

The Role of HY5 (Transcription Factor) in Carbon and Nitrogen Balancing

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Introduction

Plants are sessile organisms, and they developed sophisticated sensing and signaling systems that enable them to vigilantly monitor and react properly to the variable changes in their environment. Carbon (C) and nitrogen (N) are necessary for plants to carry out normal and basic cellular functions. Photosynthetic byproducts such as sucrose and glucose supply the energy for cellular functions and C-skeletons for amino acid synthesis (Coruzzi and Bush, 2001). N nutrients in plants include nitrate and ammonium (inorganic compounds) and amino acids (Organic compounds) which are biosynthesized by assimilating ammonium into the C-skeletons. Amino acids and resultant proteins are structural and fundamental components of the cell. Carbon and nitrogen metabolites are precisely coordinated in plants, and this ratio is referred as 'C/N balance' (Coruzzi and Zhou, 2001). C/N balance is crucial for regulating plant growth and development. C and N nutrients also serve as signalling molecules in a variety of cellular reactions (Vidal and Gutierrez, 2008). Plants have evolved a sophisticated system for sensing and reacting appropriately to the available C and N nutrient ratio. This process is called C/N-nutrient response.

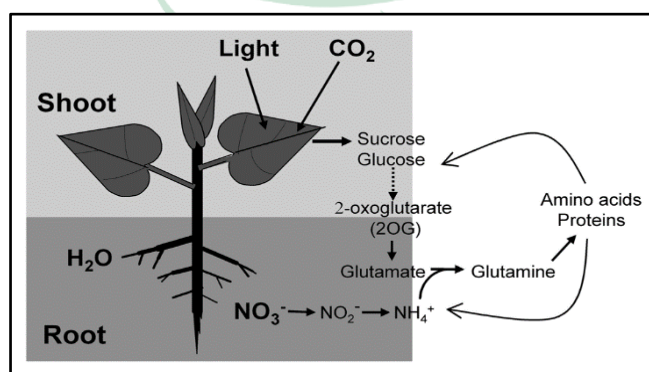


Figure: Simplified view of C and N metabolism coordination in plants

The need for close coordination of C and N metabolism is well recognised in plants. This coordination takes place at various levels. During photosynthesis, CO_2 is assimilated and the resulting glucose and sucrose are transformed into α -ketoglutarate or 2-oxoglutarate (2OG) via glycolysis and the Krebs cycle. While nitrate (NO_3^-) is reduced to nitrite (NO_2^-) by the action of nitrate reductase enzyme and further nitrite is reduced to ammonium (NH_4^+) by the action of nitrite reductase enzyme. Glutamate (Glu) is synthesised by assimilating NH_4^+ into the 2OG by using glutamate dehydrogenase enzyme. Glutamine (Gln) is synthesised by incorporating NH_4^+ into glutamate by the action of enzyme glutamine synthetase. All other amino acids synthesised by using NH_4^+ donated from the Glu and Gln. Aspartate (Asp), which serves as an active NH_4^+ donor, and asparagine (Asn), which serves as a transport/storage compound (Asn) also synthesised by using NH_4^+ donated from the Glu and Gln. For nearly all cellular functions, proteins especially enzymes are necessary. Therefore, from a metabolic perspective, it is crucial to sustain a proper balance or ratio of C and N nutrients. Sensing and communicating C/N balance across long distances is another aspect of precise coordination. Assimilation of carbon and carbon metabolism occurs predominantly in the leaf, while uptake of NO_3^- and/ or NH_4^+ is usually by the root and then they are transported to aerial parts of a plant such as the leaf. Biochemical and physiological studies have concluded that photosynthetic output was adversely affected when plants are facing nitrogen deficiency (Corozzi and Bush, 2001; Corozzi and Zhou, 2001). In order to balance the coordination between N availability and photosynthesis, plants have evolved a system that senses the amount of N present in the soil environment and root system and coordinates it with the leaf sensory machinery where the photosynthesis is carried out.

Plants, which are sessile organisms, have developed strategies to adjust to changes in their environment, including variations in nutrients and light availability. Reprogramming of the metabolism and allocation of resources are two examples of such adaptations (Shaw and Cheung, 2018). In a variable environment, coordination of root inorganic nitrogen uptake with shoot photosynthetic carbon fixation enhances plant efficiency. Plant roots and shoots have different developmental paths but their biology is closely coordinated to maximise the performance of the plant in a variable environment. Atmospheric carbon is fixed by shoots and soil inorganic nitrogen acquired by roots, coordination between these metabolic assimilations is very important (Ho *et al.*, 2009).

Role of HY5 in C/N balance

In an experiment by Chen *et al.*, (2016) with *A. thaliana*, it was found that a mutant specifically disrupted the shoot illumination-promoted root growth contained a new *HY5* loss-of-function allele. Further analysis showed that shoot-illumination-promoted root growth is abolished by the *hy5* null allele. Photomorphogenic bZIP transcription factor HY5 encoded by the *HY5*.COP1 ubiquitin ligase regulates HY5 and, in the dark COP1 targets HY5 for proteolytic degradation. Findings revealed that loss of function in *COP1-4* (*cop1-4* mutants) exhibits shoot-illumination promotion of root growth when the seedlings are grown in dark. These results suggested that the promotion of root growth induced by shoot illumination involves mediation of HY5. Uptake of NO_3^- by the root is promoted when the shoots are illuminated, but this was absent when only the roots are illuminated. The promotion of NO_3^- uptake by root when shoots are illuminated is mainly dependent on *NRT2.1*. In *hy5* mutants, shoot-illumination promotion of root NO_3^- uptake is reduced drastically. Experiment using hypocotyl graft chimeras reveal that root growth and NO_3^- uptake is promoted by illumination of the shoot and is mediated by HY5 which is moved from scion to root. All these suggest that shoot-derived signal regulates root growth and NO_3^- uptake is HY5 dependent.

In response to environmental light circumstances, mobile HY5 is involved in regulating the homeostasis of C and N metabolism. Studies demonstrated that HY5 regulates the expression of chlorophyll biosynthesis genes and the expression of photosynthesis-related genes thereby modulating photosynthetic capacity. For example, HY5 promotes PHYTOENE SYNTHASE (*PSY*) expression by directly binding to the *PSY* promoter. Fixed C is mainly transported through the phloem in the form of sucrose to sink tissues (e.g., roots) and the Trehalose-6-phosphate (T6P), a precursor of trehalose, acts as a proxy for photosynthetic carbohydrate status. Both sucrose metabolism and shoot-root transport of sucrose are affected by HY5 by promoting the expression levels of *TPS1*, a gene encoding trehalose-6-phosphate synthase, and *SWEET11* and *SWEET12* genes encoding sucrose efflux transporters. Experiments confirmed in vivo binding of HY5 to the *TPS1*, *SWEET11*, and *SWEET12* promoters. Thus, HY5 regulates the initial C fixation and movement of fixed C into phloem cells for shoot-to-root translocation. Both sucrose and glucose enhance the shoot-illumination promotion of root *NRT2.1* expression and NO_3^- uptake. These effects are downregulated significantly in *hy5*. Whatever the mechanism,



sucrose induction of *NRT2.1* expression and NO₃⁻ uptake is dependent upon HY5. Taken together, these results indicate that HY5 responds to sugar signals in the regulation of *NRT2.1*-dependent NO₃⁻ uptake, thus contributing to the coordinated homeostatic balancing of C and N metabolism.

Conclusion

HY5 is a shoot-root mobile signal that mediates light-regulated coupling of C assimilation and shoot growth with N uptake and root growth. This coupling is accomplished via HY5 regulation of C fixation in the shoot and via sucrose-enhanced promotion of HY5-dependent N uptake in the root. In consequence, HY5 mediates homeostatic regulation of whole-plant C versus whole-plant N status.

References

- Chen, X., Yao, Q., Gao, X., Jiang, C., Harberd, N. P., & Fu, X. (2016). Shoot-to-root mobile transcription factor HY5 coordinates plant carbon and nitrogen acquisition. *Current Biology*, 26(5), 640-646.
- Coruzzi, G. M., & Zhou, L. (2001). Carbon and nitrogen sensing and signaling in plants: emerging 'matrix effects'. *Current opinion in plant biology*, 4(3), 247-253.
- Coruzzi, G., & Bush, D. R. (2001). Nitrogen and carbon nutrient and metabolite signaling in plants. *Plant physiology*, 125(1), 61-64.
- Ho, C. H., Lin, S. H., Hu, H. C., & Tsay, Y. F. (2009). CHL1 functions as a nitrate sensor in plants. *Cell*, 138(6), 1184-1194.
- Shaw, R., & Cheung, C. M. (2018). A dynamic multi-tissue flux balance model captures carbon and nitrogen metabolism and optimal resource partitioning during Arabidopsis growth. *Frontiers in plant science*, 9, 884.
- Vidal, E. A., & Gutierrez, R. A. (2008). A systems view of nitrogen nutrient and metabolite responses in Arabidopsis. *Current opinion in plant biology*, 11(5), 521-529.