Journal of
Plant Biochemistry & Physiology
ISSN: 2329-9029



Editorial
Open Access

# Follow the Money: A Spotlight on the Carbon and Nitrogen Control of Plant Growth and Development

**Nijat Imin***

*Plant Science Division, Research School of Biology, College of Medicine, Biology and Environment, The Australian National University, Canberra ACT 0200, Australia*

Carbon (C) and Nitrogen (N) are two essential macronutrients that are fundamental for the survival of all organisms including plant growth and development. Shoots and leaves fix C through photosynthesis into carbohydrate (sugars and starches), the primary source of energy that is required for growth. By contrast, nitrogen along with water and other nutrients (phosphorous, potassium, secondary- and micro-nutrients) is taken up from the soil by roots and is a major nutrient for growth as it is needed to synthesise amino acids, which are the building elements of protein, nucleotides, chlorophyll, and numerous other metabolites and cellular components. At the global scale, the interactions between the N and C cycle are key players in Earth's climate and other planetary processes [1]. Many decades of research has shed light into the various aspects of how C and N availability and allocation coordinates growth and plant response to environment (biotic and abiotic stresses) and it is one on the major questions in many areas of plant biology, from general physiology to cell biology, from molecular biology to ecology and stress biology. Therefore, not only to understand plant growth and development but also how plants response to environment, it is important to "Follow C and N" and this core theme is well-deserved to be in the spotlight.

C is acquired through photosynthesis and carbon assimilation principally in leaf mesophyll cells. For distribution to distal tissues, fixed carbon must move out of the photosynthetic cells and into the phloem. To distribute resources such as C and N, plants have a vasculature composed of phloem and xylem. The xylem conducts water, N and minerals from the roots up to the shoots. The distribution of carbon- and nitrogen-containing compounds occurs by their loading into the phloem and transporting them from the photosynthetic "sources" (predominantly leaves) to the heterotrophic "sinks" (meristems, roots, flowers, and seeds) where these compounds is unloaded [2]. This process is called carbon partitioning in which assimilates are distributed throughout the plant body from photosynthetic tissues. Sucrose is synthesised in leaf mesophyll cells and diffuses cell-to-cell through plasmodesmata toward the phloem which is the specialised tissue involved in long-distance sucrose transport via sucrose- and monosaccharide- transporters [2-5]. However, it has also been shown that down-regulating a sucrose transporter gene does not inhibit phloem loading [6]. Prior to sucrose be transported in the phloem, it must effuse from inside the cell into the cell wall proactively and recently it was shown that sucrose effluxers play a key role in this process [7]. Several other transporters/channels of sucrose, K+ and water have been characterised for their contribution to the sucrose transport in the phloem [2-5]. Apart from transporters, there are other proteins are also involved in phloem loading and carbohydrate partitioning [8,9]. Besides C fixation through photosynthesis, the proper and efficient allocation of carbohydrates is also fundamental for plant growth. On the other hand, N availability is a major limiting factor for plant growth, development and productivity. Biologically available N forms (e.g. nitrate or ammonia) are in short supply in nature as well as in agricultural systems. N removed from the soil in crop products must be replaced to sustain agricultural productivity. N fertilisers (e.g. urea and ammonium nitrate) are the main sources of N applied to crops and represent up to 50% of the operational costs in agriculture [10]. Furthermore, unutilised N (more than half of the applied N) is not used by crops and hence is lost into the soil or is released to the atmosphere as nitrogen gases such as nitrous oxide which is the third contributor to global warming and excess N can cause eutrophication of terrestrial and aquatic systems.

C and N metabolism are intimately linked. N deficiency decreases C assimilation, while C starvation reduces N utilisation in plants. N deficiency therefore affects, to various extents, primary photosynthesis, sugar metabolism and/or carbohydrate partitioning between source and sink tissues [11]. N along with water and other nutrients are principally acquired by roots. C allocation below ground is often greater than that allocated above ground [12]. N metabolism is severely impaired when photosynthesis rate is decreased [13]. On the other hand, photosynthesis rate is significantly reduced when N availability is limited [14]. Therefore, the balance between C and N is critical to ensure optimal nutrient utilisation for growth, development and response to environment (biotic and abiotic stresses) via complex coordinated metabolic responses and signalling pathways. C and N availability and allocation is also a major topic of ecological interest [15].

However, the molecular mechanisms underlying the co-regulation of C and N are not understood. Can a plant sense the C/N ratio (or balance)? If so, what is the molecular mechanism(s) involved in this process? These are some of the key questions still remain elusive. Despite this, it is well accepted that C and N are not only important energy sources and structural components, but also central regulatory molecules controlling gene expression, metabolism, physiology, and growth and development [16-19].

Glucose, sucrose and trehalose have been suggested to act as C signals [20,21]. A glucose-specific sensor HEXOKINASE1 has been identified [22]. Despite a decade-long search, a sucrose-specific sensor remains to be discovered, although sucrose-specific pathways have been demonstrated. Sucrose-specific signalling is difficult to study since sucrose is readily hydrolysed into hexoses, which are powerful signalling molecules as well [23]. Several transcriptional regulators are implicated in coordinating C signalling. Arabidopsis transcription factors bZIP and master clock control CIRCADIAN CLOCK ASSOCIATED1 are well known transducers of sucrose-specific signals [24-26].

***Corresponding author:** Nijat Imin, Plant Science Division, Research School of Biology, College of Medicine, Biology and Environment, The Australian National University, Canberra ACT 0200, Australia, E-mail: nijat.imin@anu.edu.au

**Received** January 04, 2013; **Accepted** January 07, 2013; **Published** January 07, 2013

**Citation:** Imin N (2013) Follow the Money: A Spotlight on the Carbon and Nitrogen Control of Plant Growth and Development. J Plant Biochem Physiol 1: e104. doi:10.4172/jpbp.1000e104

For N signalling, the low-affinity NITRATE TRANSPORTER 1.1 protein is identified as involved in both nitrate perception and transport. Additionally, the high-affinity NITRATE TRANSPORTER 2.1 (NRT2.1) is one of several primary nitrate response genes that show a rapid induction of gene expression in response to nitrate treatments independent of protein synthesis. NRT2.1 represses lateral root initiation in response to nutritional cues by acting either as a nitrate sensor or signal transducer [27]. Similarly, the role of AMMONIUM TRANSPORTER 1.3 in regulating lateral root branching in response to ammonium is independent of ammonium transport, suggesting a signalling role for this transporter [28]. Several regulatory factors involved in N responses have been identified. These include a MADS box transcription factor ARABIDOPSIS NITRATE REGULATED 1 which promotes lateral root development in response to nitrate, a NIN-LIKE PROTEIN 7 which is required for normal nitrate regulation of N-assimilatory genes, members of the LATERAL ORGAN BOUNDARY DOMAIN (LBD37/38/39) which repress anthocyanin biosynthesis and many known N-responsive genes, ELONGATED HYPOCOTYL 5 which positively regulates NITRATE REDUCTASE 2 and negatively regulates NRT1.1 and SQUAMOSA PROMOTER BINDING PROTEIN–LIKE 9 which negatively regulates nitrite and nitrate reductases.

Interestingly, some of the transcription factors such as bZIP and CIRCADIAN CLOCK ASSOCIATED 1 which regulated by C are also known to be regulated by N and may function as integrators of C and N signalling [26,29]. It is also known that root system architecture, which is critical for N uptake and regulated by N, is also regulated by sucrose uptake in the aerial tissues [30]. However, the underlying molecular mechanism(s) for how plant senses the C/N ratio and mediates growth, development and response to environment are remains to be identified.

The world population is estimated to reach nine billion by mid-twenty-first-century (United Nations, http://esa.un.org/unpd/wpp/index.htm). The increased demand for food will impose a substantial strain on agriculture. Urgency is required to develop more sustainable, economically-viable "Second Green Revolution" crops for food production with higher photosynthesis rate and better N use efficiency. To achieve this, it is necessary to understand the molecular mechanisms underlying the coordination between C and N metabolism and regulation. Notably, establishment of a holistic view of how plants control C/N ratio and metabolism coordinately at the whole plant level can't be overlooked.

## Acknowledgments

This work was supported by the ARC grant (DP120101893).

## References

1. Gruber N, Galloway JN (2008) An Earth-system perspective of the global nitrogen cycle. Nature 451: 293-296.
2. Ayre BG (2011) Membrane-transport systems for sucrose in relation to whole-plant carbon partitioning. Mol Plant 4: 377-394.
3. Braun DM, Slewinski TL (2009) Genetic control of carbon partitioning in grasses: roles of sucrose transporters and tie-dyed loci in phloem loading. Plant Physiol 149: 71-81.
4. Lalonde S, Wipf D, Frommer WB (2004) Transport mechanisms for organic forms of carbon and nitrogen between source and sink. Annu Rev Plant Biol 55: 341-372.
5. Schulz A, Beyhl D, Marten I, Wormit A, Neuhaus E, et al. (2011) Proton-driven sucrose symport and antiport are provided by the vacuolar transporters SUC4 and TMT1/2. Plant J 68: 129-136.
6. Zhang C, Turgeon R (2009) Downregulating the sucrose transporter VpSUT1 in Verbascum phoeniceum does not inhibit phloem loading. Proc Natl Acad Sci U S A 106: 18849-18854.
7. Chen LQ, Qu XQ, Hou BH, Sosso D, Osorio S, et al. (2012) Sucrose efflux mediated by SWEET proteins as a key step for phloem transport. Science 335: 207-211.
8. Ma Y, Slewinski TL, Baker RF, Braun DM (2009) Tie-dyed1 encodes a novel, phloem-expressed transmembrane protein that functions in carbohydrate partitioning. Plant Physiol 149: 181-194.
9. Slewinski TL, Baker RF, Stubert A, Braun DM (2012) Tie-dyed2 encodes a callose synthase that functions in vein development and affects symplastic trafficking within the phloem of maize leaves. Plant Physiol 160: 1540-1550.
10. Hirel B, Tétu T, Lea PJ, Dubois F (2011) Improving Nitrogen Use Efficiency in Crops for Sustainable Agriculture. Sustainability 3: 1452-1485.
11. Scheible WR, Morcuende R, Czechowski T, Fritz C, Osuna D, et al. (2004) Genome-wide reprogramming of primary and secondary metabolism, protein synthesis, cellular growth processes, and the regulatory infrastructure of Arabidopsis in response to nitrogen. Plant Physiol 136: 2483-2499.
12. Jackson RB, Mooney HA, Schulze ED (1997) A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci U S A 94: 7362-7366.
13. Joy KW (1988) Ammonia, glutamine, and asparagine: a carbon-nitrogen interface. Can J Bot 66: 2103-2109.
14. Longstreth DJ, Nobel PS (1980) Nutrient Influences on Leaf Photosynthesis: EFFECTS OF NITROGEN, PHOSPHORUS, AND POTASSIUM FOR GOSSYPIUM HIRSUTUM L. Plant Physiol 65: 541-543.
15. Franklin O, Johansson J, Dewar RC, Dieckmann U, McMurtrie RE, et al. (2012) Modeling carbon allocation in trees: a search for principles. Tree Physiol 32: 648-666.
16. Gutierrez RA (2012) Systems biology for enhanced plant nitrogen nutrition. Science 336: 1673-1675.
17. Jang JC, Leon P, Zhou L, Sheen J (1997) Hexokinase as a sugar sensor in higher plants. Plant Cell 9: 5-19.
18. Krouk G, Ruffel S, Gutierrez RA, Gojon A, Crawford NM, et al. (2011) A framework integrating plant growth with hormones and nutrients. Trends Plant Sci 16: 178-182.
19. Vidal EA, Gutierrez RA (2008) A systems view of nitrogen nutrient and metabolite responses in Arabidopsis. Curr Opin Plant Biol 11: 521-529.
20. Iturriaga G, Suarez R, Nova-Franco B (2009) Trehalose metabolism: from osmoprotection to signaling. Int J Mol Sci 10: 3793-3810.
21. Rolland F, Baena-Gonzalez E, Sheen J (2006) Sugar sensing and signaling in plants: conserved and novel mechanisms. Annu Rev Plant Biol 57: 675-709.
22. Gibson SI (2005) Control of plant development and gene expression by sugar signaling. Curr Opin Plant Biol 8: 93-102.
23. Wind J, Smeekens S, Hanson J (2010) Sucrose: metabolite and signaling molecule. Phytochemistry 71: 1610-1614.
24. Price J, Laxmi A, St Martin SK, Jang JC (2004) Global transcription profiling reveals multiple sugar signal transduction mechanisms in Arabidopsis. Plant Cell 16: 2128-2150.
25. Weltmeier F, Rahmani F, Ehlert A, Dietrich K, Schutze K, et al. (2009) Expression patterns within the Arabidopsis C/S1 bZIP transcription factor network: availability of heterodimerization partners controls gene expression during stress response and development. Plant Mol Biol 69: 107-119.
26. Gutierrez RA, Stokes TL, Thum K, Xu X, Obertello M, et al. (2008) Systems approach identifies an organic nitrogen-responsive gene network that is regulated by the master clock control gene CCA1. Proc Natl Acad Sci U S A 105: 4939-4944.
27. Little DY, Rao H, Oliva S, Daniel-Vedele F, Krapp A, et al. (2005) The putative high-affinity nitrate transporter NRT2.1 represses lateral root initiation in response to nutritional cues. Proc Natl Acad Sci U S A 102: 13693-13698.
28. Lima JE, Kojima S, Takahashi H, von Wiren N (2010) Ammonium triggers lateral root branching in Arabidopsis in an AMMONIUM TRANSPORTER1;3-dependent manner. Plant Cell 22: 3621-3633.
29. Sang Y, Sun W, Yang Z (2012) Signaling mechanisms integrating carbon and nitrogen utilization in plants. Front Biol 7: 548-556.
30. Macgregor DR, Deak KI, Ingram PA, Malamy JE (2008) Root system architecture in Arabidopsis grown in culture is regulated by sucrose uptake in the aerial tissues. Plant Cell 20: 2643-2660.