). Plant signaling processes are dependent on ROS and soluble antioxidants, while stable oxidants (like hydrogen peroxide [H_2O_2]) and antioxidants are the sensors of oxidative status in the cells (Noctor et al., 2002; Schieber and Chandel, 2014; Hussain et al., 2016a, b; Hussa 14 al., 2018). Sies (2017) concluded that H_2O_2 has the ability to serve as a messenger to carry a redox signal from the site of its production to a target site, and it is regarded as the most suitable for redox signaling among the various oxygen metabolites. Moreover, Heneberg (2018) suggested that hexokinases are responsible for regulating various cellular processes, such as the stimulation of mitochondrial redox signaling. Rhee et al. (2018) suggested that H 40 is produced on the induction of many cell surface receptors and acts as an intracellular messenger in the regulation of various physiological processes, mainly by oxidizing the cysteine residues of effector proteins. A mild increase in the oxidative load helps plants to acclimatize and increase resistance, while further increases and sustained oxidative loads overshadow the beneficial aspect and can cause senescence and death (Schieber and Chandel, 2014; Hancock et al., 2017; Mittler, 2017). Thus, it is appropriate to investigate the optimum level of oxidative load to better equip the plants to cope with stressful conditions. Previous studies have indicated that modified stasis between the production of ROS and the antioxidant system perturb the balance of antioxidative enzymes and are also involved in the hypersensitive respons 65 pathogen attacks (Smirnoff, 1993; Levine et al., 1994; Noctor and Foyer, 1998; Veljovic-Joanovic et al., 2001). Furthermore, gene expression and signaling pathways involved in photorespiration 18 reported to have an affiliation with H_2O_2 and glutathione (Levine et al., 1994; Foyer et al., 1995, 1997; Willekens et al., 1997; Locato et al., 2017; Mhamdi et al., 2017; Demidchik et al., 2018), which have key roles in host responses to environmental stresses and pathogens.

3.2. Photorespiration as an alternative electron sink

Photorespiration usually occurs in C_3 plants at high rates (Foyer and Noctor, 2000), where net photosynthesis relies on the ratio of photorespiration to total photosynthesis (Ehlers et al., 2015). The substantial amount of energy used in the photorespiratory pathway reduces the overall yield of photosynthesis, and hence a reduction in fixed CO_2. This event may have physiological advantages during stress conditions, su 31 as drought, where CO_2 availability to the photosynthetic apparatus is reduced by stomatal closure (Foyer and Noctor, 2000). The metabolism of photosynthetic products by an augmented share of energy to photorespiration could alleviate detrimental effects, such as photoinhibition (Osmond and Grace, 1995). Although the decrease in photoinhibition could weaken ROS production in chloroplasts, the photorespiratory cycle is associated with the mandatory production of H_2O_2 in peroxisomes. Enhanced photorespiratory flow during drought worsens the oxidative load in photosynthetic cells. The photorespiratory pathway in C_3 plants promotes the light dependent H_2O_2 depositio 42 utside the chloroplast, where it evokes acclimatization events in abiotic stresses, such as drought (Ku et al., 1996; Noctor et al., 2002).

Furthermore, the conversion of inorganic nitrogen to nitrate and its subsequent assimilation by photorespiration is required for plant growth. This observation demonstrates why photorespiratory suppressed plants cannot grow in photorespiratory conditions (Rachmilevitch et al., 2004).

3.3. The negative correlation between CO_2 level and nitrogen availability

Higher plants respond to increased CO_2 availability by producing more biomass; this, accompanied by a decreased level of nitrogen status, reduces the maximum capacity of the photosynthetic yield. A previous study suggested that the availability of soil ammonium and nitrogen will be critical in deciding the plant quality and yield (Bloom et al., 2010).

The two possible hypotheses in this regard are as follows: 1) plants in CO_2 enriched environments take up more CO_2 into carbohydrates than they can assim 20 into their developing tissues, resulting in the depreciation of CO_2 assimilation by reducing the levels of Rubisco and other proteins (Long et al., 2004); and 2) plants accumulate carbohydrates faster than they can assim 49 nitrogen, leaving plants with a reduced nitrogen content (Norby et al., 2001; Hungate et al., 2003). Increased levels of litter in the environment causes soil microbes to bind to nitrogen, further reducing the available nitrogen; this would inhibit plant protein synthesis and photosynthesis, leading to restricted growth.

Nitrogen use efficiency in plants is associated with the quantity absorbed and utilized for grain formation. Hence, the partitioning of N in vegetative parts and grains is fundamental for higher yields. The major uptake forms of nitrogen in crop plants are ammonium and nitrate. Both of these forms are equally effective in the uptake process; nevertheless, the uptake of ammonium and/or nitrate by plants depends on the quantity of nitrogen forms in the soil. It was found that photorespiration rates were co 27 ted with nitrate assimilation in hydroponically grown *Arabidopsis* and wheat (Rachmilevitch et al., 2004; Bloom et al., 2010). This relationship has even been suggested to explain the lower-than-expected growth increases in plants grown under elevated CO_2, and could explain why many C_3 plants grow more slowly when fed with nitrate as a sole nitrogen source (Bloom et al., 2010). The

exact mechanism exploring such co-dependency is still unclear, but might be related to the photosynthesis-dependent export of malate from the chloroplast, which enhances the cytosolic NADH levels and thus provides the reducing equivalents for nitrate reduction (Bloom et al., 2010).

In most of the soils, the predominant form of available nitrogen is nitrate; however, the uptake of nitrate generally requires more energy (about five times) compared to that of ammonium. From this, it is possible that reducing the photorespiratory rates of crops (that mainly use nitrate) may lead to nitrogen deprivation. However, reliance on ammonium fertilizers may not always be effective, since many plants show toxicity symptoms when grown using ammonium as the sole nitrogen source.

4. Allantoin as a backup source of nitrogen, artificial horizontal gene transfer, and cluster formation in photorespiratory suppressed *Arabidopsis*

The discovery of the allantoin transporter "AtUPS1" indicated that in *Arabidopsis*, allantoin can be used as a backup source for nitrogen when the primary sources are limited (Desimone et al., 2002). The two functional allantoinase genes responsible for the degradation of allantoin, AtALN and RpALN, were reported to be overexpressed in the absence of other nitrogen sources, hence providing evidence for allantoin as an alternative nitrogen source (Yang and Han, 2004). Nitrogen is very important for sustainable yields; hence, we hypothesized that allantoin could be used as source of nitrogen by partially photorespiratory suppressed *Arabidopsis* plants. These observations allowed us to suspect that sustainable biomass production in partially photorespiratory suppressed *Arabidopsis* plants might be caused by the formation of a favorable gene cluster to use allantoin as a nitrogen source.

4.1. Gene clustering in microorganisms and plants

The generation of gene clusters to produce secondary metabolites is well known in microorganisms (Jacob and Monod, 1961; Koonin, 2009). Gene clusters for the synthesis of antibiotics in actinomycetes and toxins are well known in filamentous fungi. Gene clusters in plants for metabolic pathways were discovered recently; however, five plant gene clusters have been identified, all of which were associated with the generation of defense compounds (Chu et al., 2011). Horizontal gene transfer from microorganisms could be responsible for eukaryotic gene clusters, although there are hints that this is not true in this case; translocations duplications have been observed. It is worth mentioning that in all five reported plant secondary metabolic gene clusters, the enzymes from the primary metabolic pathway are induced in the secondary pathway as a first step (Chu et al., 2011).

There are known non-homologous gene clusters that are required for growth and survival under specific environmental conditions in unicellular eukaryotes and animals, which are termed adaptive gene clusters (Osbourn and Field, 2009; Osbourn, 2010a;b). Clusters for catabolic pathways in yeast (*Saccharomyces cerevisiae*), such as DAL and GAL clusters, that allow the use of new nitrogen or carbon sources (Hittinger et al., 2004; Wong and Wolfe, 2005).

Gene clustering is uncommon in plants; for example, the genes for well-known secondary metabolic pathways in plants are not linked. Anthocyanin synthesis genes in maize are one such example. For the few gene clusters that are present in plants, the obvious assumption is that these clusters arose by horizontal gene transfer from microbes; nonetheless, the evidence indicates that this is not the most likely occurrence. The genes and the products used in the earlier steps in these pathways can be considered to be indicator genes or enzymes and are necessary for the composition of the skeleton structure of secondary metabolites (Osbourn, 2010b). These indicator genes commenced from plants instead of microbes, and share homology with the genes responsible for encoding enzymes for primary plant metabolism. It is possible that they are regulated directly or indirectly due to gene duplication and the procurement of new functions. In lieu of this, it is also possible that the genes for primary metabolites and their indicator gene analogue originated from a common ancestor (Chu et al., 2011). Moreover, the genes for altering enzymes are necessary, in addition to indicator genes, for the further processing of the skeleton structures along with cytochrome P450s and other acyltransferases, methyl transferases, oxidoreductases, and sugar transferases (Osbourn, 2010a).

4.2. *E. coli* can use allantoin as a sole source of nitrogen

In *E. coli*, the degradation of purines through uric acid leads to allantoin, which is used as an N source by *E. coli* under anaerobic conditions (Vogels and Van der Drift, 1976). For N assimilation, allantoinase (AllB) and allantoate amidohydrolase (AllC) are used to convert allantoin to ureidoglycolate (Vogels and Van der Drift, 1976; Chang et al., 1993). Ureidoglycolate is then metabolized by two different pathways. In the first pathway, 3PGA is formed from ureidoglycolate by the action of AllA, involving ureidoglycolate hydrolase, GCL and tartronic semialdehyde reductase (GlxR) and glycerate kinase (GlxK). Then, 3PGA is integrated into key energy metabolism. The second metabolic route of ureidoglycolate is its conversion to oxalurate by ureidoglycolate dehydrogenase (AllD), which leads to the production of oxamate and carbamoyl phosphate (Cusa et al., 1999), which are then further processed to yield $3NH_4^+$, used for the synthesis of amino acids via glutamine (Hasegawa et al., 2008). The DNA binding transcription factor AllR, together with AllS, plays a key role in shifting control of the two pathways between N assimilation and energy production in *E. coli*. The substrate, allantoin, which is common to both pathways, activates the repressive function of AllR, which switches off the energy production genes. In contrast, the accumulation of glyoxylate deactivates AllR, which activates the energy production genes. The master regulator for pyrimidine and arginine production, RutR, is also involved in the switching control of this pathway (Hasegawa et al., 2008).

4.3. S-allantoin as a source of nitrogen in Arabidopsis thaliana

Many organisms, including plants, some fungi, and several bacteria, can utilize S-allantoin to exploit its stored N, carbon, and energy. Soybean, a N-fixing leguminous crop, depends on allantoin degradation as its primary N supply in low-turgor-pressure tissues. The hydrolysis of allantoin by allantoinase to produce allantoate is the common starting reaction in of the organisms that metabolize allantoin. In *Arabidopsis*, S-allantoin is converted to allantoate by the action of allantoicase, which is further processed to synthesize S-ureidoglycine by allantoate amidohydrolase (AAH), releasing CO_2 and ammonia. S-ureidoglycine is acted upon by allantoate amidohydrolase to produce S-ureidoglycolate (Fig. 3).

Here, we propose transferring the whole set of genes (*GDH, GCL*, and *TSR* from *E. coli*) to short-circuit the photorespiratory pathway. Kebeish et al. (2007) documented that triggered genes of the photorespiratory bypass pathway and S-allantoin degradation pathway form a possible gene cluster to eventually provide plants with energy from glycolate metabolism in chloroplasts and N from degrading S-allantoin. The sequence analysis of allantoinase from *Arabidopsis* and *E. coli* showed conserved domains of the metallo-dependent hydrolases superfamily, while the genes involved in the degradation of allantoin in *E. coli*, *GCL* and *TSR*, were transformed to *Arabidopsis*, along with *GDH*. In *E. coli*, these genes are responsible for glycolate metabolism as well as allantoin degradation under low N conditions. *GDH*, *GCL*, and *TSR* collectively enable transformed *Arabidopsis* plants to metabolize glycolate in the chloroplasts. *GCL* and *TSR* are also involved in degrading allantoin into a N source in *E. coli*. This dual function of *GCL* and *TSR* led us to search for the substrate allantoin in the chloroplasts or peroxisomes, the presence of which was experimentally confirmed by Lamberto et al. (2010). The enzymes responsible for S-allantoin

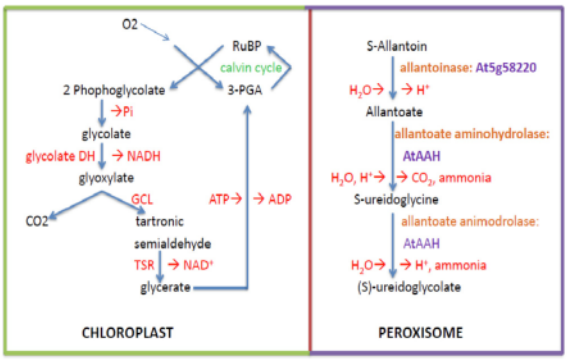

Fig. 3. Linking bypass Photorespiratiory pathway to Allantoin degradation Pathway.

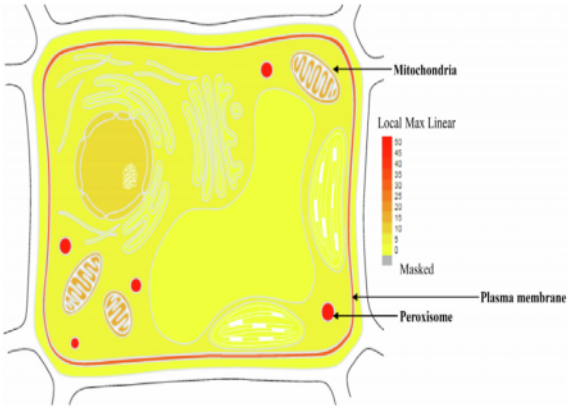

Fig. 4. The Cell eFP Viewer depicts the subcellular localization of the gene product At5g58220, ALNS, allantoinase. The color gradient (black to dark red) represents the quality of the localization information in each organelle from the SUBA database. Data are from Tanz et al. (2012) SUBA3: a database for integrating experimentation and prediction to define the SUBcellular location of proteins in *Arabidopsis*. Nucleic Acids Res. 41, D1185-91.

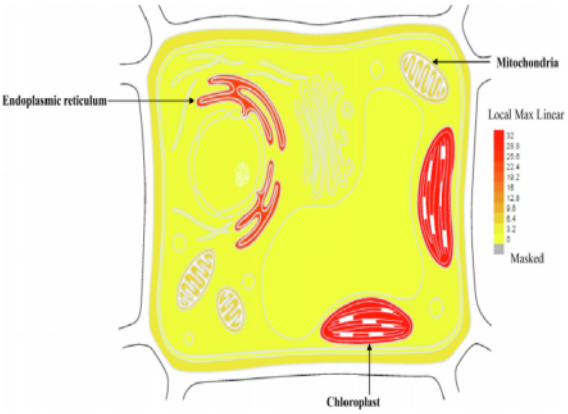

Fig. 5. The Cell eFP Viewer depicts the subcellular localization of the gene product At4g20070, AtAAH, aminohydolase. The color gradient (black to dark red) represents the quality of the localization information in each organelle from the SUBA database. Data are from Tanz et al. (2012) SUBA3: a database for integrating experimentation and prediction to define the SUBcellular location of proteins in *Arabidopsis*. Nucleic Acids Res. 41: D1185-91.

degradation are localized in the endoplasmic reticulum, while their presence is also predicted in the peroxisomes. This further strengthens the hypothesis for possible gene clustering or the direct impact of *GCL* or *TSR* on the allantoin degradation pathway during N demand; these are the exogenous genes overexpressed in transformed *Arabidopsis* by Kebeish et al. (2007) to install a novel glycolate metabolizing pathway from *E. coli*. Thus, we propose the further characterization of *GDH*, *GCL*, and *TSR* in transformed plants in relation to allantoin degradation. Figs. 4 and 5 show the prediction of S-allantoin degradation enzymes localized in the peroxisomes, chloroplasts, and other organelles. Further support for this hypothesis comes from the observation that gene clusters generally form when a signature gene for a metabolic pathway is recruited through a direct or indirect method. Interestingly, in the photorespiratory bypass pathway, *GDH* from *E. coli* is induced, along with two more genes, *GCL* and *TSR*. Here, *GDH* could serve as the signature gene from which the gene cluster could evolve. For the two metabolic routes of S-allantoin, the conversion of glyoxylate to 3-phosphoglycerate by photorespiratory enzymes in the peroxisomes is the energy metabolism route, while the second metabolic pathway makes the N in S-allantoin available to be used in the production of enzymes, hormones, and amino acids.

5. Conclusion and perspectives

In the last two decades, the decrease in crop productivity has been associated with a significant decline in fertilizer nutrient use efficiency (especially N) and widespread environmental damage. Efficient N management to provide a balance between N inputs and outputs is essential in modern agricultural systems, which will ultimately improve the NUE as well as crop yield. It has been well evident that respiration and N metabolism are intimately associated in plant cells, particularly because of the energy and metabolite requirements. Thus, exploitation of the flexibility of the respiratory pathways in plants has the potential to affect the NUE. In the present review, some of the examples for the manipulation of respiratory processes were discussed in order to highlight the more efficient driving force for N in plants. Several efforts have been carried out in order to manipulate the photorespiration to increase the plant biomass and yield; nevertheless, most of these approaches have been made using model plants (with some notable exceptions). For instance, the approach used by Peterhansel's group to overcome photorespiration in *Arabidopsis* not only increased the CO_2 concentration and photosynthetic efficiency of the chloroplasts, but had also a possible effect on the plant genes responsible for using S-allantoin as a source of N by prompting gene clustering. This effort also showed that bacterial *GCL* and *TSR* had a possible direct effect on allantoin degradation (Fig. 6). This is an example of favorable horizontal gene transfer, which can trigger functionally related or physically interacted genes to form gene clusters to overcome nutritional requirements in a controlled regulated manner by evolving transcription factor regulators. The introduction and function of such a novel photorespiratory pathway in crops, and the possibility of using allantoin as source of N in photorespiratory suppressed plants, will certainly be a scientific breakthrough, as it could improve crop production in the future. However, a great challenge exists to transfer these advances to the major grain crops, which are generally more recalcitrant to genetic manipulation. A rational bio-engineering of the plants with altered photorespiration should be taken into consideration, as this pathway is tightly linked with several other aspects of plant metabolism.

Conflict of interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

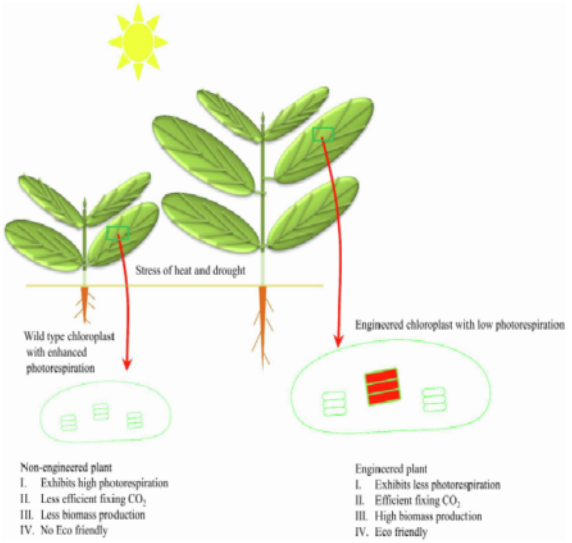

Fig. 6. Comparison model of plants to illustrate features of engineered chloroplast.

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