



OPEN ACCESS

EDITED AND REVIEWED BY
Anna N Stepanova,
North Carolina State University,
United States

*CORRESPONDENCE

María José García
✉ b92gadem@uco.es
Francisco Javier Romera
✉ ag1roruf@uco.es
Wenna Zhang
✉ wennafhxy@163.com
Rafael Pérez-Vicente
✉ bv1pevir@uco.es

RECEIVED 10 May 2023
ACCEPTED 01 June 2023
PUBLISHED 13 June 2023

CITATION

García MJ, Romera FJ, Zhang W and Pérez-Vicente R (2023) Editorial: Role of shoot-derived signals in root responses to environmental changes.
Front. Plant Sci. 14:1220592.
doi: 10.3389/fpls.2023.1220592

COPYRIGHT

© 2023 García, Romera, Zhang and Pérez-Vicente. This is an open-access article distributed under the terms of the [Creative Commons Attribution License \(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

Editorial: Role of shoot-derived signals in root responses to environmental changes

María José García^{1*}, Francisco Javier Romera^{1*}, Wenna Zhang^{2*} and Rafael Pérez-Vicente^{3*}

¹Department of Agronomy (DAUCO-María de Maeztu Unit of Excellence), Edificio Celestino Mutis (C-4), Universidad de Córdoba, Córdoba, Spain, ²Beijing Key Laboratory of Growth and Developmental Regulation for Protected Vegetable Crops, College of Horticulture, China Agricultural University, Beijing, China, ³Department of Botany, Ecology and Plant Physiology, Edificio Celestino Mutis (C-4), Universidad de Córdoba, Córdoba, Spain

KEYWORDS

long distance signals, MicroRNAs, hormones, phloem peptides, shoot-root communication, environmental changes

Editorial on the Research Topic

Role of shoot-derived signals in root responses to environmental changes

Shoot-root communication in plants is essential for the correct integration of responses to environmental changes. As sessile organisms, plants are continuously subjected to changing environmental conditions that in most cases constitute a form of stress. Plants, then must be able to manage the distinct signals perceived by the different organs and produce an integrated response. In this important task, root- and shoot-derived signals play a key role. Shoots and roots deliver messages to each other to induce systemic responses. Shoot growth is modulated by root-derived signals, while nutrient uptake activity in the root is regulated by shoot-derived signals (Notaguchi and Okamoto, 2015; Ko and Helariutta, 2017).

In recent years, several molecules have been identified as systemic signals such as RNAs and microRNAs (Aung et al., 2006; Chiou, 2007; Lin et al., 2008; Buhtz et al., 2010; Liu et al., 2023), small peptides (Koen et al., 2012; Shanmugam et al., 2012; Shanmugam et al., 2015; Grillet et al., 2018; Hirayama et al., 2018; Ota et al., 2020; Kobayashi et al., 2021; Shee et al., 2022; Tabata, 2023), and phytohormones (Kohlen et al., 2011; Borghi et al., 2016; Ko and Helariutta, 2017; Li et al., 2021) that play an essential role in shoot-root communication.

MicroRNAs are 20- to 24-nucleotide RNAs that regulate eukaryotic gene expression posttranscriptionally and transcriptionally as well (by mediating gene silencing) (Brodersen et al., 2008). The knowledge about the implication of shoot-derived RNAs in the regulation of several responses to pathogen and abiotic stresses has been increasing in the last few years and numerous RNAs have been identified. The role of these RNAs in plant development has been thoroughly reviewed very recently by Liu et al. (2023). Thus, we can find shoot-derived RNAs involved in the regulation of root responses to different stresses such as drought [miRNA166 (*O. sativa*) and miRNA390 (*N. tabacum*)]; chilling [*CmoASCL*, *CmoSDC*, *CmoCEK1* (*C. moschata*); *CsaACSL*, *CsaCEK1*, *CsaP450s* (*C.*

sativus); nutritional stresses such as phosphate [miRNA172 (*C. sativus*), miRNA399, miRNA827 and miRNA2111 (*A. thaliana*)] and sulfate [miRNA395 (*A. thaliana*)] deficiencies; and injury response [Prosystemin (PS) (*S. lycopersicum*)] (Liu et al., 2023).

Among the small peptides involved in shoot-root communication are glutathione (GSH; Koen et al., 2012; Shanmugam et al., 2012; Shanmugam et al., 2015) and Iron Man (IMA) peptides (García et al., 2018; Grillet et al., 2018; Hirayama et al., 2018; Gautam et al., 2021; Kobayashi et al., 2021; García et al., 2022; Meng et al., 2022; Peng et al., 2022; Tabata, 2023). Both have been involved in the regulation of the Fe deficiency response. However, while IMA peptides are exclusive for the Fe deficiency response regulatory network, GSH has also been linked to sulfur nutrition (Liu et al., 2009; Koprivova and Kopriva, 2014). Another important peptide in long-distance signaling is the phloem-mobile CEPD-like 2 (CEPDL2) polypeptide which is involved in plant responses to decreased shoot N status. Its expression increases in the leaf vasculature in response to decreased shoot N content and, after translocation to the roots, promotes high-affinity uptake and root-to-shoot transport of nitrate (Ota et al., 2020).

The present Research Topic includes four papers: one review and three original research articles. The review by Bai et al. summarizes the new experimental methods available in the area of synthetic biology to improve the characteristics of natural heavy metal hyperaccumulators and include these characteristics into non-food and high-biomass plant species for phytoremediation of heavy metals. In this review, synthetic biology is presented as an innovative way to build modules with new functions that could be applied to get more efficient natural hyperaccumulator plants in phytoremediation of heavy metals from soil. The authors summarize the new experimental methods for the discovery of synthetic biological elements as well as the knowledge about the construction of circuits and take into account the signaling between the different modules to enable their proper function in the transgenic lines generated.

In Glanz-Idan et al. the importance of a cytokinin (CK) mediated root–shoot communication network is shown in the regulation of leaf senescence. The authors propose that a CK-mediated signal is translocated through the xylem to the leaves where this signal alters CK biosynthesis, resulting in delayed senescence.

García et al. studied the relationship among several regulatory signals related to the Fe deficiency response. IMA peptides were discovered very recently (Grillet et al., 2018; Hirayama et al., 2018) and presented as key regulators of the Fe deficiency response, however their relationship with other known factors that regulate this response, such as ethylene (activating signal) and LODIS (LOng-Distance Iron Signal), a repressive signal (García et al., 2018), was unknown until the publication of this work.

Finally, the third original paper of the present Research Topic by Li et al. attempts to clarify how nitrate inhibits nodule growth

and nodule nitrogenase activity in *Glycine max* (L.) Merr roots. The authors employ a dual-root growth system in which both halves of the root are inoculated with rhizobia and only one side is subjected to nitrate treatment. Results obtained suggest that the mechanism by which the plant systemically suppresses nodulation under nitrogen-replete conditions is the reduction of carbon fluxes from shoots to nodules and roots.

To date, most research about plant responses to biotic or abiotic stresses has been carried out in roots or shoots separately without considering possible systemic signals that connect them. However, integration of all signals received from the environment is essential for the correct development of plants, allowing them to respond coordinately and leading to a fine adjustment of their responses in each environmental condition. The knowledge of the signals involved in shoot-root communication will be essential in the near future to developing new plant varieties that are more efficient and better adapted to the changing environmental conditions.

Author contributions

MG wrote a first draft of the manuscript that was corrected and improved by all the authors. All authors revised the manuscript and approved the submitted version.

Funding

We acknowledge financial support from the Spanish Ministry of Science and Innovation, the Spanish State Research Agency, through the Severo Ochoa and María de Maeztu Program for Centers and Units of Excellence in R&D (Ref. CEX2019-000968-M).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

References

- Aung, K., Lin, S. I., Wu, C. C., Huang, Y. T., Su, C. L., and Chiou, T. J. (2006). *pho2*, a phosphate overaccumulator, is caused by a nonsense mutation in a microRNA399 target gene. *Plant Physiol.* 141, 1000–1011. doi: 10.1104/pp.106.078063
- Borghì, L., Liu, G. W., Emonet, A., Kretschmar, T., and Martinoia, E. (2016). The importance of strigolactone transport regulation for symbiotic signaling and shoot branching. *Planta* 243, 1351–1360. doi: 10.1007/s00425-016-2503-9
- Brodersen, P., Sakvarelidze-Achard, L., Bruun-Rasmussen, M., Dunoyer, P., Yamamoto, Y. Y., Sieburth, L., et al. (2008). Widespread translational inhibition by plant miRNAs and siRNAs. *Sci.* (1979) 320, 1185–1190. doi: 10.1126/science.1159151
- Buhtz, A., Pieritz, J., Springer, F., and Kehr, J. (2010). *Phloem small RNAs, nutrient stress responses, and systemic mobility*. Available at: <http://www.biomedcentral.com/1471-2229/10/64>.
- Chiou, T. J. (2007). The role of microRNAs in sensing nutrient stress. *Plant Cell Environ.* 30, 323–332. doi: 10.1111/j.1365-3040.2007.01643.x
- García, M. J., Angulo, M., Romera, F. J., Lucena, C., and Pérez-Vicente, R. (2022). A shoot derived long distance iron signal may act upstream of the IMA peptides in the regulation of Fe deficiency responses in Arabidopsis thaliana roots. *Front. Plant Sci.* 13. doi: 10.3389/fpls.2022.97177
- García, M. J., Corpas, F. J., Lucena, C., Alcántara, E., Pérez-Vicente, R., Zamarreño, Á.M., et al. (2018). A shoot Fe signaling pathway requiring the opt3 transporter controls gsn reductase and ethylene in Arabidopsis thaliana roots. *Front. Plant Sci.* 9. doi: 10.3389/fpls.2018.01325
- Gautam, C. K., Tsai, H. H., and Schmidt, W. (2021). IRONMAN tunes responses to iron deficiency in concert with environmental pH. *Plant Physiol.* 187, 1728–1745. doi: 10.1093/plphys/kiab329
- Grillet, L., Lan, P., Li, W., Mokkapat, G., and Schmidt, W. (2018). IRON MAN is a ubiquitous family of peptides that control iron transport in plants. *Nat. Plants* 4, 953–963. doi: 10.1038/s41477-018-0266-y
- Hirayama, T., Lei, G. J., Yamaji, N., Nakagawa, N., and Ma, J. F. (2018). The putative peptide gene FEP1 regulates iron deficiency response in Arabidopsis. *Plant Cell Physiol.* 59, 1739–1752. doi: 10.1093/pcp/pcy145
- Ko, D., and Helariutta, Y. (2017). Shoot–root communication in flowering plants. *Curr. Biol.* 27, R973–R978. doi: 10.1016/j.cub.2017.06.054
- Kobayashi, T., Nagano, A. J., and Nishizawa, N. K. (2021). Iron deficiency-inducible peptide-coding genes OsIMA1 and OsIMA2 positively regulate a major pathway of iron uptake and translocation in rice. *J. Exp. Bot.* 72, 2196–2211. doi: 10.1093/jxb/eraa546
- Koen, E., Szymańska, K., Klinguer, A., Dobrowolska, G., Besson-Bard, A., and Wendehenne, D. (2012). Nitric oxide and glutathione impact the expression of iron uptake- and iron transport-related genes as well as the content of metals in a thaliana plants grown under iron deficiency. *Plant Signal Behav.* 7, 1246–1250. doi: 10.4161/psb.21548
- Kohlen, W., Charnikova, T., Liu, Q., Bours, R., Domagalska, M. A., Beguerie, S., et al. (2011). Strigolactones are transported through the xylem and play a key role in shoot architectural response to phosphate deficiency in nonarbuscular mycorrhizal host Arabidopsis. *Plant Physiol.* 155, 974–987. doi: 10.1104/pp.110.164640
- Koprivova, A., and Kopriva, S. (2014). Molecular mechanisms of regulation of sulfate assimilation: first steps on a long road. *Front. Plant Sci.* 5. doi: 10.3389/fpls.2014.00589
- Li, H., Testerink, C., and Zhang, Y. (2021). How roots and shoots communicate through stressful times. *Trends Plant Sci.* 26, 940–952. doi: 10.1016/j.tplants.2021.03.005
- Lin, S. I., Chiang, S. F., Lin, W. Y., Chen, J. W., Tseng, C. Y., Wu, P. C., et al. (2008). Regulatory network of microRNA399 and PHO2 by systemic signaling. *Plant Physiol.* 147, 732–746. doi: 10.1104/pp.108.116269
- Liu, T. Y., Chang, C. Y., and Chiou, T. J. (2009). The long-distance signaling of mineral macronutrients. *Curr. Opin. Plant Biol.* 12, 312–319. doi: 10.1016/j.pbi.2009.04.004
- Liu, Z., Wang, C., Li, X., Lu, X., Liu, M., Liu, W., et al. (2023). The role of shoot-derived RNAs transported to plant root in response to abiotic stresses. *Plant Sci.* 328, 1–8. doi: 10.1016/j.plantsci.2022.111570
- Meng, X., Li, W., Shen, R., and Lan, P. (2022). Ectopic expression of IMA small peptide genes confers tolerance to cadmium stress in Arabidopsis through activating the iron deficiency response. *J. Hazard Mater.* 422, 1–14. doi: 10.1016/j.jhazmat.2021.126913
- Notaguchi, M., and Okamoto, S. (2015). Dynamics of long-distance signaling via plant vascular tissues. *Front. Plant Sci.* 6. doi: 10.3389/fpls.2015.00161
- Ota, R., Ohkubo, Y., Yamashita, Y., Ogawa-Ohnishi, M., and Matsubayashi, Y. (2020). Shoot-to-root mobile CEPD-like 2 integrates shoot nitrogen status to systemically regulate nitrate uptake in Arabidopsis. *Nat. Commun.* 11, 1–9. doi: 10.1038/s41467-020-14440-8
- Peng, F., Li, C., Lu, C., Li, Y., Xu, P., and Liang, G. (2022). IRONMAN peptide interacts with OsHRZ1 and OsHRZ2 to maintain Fe homeostasis in rice. *J. Exp. Bot.* 73, 6463–6474. doi: 10.1093/jxb/erac299
- Shanmugam, V., Tsednee, M., and Yeh, K. C. (2012). Zinc tolerance induced by iron 1 reveals the importance of glutathione in the cross-homeostasis between zinc and iron in Arabidopsis thaliana. *Plant J.* 69, 1006–1017. doi: 10.1111/j.1365-3113.2011.04850.x
- Shanmugam, V., Wang, Y. W., Tsednee, M., Karunakaran, K., and Yeh, K. C. (2015). Glutathione plays an essential role in nitric oxide-mediated iron-deficiency signaling and iron-deficiency tolerance in Arabidopsis. *Plant J.* 84, 464–477. doi: 10.1111/tpj.13011
- Shee, R., Ghosh, S., Khan, P., Sahid, S., Roy, C., Shee, D., et al. (2022). Glutathione regulates transcriptional activation of iron transporters via S-nitrosylation of bHLH factors to modulate subcellular iron homeostasis. *Plant Cell Environ.* 45, 2176–2190. doi: 10.1111/pce.14331
- Tabata, R. (2023). Regulation of the iron-deficiency response by IMA/FEP peptide. *Front. Plant Sci.* 14. doi: 10.3389/fpls.2023.1107405