Transcriptomic regulatory network underlying morphological and physiological acclimation to nitrogen starvation and excess in poplar roots and leaves

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Nitrogen (N) is an essential macronutrient that plays a pivotal role in plant growth and development. It is a component of many biomolecules, including amino acids, chlorophylls and nucleic acids. High N availability is a prerequisite for plants to achieve high productivity. This is particularly important for fast growing woody plants, such as Populus species, which often grow on N poor soils (Rennenberg et al. 2010). For instance, the aboveground biomass production of eastern cottonwood (Populus deltoides Bartr.) in the southeastern USA was significantly elevated when N fertilizers were applied (Coyle et al. 2013). During the last few decades, with the development of short-rotation forest plantations, N fertilizers have often been applied to the soil to achieve higher productivity (Coleman et al. 2006, Paris et al. 2011). However, excess N may not only increase the costs of growers but may also lead to serious environmental pollution. Nitrogen availability markedly affects the morphological and physiological characteristics of woody plants (Rennenberg et al. 2009, 2010, Zhao et al. 2011, Zhang et al. 2014). Nitrogen fertilization stimulates photosynthetic rates and leaf area of most woody plants, while low N availability has the opposite effects (Hyvönen et al. 2007, Chen et al. 2011, Li et al. 2011, Luo et al. 2013a). In comparison with an appropriate N supply, a high N supply shifts allocation away from roots, whereas a low N level increases root length and biomass (Ingestad and Ågren 1988, Li et al. 2012, Luo et al. 2013a).

Although the morphological and physiological responses of trees to changes in N availability have been studied intensively, the molecular regulatory mechanisms underlying the morphological and physiological acclimation to different N levels remain largely unknown. Understanding these mechanisms is of great importance not only for the scientific community of tree biology but also for practical tree breeders, as knowledge of trees’ responses to N availability enables breeding trees with a high N use efficiency. To shed light on this knowledge gap, Luo et al. (2015) in this issue employed a comprehensive approach to dissect the transcriptomic regulatory network underpinning morphological and physiological acclimation to N starvation and excess in poplar roots and leaves.

In the study reported by Luo et al. (2015), the authors treated cuttings of Populus simonii Carr. with contrasting levels of N supplies, i.e., 0 (N starvation), 2 (control) or 10 (N excess) mM NH\textsubscript{4}\textsuperscript{+}, NO\textsubscript{3}\textsuperscript{−}, amino acids, total N and phytohormones, as well as mineral nutrients, and related those results to transcriptomic changes. The comprehensive approach used in this study is unique. The combined utilization of information on morphological parameters, biochemical and metabolic measurements, and genome-wide RNA sequencing analysis provides an integrative approach to dissecting the complex regulatory mechanisms of trees exposed to changing N availability. Although a few previous reports have shown the transcriptional responses of woody plants to N fertilization or low N availability (Cooke et al. 2003), the links between differentially expressed genes and morphological and/or...
physiological changes have usually been weak or even lacking (Pitre et al. 2010, 2014, Plavcová et al. 2013). Using an integrative approach, Luo et al. (2015) provide holistic insights into the transcriptomic regulatory network underpinning morphological and physiological acclimation to altered N levels in roots and leaves of poplars.

One of the novel findings presented by Luo et al. (2015) is that poplar roots and leaves not only display tissue-specific transcriptomic responses to N starvation and excess, but both root and leaf tissues also exhibit common molecular responses to changing N levels. In roots, gene ontology (GO) terms were enriched in ion transport and responses to auxin stimulus, whereas the GO term for responses to abscisic acid (ABA) stimulus was overrepresented in leaves under N starvation and excess. NH$_4^+$ and NO$_3^-$ are major inorganic N ions, which can be absorbed by the roots of trees (Luo et al. 2013b). Due to the fluctuating levels of these nutritional ions in soil, roots have to differentially regulate gene expression to keep pace with resource changes. Moreover, root morphology is sensitive to N availability, and root architecture can be rapidly modified with the mediation of phytohormones, such as ABA and auxin, to acclimate to external N levels (Kiba et al. 2011). In contrast to roots, leaves are the primary producers of photosynthates, which provide the precursors for carbon (C) skeletons to biosynthesize various metabolites. Carbon dioxide assimilation in leaves is controlled by means of ABA-mediated stomatal movement and leaf N availability, which helps to maintain the homeostasis of N and C at the whole-plant level. The presence of root- and leaf-specific GO terms in N-treated poplars discovered by Luo et al. (2015) suggests that poplar roots and leaves, respectively, play specific roles in resource acquisition in response to altered N availability. In addition to the specific GO terms in root and leaf tissues, common GO terms for development, N metabolism, stress response and hormone stimulus were also found in root and leaf tissues of poplars treated with N starvation or excess, suggesting that these biological processes are essential for both tissues in response to altered N supply. The finding of specific and common GO terms in root and leaf tissues of poplars treated with N starvation and excess is of particular significance for using candidate genes as part of the tool kit in tree breeding or screening of natural populations for the selection of individuals with improved N use efficiency.

The second important finding in the study presented by Luo et al. (2015) is that ~30–40% of the differentially expressed genes were coexpressed and formed a transcriptomic regulatory network in the roots and leaves of poplars treated with N starvation or excess. Although a number of transcriptional profiles have been investigated in trees treated with low or high N supply levels (Cooke et al. 2003, Pitre et al. 2010, Plavcová et al. 2013), to date, only two studies on Populus have reported coexpressed regulatory networks of differentially expressed genes, namely an experiment on fine roots exposed to low N (Wei et al. 2013) and an experiment on stem elongation in Populus treated with N fertilization (Euring et al. 2014). The coexpressed networks identified by Luo et al. (2015) suggest that poplars coordinate various molecular regulatory pathways to work together in roots and leaves to allow acclimation to N starvation or excess. Importantly, Luo et al. (2015) further identified highly connected hub genes, which may be responsible for essential biological processes in poplar roots and leaves in acclimation to N starvation or excess. For instance, transcript levels of TIP2;3, involved in NH$_4^+/NH_4^+$ transport, and NRT 1;5, participating in NO$_3^-$ translocation, were repressed in N-starved roots of poplars. In poplar roots treated with N excess, two hub genes, i.e., ABCB4 encoding an auxin efflux transmembrane transporter (Kubeš et al. 2012) and PDR9 regulating auxin distribution and homeostasis (Ruzicka et al. 2010), decreased their transcript levels. Notably, the differential expression of these hub genes is in agreement with the changes in NH$_4^+$, NO$_3^-$ and auxin levels in poplar roots exposed to altered N availability. Thus, the identified hub genes are probably key players in poplars in acclimation to changing N availability. From this point of view, the findings by Luo et al. (2015) are of particular significance when further elucidating the function and characteristics of hub genes for potential applications, including transgenic trees with more efficient N utilization characteristics.

In trees and other plants, an obvious stress response to adverse environmental conditions is changes in phytohormone homeostasis. Although phytohormones, such as ABA and indole-3-acetic acid (IAA), can combine with N signals to modulate root growth and development in herbaceous plants (Kiba et al. 2011, Vidal et al. 2013), no information is currently available on the involvement of phytohormones in mediating the responses of trees to altered N availability. However, Luo et al. (2015) found that poplars alter transcript levels of genes involved in phytohormone metabolism and signaling pathways, and they change their hormone status in both roots and leaves when acclimatizing to N starvation and excess. In Arabidopsis, ABA represses lateral root growth in the presence of a high nitrate supply (Signora et al. 2001). In N-starved roots of P. simonii, the increased transcript level of the Arabidopsis homolog, the ABA-degraded CYP707A1 gene (Okamoto et al. 2009), was in agreement with the reduced ABA level, and the decreased mRNA level of carotenoid cleavage dioxygenase 7, involved in ABA metabolism (Booker et al. 2004), probably contributed to the elevated ABA level in roots with high N fertilization. Such changes in ABA levels can affect root characteristics of P. simonii under N starvation or excess. In Arabidopsis thaliana and Medicago truncatula Gaertn., ABA is involved in modulating lateral root growth and development under altered N supply levels (Zhang et al. 2007, Yendrek et al. 2010). Additionally, IAA plays a role in regulating the lateral root initiation and development of herbaceous plants in response to changes
in N supply levels (Fukai and Tasaka 2009, Ma et al. 2014). In the study by Luo et al. (2015), the reduced IAA levels in P. simonii roots exposed to N excess suggest that IAA metabolism is also associated with N physiology in woody plants. Based on the morphological changes of roots, alterations in phytohormone levels and the presence of differentially expressed genes involved in stress responses and root development, Luo et al. (2015) suggest that poplars employ stress pathways (particularly phytohormone metabolism and signaling pathways) to regulate the growth of roots and leaves in response to N starvation and excess. This finding is novel because it provides new insights into phytohormone-mediated growth responses of trees when acclimatizing to changes in N availability.

The study by Luo et al. (2015) provides a better and more comprehensive understanding of the mechanisms of transcriptomic regulatory mechanisms underlying morphological and physiological acclimation to N starvation and excess in roots and leaves of poplars. Undoubtedly, based on the knowledge gained from the investigation by Luo et al. (2015), future studies will be able to elucidate further the functions of various hub genes, and breeders will have a chance to develop trees with improved N use efficiency.

References


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