



REVIEW PAPER

OPEN ACCESS

Investigating the effect of carbohydrate buildup and sink limitation to photosynthetic rate: A review

Christine B. Dalogdog, Caitlin Andrea M. Perral*, Cecille N. Gementiza,
Mauricio S. Adlaon

*MAED-General Science 1A, Graduate School, Surigao del Norte State University,
Surigao del Norte, Philippines*

Key words: Carbohydrate, Photosynthesis, Photosynthetic rate, Sink limitation, Sugar

<http://dx.doi.org/10.12692/ijb/23.2.106-112>

Article published on August 04, 2023

Abstract

In crops, the physiological basis of dry matter production depends on the source-sink notion and the capability to utilize photosynthetic products. When the sink exceeds the source, it declines prematurely due to lack of assimilates. The source organs are leaves while the sink organs are the fruit of the plant. In process of photosynthesis, chlorophyll absorbs energy from sunlight to build carbohydrates in the chloroplasts of the leaves, and aerobic cellular respiration releases that stored energy by using oxygen to break down carbohydrates. Both organelles use electron transport chains to generate the energy necessary to drive other reactions. It was suggested by (Tejera-Nieves *et al.*, 2023) that sink limitation is an important mechanism that drives photosynthetic decline. In their study, the starch (a carbohydrate) in the rhizome of perennial switch grass reached highest concentrations at the same the leaf photosynthesis rate is low. Strategies to mitigate sink limitation must be included to breeding practice to increase yields. The balance of sources and sinks is the subject of two recent papers, highlighting the possibility of combining improvements in both source and sink capacities (Paul *et al.*, 2020; Sonnewald & Fernie, 2018). In this review, the effect of carbohydrate buildup and sink limitation to photosynthetic rate was investigated.

* **Corresponding Author:** M. Perral ✉ caitlinandraperral98@gmail.com

Introduction

Photosynthesis is the process by which plants use sunlight, water, and carbon dioxide to create oxygen and convert it into biochemical energy, which is subsequently used to support nearly all life on Earth. Plant growth depends on photosynthesis. Water undergoes oxidation, which means it loses electrons, while carbon dioxide is reduced, which indicates it obtains electrons, within the plant cell. This process absorbs energy from sunlight to build carbohydrates in the chloroplasts, and aerobic cellular respiration releases that stored energy by using oxygen to break down carbohydrates. Both organelles use electron transport chains to generate the energy necessary to drive other reactions.

Carbohydrates are of unique importance because they are direct products of photosynthesis and the primary energy storage compounds. These are the basic organic substances from which most other organic compounds found in plants are synthesized. As carbon dioxide concentration increases, the rate of carbon that incorporated into carbohydrate also increases in the light-independent reaction of photosynthesis. Sink regulation of photosynthesis is highly dependent on the physiology of the rest of the plant. It regulates photosynthesis through signal transduction pathways that coordinate the plant carbon-nitrogen balance, which matches photosynthetic capacity to growth and storage capacity and underpins and can override the direct short-term control of photosynthesis by light and CO₂ (Paul *et al.*, 2001).

It was suggested by Tejera-Nieves *et al.* (2023), that sink limitation is an important mechanism that drives photosynthetic decline. In their study, the starch (a carbohydrate) in the rhizome of perennial switch grass reached highest concentrations at the same the leaf photosynthesis rate is low. Strategies to mitigate sink limitation must be included to breeding practice to increase yields. The aim of this study is to investigate the effect of carbohydrate buildup and sink limitation to Photosynthetic Rate. A diagram is crafted to comprehensively understand the concept.

Source-Sink Relationship

In crops, the physiological basis of dry matter production depends on the source-sink notion and the capability to utilize photosynthetic products. When the sink exceeds the source, it declines prematurely due to lack of assimilates. Sink limitation is one of the most common causes of yield loss. Source limitation is caused basically by leaf defoliation caused by bad weather, disease, or attack by sucking insects, which limits leaf area development and affects source size. Decreased light source activity is also attributed to decreased light intensity above the plant canopy. Sink limitation exists caused by floret sterility, insect damage, nutrient boundary, canopy temperature, hormonal fluctuations, waterlogging, salinity, and other causes. Adverse climatic conditions, such as heat stress, can affect both floret assembly and sink activity. In certain wheat genotypes, changes in photoperiod sensitivity and fertilization due to high temperatures affect anther and pollen viability, leading to spikelet sterility (Aiqing *et al.*, 2018; Prieto *et al.*, 2018; Hütsch *et al.*, 2019).

Source-Sink Relationships in Crop Plants and Their Influence on Yield Development and Nutritional Quality

Many crops rarely reach their maximal output potential in terms of yield. The difference between the average yield at the farm gate and the crop production potential for a certain land area is known as the resulting yield gap. According to Evans and Fischer (1999), crop yield potential is the yield of a cultivar grown under ideal conditions where abiotic and biotic stressors are successfully managed. According to these ideas (Evans and Fischer, 1999; Lobell *et al.*, 2009; Van Ittersum and Cassman, 2013), producers and researchers can assess production disparities, particularly the sensitivity of output to manageable pressures, and target changes accordingly. However, there are constraints in the pursuit of the aspirational goal of decreasing the yield gap. The yield gap is a less precise measurement that is susceptible to increases in yield potential (Lobell *et al.*, 2009). Targeting the yield gap similarly ignores economic production factors like input costs or the price paid for product quality (Lobell *et al.*, 2009; Fischer *et al.*, 2014).

However, as crop production potential improvements are insufficient to satisfy future demand (Ray *et al.*, 2013), closing the yield gap is a crucial part of interdisciplinary efforts to promote food security.

As a result of enhanced accumulation of soluble sugars, amino acids, and proteins to the grain, it was discovered that under drought stress, chickpea output had a higher nutritional quality (Behboudian *et al.*, 2001). Such reactions may be accounted for by changes in architecture that subsequently affect access to vital nutrients like calcium or phosphorus as rooting depth rises in pursuit of additional water (Chaves *et al.*, 2003). Therefore, nutrient content and concentration fluctuate as a result of drought stress, potentially changing the yield's nutritional quality. Given the size of these effects, it is likely that they will have an impact on the nutritional quality of food production, stressing the need to take yield quality and its adaptability to change.

Effects of Carbohydrate Accumulation on Photosynthesis

The buildup of carbohydrates in leaves frequently results in the cytosolic accumulation of sugar phosphates and feedback inhibition of sucrose production. The antiport of triose phosphate orthophosphate through the chloroplast envelope is suppressed by the buildup of sugar phosphates because it lowers the cytosolic concentration of orthophosphate (Stitt and Quick 1989). Low stromal orthophosphate availability inhibits the synthesis of ATP and the conversion of PGA to triose phosphate, both of which are necessary for photosynthesis (Stitt 1986; Sharkey and Vanderveer 1989). At saturating CO₂ concentrations, the phosphate-limited photosynthesis is most likely to take place (Sharkey, 1985). Low levels of orthophosphate in the stroma may also cause ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) to be less activated (Sawada *et al.*, 1992). Although they accumulated the phosphorylated intermediates, several mutants of *Arabidopsis thaliana* with decreased sucrose synthesis did not exhibit any evidence of reduced photosynthesis caused by orthophosphate depletion (Strand *et al.*, 2000; Chen *et al.*, 2005).

As a result, the limiting of phosphate is not necessarily brought on by the suppression of sucrose production.

In leaves, non-structural carbohydrate buildup inhibits photosynthesis. But between source leaves (sugar exporters) and sink leaves (sugar consumers), the degree of suppression ought to differ. These findings show that the influence of carbohydrate accumulation on photosynthesis is significant in source leaves but not in immature sink leaves, and that the key factor contributing to the carbohydrate suppression of photosynthesis was the decline in Rubisco concentration.

Optimization of source-sink for sustainable crop production

Optimizing the source-sink relationship would be another promising means of improving crop yields by improving the efficiency of photosynthesis through various mechanisms. Reduction of photorespiration, conversion of C₃ plants to C₄ signaling pathway, optimization of Calvin-Benson cycle/Rubisco and electron transport. Strong sinks can increase crop yields even under stress conditions. elevated swelling capacity, likely Muhie CABI Agriculture and Bioscience (2022). It is also required to handle sink conditions in facilities with increased source capacity. The balance of sources and sinks is the subject of two recent papers, highlighting the possibility of combining improvements in both source and sink capacities (Paul *et al.*, 2020; Sonnewald & Fernie, 2018).

Carbon partitioning within plants have a major determinant which is the source–sink balance. In the study of Andrade *et al.* (2019), they manipulated the source-sink by thinning which is an agricultural practice of changing the ratio between leaves and fruits. Equilibrium is changed which causes higher carbon buildup from leaves to the remaining fruit. It is supposed that the fruits of the Peach Tree will be increased with soluble solid content in the fruit by decreasing the fruit load of the Peach. The most abundant soluble sugar in leaves followed by sucrose which is mostly in the fruit. Thinning treatments leads Sorbitol accumulation in the leaves causing imbalance in drain capacity which leads to low photosynthetic rate and stomatal closure.

The final fruit size was not affected. Development of other sink organs (e.g. vegetative suckers) is allowed by the fruit thinning. This is an acclimation process that maintains the source-sink balance in the tree. The red pearl variety of Peach Tree under thinning, fruit development is hastened leading to later harvest maturity.

Sink-Regulation of Photosynthesis in Relation to Temperature

A study supports that low temperatures imply photosynthetic absorption limitation, which occurs at higher temperatures in sunflowers than in rape. This limit can be reduced by lowering the source: sink ratio. Cold temperatures reduce the rate of anabolic utilization more than the rate of photosynthesis (Farrar, 1988), and the short-term amount of carbohydrate accumulated in leaves when plants switch to low temperatures depends on the magnitude of the imbalance between sources and sinks. This temperature point may reflect the This temperature point. Matthew Paul and David Lawler therefore suggest that oxygen sensitivity and carbohydrate accumulation reflect anabolic utilization and may be more sink-limited in photosynthesis in sunflower than in rapeseed as a plant material base. Confirmed the discovery. The small amount of carbohydrates accumulated in plants grown in cold climates may be due to higher respiration rates than plants grown in warm conditions.

Studies on switch grass and *Haloxylon amodendron* in dry places indicate that these are the main drivers of the net rate of photosynthesis under extremely dry conditions, although photosynthesis is substantially reduced around noon when direct solar radiation is strong. finished. They could not tolerate intense sunlight and high temperatures (Zaiyou et.al, al 2022; Gao et.al, 2022). An indication that stomatal limitation of photosynthesis is dominant is when stomata approach a condition that maintains water balance within the plant and limits CO₂ entry into the leaves. The high transpiration rate caused by the high vapor pressure deficit caused severe leaf water deficit,

resulting in reduced stomatal conductivity and limited ingress of CO₂ concentration, resulting in reduced mesophyll conductivity (Gao *et al.*, 2022).

Auxin regulates source-sink carbohydrate partitioning and reproductive organ development

A key challenge in plant biology that has significant ramifications for raising agricultural yields is the understanding of the molecular mechanisms controlling source sink carbohydrate partitioning (Braun *et al.*, 2014; Yu *et al.*, 2015; Ruan *et al.*, 2014). Little is known about the interactions between auxin and sugar, despite the fact that it has long been understood that long-distance transport of auxin and sugar from the source to sink tissues is crucial for growth and developmental processes, including lateral root development, hypocotyl elongation, and shoot branching (Ruan *et al.*, 2014; Zhao, Y. 2018; Schlereth *et al.*, 2010).

According to several studies (Koch, K. 2004; Braun *et al.*, 2014; Yu *et al.*, 2015), the higher plants' sink organs, such as flowers, fruits, and seeds, are heterotrophic in nature and depend on nutrients from the photosynthetically active organs (such as leaves, referred to as source organs) for their growth and development.

Higher plants use the phloem sieve components to transfer nutrients (mostly sucrose) over long distances to organs that act as sinks. The driving force for the long-distance translocation of all other compounds, including nutrients, water, and signaling molecules in the phloem, is the turgor pressure created by the osmotic effect of sucrose loading into the phloem at the source and unloading at the sink (Braun *et al.*, 2014; Yu *et al.*, 2015; Ruan *et al.*, 2014).

The study's findings could have a significant impact on breeding crops with higher yields. Recent research has shown that altering the intensity or activity of the sink can greatly increase crop output. By better coordinating source and sink activities in crops, the discovery that auxin modulates carbohydrate partitioning during rice reproductive development may provide a workable solution to this issue.

Effects of Source Strength and Sink Size on Starch Metabolism, Starch Properties and Grain Quality

According to Motohide *et al.* (2015), the activities of the source, sink, and flow, as well as interactions between them, largely impact the quality and yield of rice. The source absorbs CO₂ from the surrounding atmosphere, converts it into sugars, and sends the sugars to the sink. The principal source of photosynthate for the growing grains is typically thought to be the flag leaf (Schnyder, H., 1993; and Kong *et al.* 2010). According to Biswas *et al.* (1986), grains are the main organs that act as sinks. The relationship between the sources and sinks determined grain yields. The ratio of leaf area to spikelet number, which expresses the capacity of the source supply to meet each spikelet's needs, may be a key factor in determining grain weight (Nagato *et al.*, 1970). The most often used technique to change the source-sink relationship is leaf-cutting, spikelet-thinning, and shadowing. The effects of source strength or sink size on plant development and crop output have been the subject of numerous studies (Gao *et al.*, 2021).

The synthesis of starch may be impacted by the strength of the source and sink, altering its fine structure, physicochemical properties, and grain quality. The effects of changing the source-sink link on rice starch production were demonstrated by the results. We outlined the complex interaction between the CLD and key starch metabolism enzyme gene expression. We also discussed the potential for enhancing grain quality through source-sink interactions.

A Wiring Diagram for sink strength

As a result, plant development profiles that encourage spike growth in the pre-anthesis phase will also increase post-anthesis source strength through enhanced spike photosynthesis (Araus *et al.*, 1993; Tambussi *et al.*, 2005, 2007; Maydup *et al.*, 2010; Sanchez-Bragado *et al.*, 2014). Spike photosynthesis also plays an important role as a source of photoassimilates during grain filling.

All hypotheses and models involving the transfer of source photoassimilates to the sink must consider not

only the rates of photodynthate generation and the variety of uses it is put to in source materials, including storage, but also the efficacy of transport to sink tissue in order to achieve high sink growth activities.

Understanding source-sink interactions: Progress in model plants and translational research to crops in controlled and field conditions

Basic research in model systems under regulated growth conditions and how the outcomes apply to crops in the field are examples of source-sink interactions. It is possible to enhance and/or combine the C₃, C₄, and CAM modes of photosynthesis, change the electron transport chain in chlorophyll, control photorespiration, add bacterial/algenic carbon concentration processes, and boost nitrogen and water use efficiency. Outstanding contribution to the sink's source optimization. For the source-sink sector to operate at its best, structural elements of storage organ shape that encourage storage organ cell proliferation are crucial (Miyashima *et al.*, 2019).

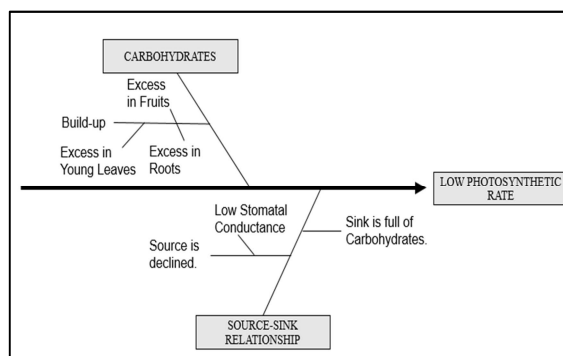


Fig. 1. Cause-Effect Diagram of the Effect of Carbohydrate Build-up and Sink Limitation on Photosynthetic Rate.

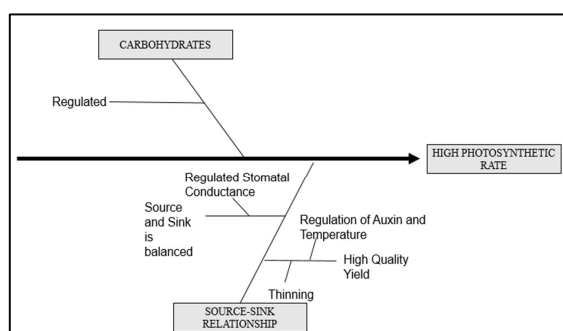


Fig. 2. Cause-Effect Diagram of the Effect of Regulated amount of Carbohydrates and Source-Sink Balance on Photosynthetic Rate.

Concluding remarks and perspectives

Recent studies show that the photosynthetic rate is affected by Carbohydrate build-up. Regular levels of carbohydrate build up can serve as energy source for the plant increasing the photosynthetic rate under suboptimal conditions. Excessive build-up of carbohydrates signals the plant to slow down or stop the photosynthesis. Roots, fruits and developing leaves are full of carbohydrates and there are too much of which the phenomenon is called Sink Limitation. Both Carbohydrate build-up and Sink Limitation will decrease the photosynthetic rate. Strategies to mitigate Carbohydrate build-up and Sink Limitation are Thinning, Auxin Regulation and Temperature Regulation.

Author contributions

No conflict of interest is declared.

References

Aiqing S., Somayanda I., Sebastian SV., Singh K., Gill K., Prasad PVVV., Jagadish SVK. 2018. Heat stress during flowering affects time of day of flowering, seed set, and grain quality in spring wheat. *Crop Science*, **58**, 380-392.

Andrade D, Covarrubias MP, Benedeto G, Pereira G, Almeida AM. 2019. Differential source-sink manipulation affects leaf carbohydrate and photosynthesis of early- and late-harvest nectarine varieties. Retrieved March 5, 2023 at https://www.researchgate.net/publication/333252509_Differential_source-sink_manipulation_affects_leaf_carbohydrate_and_photosynthesis_of_early_and_late-harvest_nectarine_varieties.

Behboudian MH., Ma QF., Turner NC., Palta, JA. 2001. Reactions of chickpea to water stress: yield and seed composition. *J. Sci. Food Agric.* **81**, 1288-1291. DOI: 10.1002/jsfa.939

Biswas AK., Mondal SK. 1986. Regulation by kinetin and abscisic acid of correlative senescence in relation to grain maturation, source-sink relationship and yield of rice (*Oryza sativa* L.). *Plant Growth Regul.* **4**, 239-245.

Braun DM. 2022. Phloem Loading and Unloading of Sucrose: What a Long, Strange Trip from Source to Sink. *Annu. Rev. Plant Biol.* **73**, 553-584. <https://doi.org/10.1146/annurev-arplant-070721.083240>

Chaves MM., Maroco JP., Pereira JS. 2003. Understanding plant responses to drought from genes to the whole plant. *Funct. Plant Biol.* **30**, 239-264. DOI: 10.1071/FP02076

Chen S., Hajirezaei M., Peisker M., Tschersch H., Sonnewald U., Börnke, F. 2005. Decreased sucrose-6-phosphate phosphatase level in transgenic tobacco inhibits photosynthesis, alters carbohydrate partitioning and reduces growth. *Planta* **221**: 479-492.

Evans LT., Fischer RA. 1999. Yield potential: Its definition, measurement and significance. *Crop Sci.* **39**, 1544-1551. DOI: 10.2135/cropsci1999.3961544x

Farrar JF. 1988. Temperature and the partitioning and translocation of carbon in plants and temperature. Eds SP. Long and FI. Woodward. The Company of Biologists Limited. Pp. 203-35.

Fischer RA., Byerlee D., Edmeades GO. 2014. *Crop Yields and Global Food Security: Will Yield Increase Continue to Feed the World.* ACIAR Monograph No. 158. Canberra: Australian Centre for International Agricultural Research.

Gao G, Feng Q, Liu X, Yu T, Wang R. 2022. The Photosynthesis of *Populus euphratica* Oliv. Is Not Limited by Drought Stress in the Hyper-Arid Zone of Northwest China. doi.org/10.3390/f13122096. <https://www.mdpi.com/1999-4907/13/12/2096>

Muhie SH. 2022. Optimization of photosynthesis for sustainable crop production. *CABI Agriculture and Bioscience* **3(1)**. <https://doi.org/10.1186/s43170022-00117-3>

Paul MJ., Foyer CH. 2001. Sink regulation of photosynthesis. *J. Exp. Bot.* **52**, 1383-1400. DOI: 10.1093/jexbot/52.360.1383

- Prieto P., Ochagavía H., Savin R., Griffiths S., Slafer GA.** 2018. Dynamics of floret initiation/death determining spike fertility in wheat as affected by Ppd genes under field conditions. *Journal of Experimental Botany*, **69**, 2633-2645.
- Ray DK., Mueller ND., West PC., Foley JA.** 2013. Yield trends are insufficient to double global crop production by 2050. *PLoS One* **8**:e66428. DOI: 10.1371/journal.pone.0066428
- Tejera-Nieves M, Abraha M, Chen J, Hamilton S, Robertson GP, James BW.** 2023. Seasonal decline in leaf photosynthesis in perennial switchgrass explained by sink limitations and water deficit. *Frontiers in Plant Science*. DOI 10.3389/fpls.2022.1023571. Retrieved January 28, 2023 at https://www.researchgate.net/publication/366870852_Seasonal_decline_in_leaf_photosynthesis_in_perennial_switchgrass_explained_by_sink_limitations_and_water_deficit
- Van Ittersum MK., Cassman KG.** 2013. Yield gap analysis-rationale, methods and applications-Introduction to the special issue. *Field Crops Res.* **143**, 1-3. DOI: 10.1016/j.heares.2012.12.001
- Araus JL., Brown HR., Febrero A., Bort J., Serret MD.** 1993. Ear photosynthesis, carbon isotope discrimination and the contribution of respiratory CO₂ to differences in grain mass in durum wheat. *Plant, Cell & Environment* **16**, 383-392. DOI: 10.1111/j.1365-3040.1993.tb00884.x.
- Hütsch, B.W., Jahn, D., Schubert, S.** 2018. Grain yield of wheat (*Triticum aestivum*L.) under long-term heat stress is sink-limited with stronger inhibition of kernel setting than grain filling. *Journal of Agronomy & Crop Science.* **205(1)**, 22-32.
- Koch, K.** 2004. Sucrose metabolism: Regulatory mechanisms and pivotal roles in sugar sensing and plant development. *Curr. Opin. Plant Biol.* **7**, 235-246.
- Maydup M.L., Antonietta M., Guamet J.J., Graciano C., López J.R., Tambussi E.A.** 2010. The contribution of ear photosynthesis to grain filling in bread wheat (*Triticum aestivum* L.). *Field Crops Research* **119**, 48-58. doi: 10.1016/j.fcr.2010.06.014
- Miyashima S., Roszak P., Sevilim I., Toyokura K., Blob B., Heo, JO., Mellor N., Help-Rinta-Rahko H., Otero S., Smet W.,** 2019. Mobile PEAR transcription factors integrate positional cues to prime cambial growth. *Nature* **565**:490-494.
- Motohide S., Gabriel FF., Song XJ., Motoyuki A., Haruka N., Keiki I., Tomoyuki Y., Mayuko I., Hidemi K., Akiko SA.** 2015. Mathematical model of phloem sucrose transport as a new tool for designing rice panicle structure for high grain yield. *Plant Cell Physiol.* **56**, 605-619.
- Lobell DB., Cassman KG., Field CB.** 2009. Crop yield gaps: Their importance, magnitudes, and causes. *Annu. Rev. Environ. Resour.* **34**, 179-204.
- Yu SM., Lo SF., Ho TD.,** 2015. Source-sink communication: Regulated by hormone, nutrient, and stress cross-signaling. *Trends Plant Sci.* **20**, 844-857.
- Zhao, Y.** 2018. Essential roles of local auxin biosynthesis in plant development and in adaptation to environmental changes. *Annu. Rev. Plant Biol.* **69**, 417-435.