ON THE NATURE OF THINGS: ESSAYS
New Ideas and Directions in Botany

Crops for the future: on the way to reduce nitrogen pollution

Vladislav Gramma1, Kübra Kontbay1, and Vanessa Wahl1,2

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1 Department of Metabolic Networks, Max Planck Institute of Molecular Plant Physiology, 14476 Potsdam, Germany
2 Author for correspondence (e-mail: vanessa.wahl@mpimp-golm.mpg.de)

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Reactive nitrogen (N\textsubscript{r}) is a limiting factor for plant growth in agriculture. Traditionally, manure and cover crops are used as an N\textsubscript{r} source to support crop growth. Introduction of the Haber-Bosch process at the beginning of the last century greatly affected agriculture, offering relatively cheap access to N\textsubscript{r} from N\textsubscript{2}, and its usage in mass-produced N fertilizers considerably increased crop production. Yet, crop plants take up less than 50% of this applied N\textsubscript{r} (Cameron et al., 2013), and runoff nitrate, as the end product of nitrification in the soil, has become a key problem in many agricultural areas leading to contamination of groundwater. In the past decades, nitrate levels in groundwater often even exceeded the upper safe limit, which is currently set to 50 mg/L for short-term and 3 mg/L for long-term exposure (Ward et al., 2018). In addition, fertilizer surplus leads to increased greenhouse gas emission in form of ammonia and nitrogen oxides, contributing to climate change (Cameron et al., 2013; Erismann et al., 2013). Together, N fertilizer use has direct consequences on environmental and human health and the downsides are expected to soon outweigh the benefits of food production (Erismann et al., 2013). Hence, finding a more sustainable way to grow healthy plants that is compatible with high yield and good quality food production, urgently needs more attention. A possible approach is generating plants that are adapted to soils with minimal fertilization.

N FERTILIZATION AND PLANTS: FROM DESCRIBING TO UNDERSTANDING

Modern agriculture utilizes different mineral sources of N\textsubscript{r}, such as anhydrous ammonia, ammonium sulfate, ammonium nitrate and urea. All forms of N fertilizers are eventually transformed into nitrate at a high rate by nitrifying bacteria. Field experiments have shown that moderate N fertilization increases plant biomass (e.g., Lea and Morot-Gaudry, 2001). However, overapplication of N fertilizers can also cause a high N\textsubscript{r} stress (Fig. 1) due to its effect on soil pH and salinity resulting in the well-known, so-called fertilizer burn. Fertilization with an excessive amount of ammonia and urea also causes toxicity to plants and eventually negatively affects their growth. Many studies point at an inadequacy of standard fertilization procedures commonly used (e.g., Albornoz, 2016). Often, an increase of N\textsubscript{r}, especially when applied at the wrong developmental stage negatively affects both yield and quality of agricultural products, such as their nutritional value or storage properties (Albornoz, 2016). How these traits are regulated at a molecular level is still not fully understood.

As the major source of N\textsubscript{r} in the soil, nitrate is taken up and distributed throughout the plant by a large number of different nitrate transporters (Krapp, 2015). Assimilation of nitrate into amino acids within a plant is highly regulated at a stage-, tissue- and even cell-specific level (Krapp, 2015; Olas and Wahl, 2019). Adding to this complexity, nitrate also acts as a signaling molecule regulating the expression of genes orchestrating N metabolism and transport, and developmental programs (Krapp, 2015; Fredes et al., 2019). N\textsubscript{r} availability affects crop yield not only by regulating vegetative biomass accumulation, but also influencing the onset of developmental programs inducing secondary growth, storage organ formation, and reproductive growth such as flowering and tuber induction (van Dingenen et al., 2019; Fernie et al., 2020). Despite positive effects on growth, a higher level of N\textsubscript{r} can also reduce yield by shifting the
anthropogenic Nr pollution, research should now focus on developing detrimental consequences for the environment. Toward decreasing the adapts to Nr levels within a species-specific range, beyond which plant between positive and negative effects should be considered. Each crop causing “high Nr stress” . Most importantly, surplus Nr has significant even exceeding the upper limit of the “crop-specific adaptation” range, “crops for the future” with better adaptation to lower levels of Nr, through increased NUE and Nr responsiveness.

Crops for the future

\[ \text{NUE and Nr responsiveness} \]

- unravel molecular mechanisms
- targeted breeding programs
- genetic modifications
- wild-species resources

\[ \text{LOW Nr} \rightarrow \text{Crop-specific ADAPTATION} \rightarrow \text{HIGH Nr} \]

FIGURE 1. Despite an obvious positive correlation between the level of Nr in the soil and plant growth, when applying Nr fertilizers, balancing between positive and negative effects should be considered. Each crop adapts to Nr levels within a species-specific range, beyond which plant development is hampered due to Nr stress. Moderate soil fertilization avoids “low Nr stress”, increases crop yield, while achieving high quality with minimal environmental impact. Aiming at high yield, current intensive fertilization practices operate with an excess of Nr, sometimes even exceeding the upper limit of the "crop-specific adaptation" range, causing “high Nr stress”. Most importantly, surplus Nr has significant detrimental consequences for the environment. Toward decreasing the anthropogenic Nr pollution, research should now focus on developing “crops for the future” with better adaptation to lower levels of Nr, through increased NUE and Nr responsiveness.

The N trade-off

\[ \text{N availability} \]

\[ \text{LOW Stress} \rightarrow \text{Crop-specific ADAPTATION} \rightarrow \text{HIGH Stress} \]

FUTURE DIRECTIONS OF N RESEARCH

Currently, many breeding programs aim at developing crop varieties with high yield on soil with limited Nr fertilization by focusing on increasing plant nitrogen use efficiency (NUE) via improving Nr uptake, its transport within a plant, and Nr metabolism (Fernie et al., 2020). Knowledge of genes regulating these processes allows accelerating the breeding by using more targeted approaches, e.g., crossing varieties with favorable versions of particular genes associated with NUE. Our current understanding of NUE-associated gene functions, however, mainly originates from research in model plants. Studies of genetic modification of the homologous genes in crops have rarely resulted in improved NUE (Fernie et al., 2020), highlighting the need to acquire a deeper understanding of species-specific N signaling mechanisms, regulating NUE and developmental processes directly, and the importance of standardized growth regimes and the fundamental research basis for each crop species on the way to the development of future crops (Seibert et al., 2019) (Fig. 1).

Unlike modern crops, some ancestral wild species and old varieties were found to better adapt to limited Nr conditions due to their more efficient usage of the available Nr (Hawkesford, 2017; van Dingenen et al., 2019). Many traits valuable for plant adaptation to limited Nr have likely been lost during domestication of ancestral crop species because the artificial selection of the modern high yield crops has been performed on high Nr soils where NUE and the tolerance to Nr limitation were not considered. Using the approach described by Swarbreck and colleagues (2019) to investigate varieties based on Nr responsiveness in addition to NUE as traits will likely increase our basic understanding of the rich source of adaptation strategies of crop wild relatives and might identify target genes for genetic modification in modern crops. We consider this strategy very promising in the endeavor to generate “crops for the future” with minimal Nr requirement (Fig. 1).

The demand for the development of sustainable agronomic practices also requires the more efficient use of Nr fertilizers. Modern knowledge-based methods of Nr fertilization have a potential to reduce environmental pollution. Among those are more frequent split application of fertilizers at optimal doses necessary for plant growth, use of new fertilizer forms with a slow Nr release, soil treatment with nitrification inhibitors that significantly reduce Nr losses and increases crop yield (Xia et al., 2017). Therefore, modern Nr fertilizing management techniques should become mandatory to minimize Nr losses.

Lastly, future food production must take into consideration the detrimental consequences of environmental pollution. As such the global Nr challenges are manifold, including the removal of damage already done. We also strongly believe that it is also important to
improve relevant communication between different research fields and dissemination of new achievements to farmers and the public. Attempts have been made to reduce agricultural N pollution by setting strict restrictions and penalties for farmers. Although this policy has been effective in some countries (Swarbreck et al., 2019), farmers often oppose these restrictions, due to the common belief that decreasing fertilizer application reduces profit. As opposed to a penalty-driven system, better training methods for farmers should be developed to foster implementation of advanced crop management strategies in the field (e.g., Eanes et al., 2017).

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LITERATURE CITED

Albornoz, F. 2016. Crop responses to nitrogen overfertilization: a review. Scientia Horticulturae 205: 79–83.

Cameron, K. C., H. J. Di, and J. L. Moir. 2013. Nitrogen losses from the soil/plant system: a review. Annals of Applied Biology 162: 145–173.

Eanes, F. R., A. S. Singh, B. R. Bula, P. Ranjan, L. S. Prokopy, M. Fales, B. Wickerham, and P. J. Doran. 2017. Midwestern US farmers perceive crop advisers as conduits of information on agricultural conservation practices. Environmental Management 60: 974–988.

Erisman, J. W., J. N. Galloway, S. Seitzinger, A. Bleeker, N. B. Dise, A. M. Petrescu, A. M. Leach, and W. de Vries. 2013. Consequences of human modification of the global nitrogen cycle. Philosophical Transactions of the Royal Society, B, Biological Sciences 368: 20130116.

Fernie, A. R., C. W. B. Bachem, Y. Helariutta, H. E. Neuhaus, S. Prat, Y. L. Ruan, M. Stitt, et al. 2020. Synchronization of developmental, molecular and metabolic aspects of source–sink interactions. Nature Plants 6: 55–66.

Fredes, I., S. Moreno, F. P. Diaz, and R. A. Gutierrez. 2019. Nitrate signaling and the control of Arabidopsis growth and development. Current Opinion in Plant Biology 47: 112–118.

Hawkesford, M. J. 2017. Genetic variation in traits for nitrogen use efficiency in wheat. Journal of Experimental Botany 68: 2627–2632.

Krapp, A. 2015. Plant nitrogen assimilation and its regulation: a complex puzzle with missing pieces. Current Opinion in Plant Biology 25: 115–122.

Lea, P. J., and J. F. Morot-Gaudry. 2001. Plant nitrogen. Springer-Verlag, Berlin, Germany.

Melino, V. J., G. Fiene, A. Enju, J. Cai, P. Buchner, and S. Heuer. 2015. Genetic diversity for root plasticity and nitrogen uptake in wheat seedlings. Functional Plant Biology 42: 942–956.

Olas, J. J., J. Van Dingenen, C. Abel, M. A. Dziakol, R. Feil, A. Krapp, A. Schlereth, and V. Wahl. 2019. Nitrate acts at the Arabidopsis thaliana shoot apical meristem to regulate flowering time. New Phytologist 223: 814–827.

Olas, J. J., and V. Wahl. 2019. Tissue-specific NIA1 and NIA2 expression in Arabidopsis thaliana. Plant Signaling & Behavior 14: 1656035.

Seibert, T., C. Abel, and V. Wahl. 2019. Flowering time and the identification of floral marker genes in S. tuberosum ssp. andigena. Journal of Experimental Botany 71: 986–996.

Srikanth, A., and M. Schmid. 2011. Regulation of flowering time: all roads lead to Rome. Cellular and Molecular Life Sciences 68: 2013–2037.

Swarbreck, S. M., M. Wang, Y. Wang, D. Kindred, R. Sylvester-Bradley, W. Shi, S. Varinderpal, et al. 2019. A roadmap for lowering crop nitrogen requirement. Trends in Plant Science 24: 892–904.

Teng, Y., Y. Liang, M. Wang, H. Mai, and L. Ke. 2019. Nitrate Transporter 1.1 is involved in regulating flowering time via transcriptional regulation of FLOWERING LOCUS C in Arabidopsis thaliana. Plant Science 284: 30–36.

van Dingenen, J., K. Hanzalova, M. Abd Allah Salem, C. Abel, T. Seibert, P. Giavalisco, and V. Wahl. 2019. Limited nitrogen availability has cultivar-dependent effects on potato tuber yield and tuber quality traits. Food Chemistry 288: 170–177.

Wahl, V., J. Ponnu, A. Schlereth, S. Arrivault, T. Langenecker, A. Franke, R. Feil, et al. 2013. Regulation of flowering by trehalose-6-phosphate signaling in Arabidopsis thaliana. Science 339: 704–707.

Ward, M. H., R. R. Jones, J. D. Brender, T. M. de Kok, P. J. Weyer, B. T. Nolan, C. M. Villanueva, and S. G. van Broda. 2018. Drinking water nitrate and human health: an updated review. International Journal of Environmental Research and Public Health 15: 1557.

Xia, L., S. K. Lam, D. Chen, J. Wang, Q. Tang, and X. Yan. 2017. Can knowledge-based N management produce more staple grain with lower greenhouse gas emission and reactive nitrogen pollution? A meta-analysis. Global Change Biology 23: 1917–1925.