

adaptation measures to ensure the success of national missions. For interactivity and two-way communications, there will be 8–10 interactive episodes based on questions, queries and letters/e-mails of the listeners and answering the questions posed at the end of each episode. The selected listeners will be provided additional materials in the form of activity kits developed specially for the serial.

Prominent subject experts, technologists and planners will highlight the scientific facets of climate change in a simple manner in the interactive episodes of the series. The series in 19 languages will also promote appropriate mechanisms that India is developing to deal with the challenges of climate change on several fronts simultaneously.

The following thrust areas are covered in the series: (a) Understanding the science of climate change and global

warming. (b) The natural and anthropogenic factors responsible for climate change. (c) The impact of climate change. (d) Preparedness of the global community to address the challenges of climate change. (e) Norms, conventions, and institutions to cope with climate change. (f) India and climate change. (g) Institutional framework in India. (h) Mitigation and adaptation.

In 2008, VP and AIR had signed a memorandum of agreement, under which radio serials are being produced and broadcast through AIR to enhance understanding of the approaches and outcome of science and technology. For the exact schedule of the broadcast day/time/frequency, etc., one may contact the nearby AIR station. Before launch of the serial, a press meet was also organized at the Constitutional Club, New Delhi on 29 March 2019.

1. IPCC, Summary for Policymakers. In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker, T. F. *et al.*), Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2013.
2. IPCC, Summary for Policymakers. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon, S. *et al.*), Cambridge University Press, Cambridge, UK and New York, NY, USA, 2007, p. 17.

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How are storage organs of root and tuber crops made? Mobile RNAs and proteins hold the promise!

Storage tuber and root crops (such as potato, yam, sweet potato, cassava, carrot, radish, sugar beet, etc.) form a significant portion of the world's subsistence food supply. Although these storage crops are nutritionally rich and have diverse roles in medicinal and industrial applications, not much research has been conducted on them. The only exception being a tuber crop potato, where extensive literature is available, largely on molecular signals that control tuber development. Since storage root crops hold an immense promise for food security purposes, studying storage root development would enable us to understand several unanswered questions. For example, what are the factors (internal and environmental) that govern the formation of below-ground storage organs? What regulates the size of the storage organs? How is the dormancy of these crops controlled post-harvest? If we could identify crucial factors involved in storage organ development, we can design biotechnological strategies to improve the overall growth performance and enhance their yields.

In all of these crops, below-ground storage organs serve as a strong reservoir for starch and storage proteins that help

plants to harness energy required during post-dormancy. Sugar molecules synthesized in leaves are transported through phloem sieve tubes that results in a massive accumulation of starch in below-ground storage organs. During the course of evolution, plants have adapted a long-distance transport mechanism through the phloem to communicate with their distant organs and regulate flowering^{1,2}, defence responses^{3,4} and nutrient deficiencies^{5,6}. Apart from sugars, many other signals, such as metabolites, hormones, proteins, lipids, small RNAs and full-length mRNAs are now known to ferry through the phloem sieve tubes as mobile molecules in response to various intrinsic and extrinsic signals⁷.

In 2007, the discovery of a phloem mobile protein as the flowering signal in *Arabidopsis* and rice paved the way to identify mobile signals for tuber development in the storage crop potato. Flowering Locus T (FT) protein is synthesized in leaves and moves to the shoot tip through the phloem to initiate flowering under favourable conditions⁸. Interestingly, early experiments from 1980s revealed that flowering and tuberization pathways share common signals⁹, where researchers observed that if a flower-

ing tobacco plant (as scion) was grafted onto non-tuberizing potato (as stock), it induces tuberization (Figure 1a). These experiments prompted other researchers to look for potential mobile signals involved in potato development. Mobile mRNA of a BEL1-like transcription factor, StBEL5, proved to be one of the major long-distance signals that moves from leaf to a below-ground modified stem (known as stolon) to induce tuber formation in potato¹⁰. Later, mRNAs of the two close homologous proteins of StBEL5 (*StBEL11* and *StBEL29*) and *Knotted1*-like class-I KNOX gene (*POTHI*) were also found to be phloem mobile signals associated with potato development. Other researchers established that over-expression of the rice FT ortholog in potato also induced both flowering and tuberization, even under unfavourable conditions. The potato FT protein ortholog StSP6A was identified as the mobile tuberization signal that moves as a protein from leaf to stolon to regulate tuber development¹¹. Potato plants having high expression of either the mobile mRNA *StBEL5* (ref. 10) or StSP6A protein¹¹ showed increased tuber yield.

The field of mobile RNAs and proteins is expanding rapidly, as revealed by

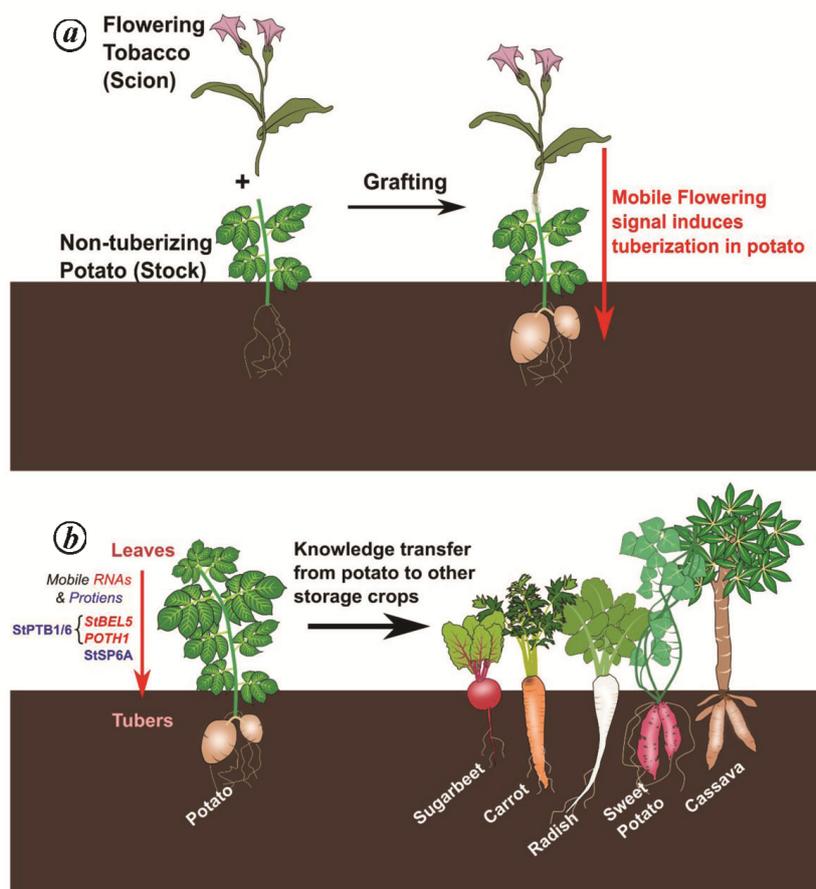


Figure 1. Diagrammatic illustration representing (a) heterograft between a flowering tobacco plant (scion) and a non-tuberizing potato (stock) induced tuber formation from the base of the stock and (b) proposed long-distance signalling mechanism of mobile RNAs and proteins in the development of below-ground storage organs of several root crops.

numerous reports from the last two decades^{1,2,12–16}. Yet, how mobile RNAs and proteins move through the phloem sieve tubes remains a puzzle. Interestingly, two studies identified RNA binding proteins (RBPs) from the pumpkin phloem sap, known as PHLOEM PROTEIN16 (ref. 17) or RBP50 (ref. 18). RBP50 was found to be associated with six different mRNA molecules as ribonucleoprotein (RNP) complex in the pumpkin phloem¹⁸. These RBPs bind to mobile RNAs selectively through a stretch of cytosine/uracil (CU) motifs in the 3' untranslated regions (UTRs). Recently, tRNAs and rRNAs have been proposed to prevent translation of mobile mRNAs during their transport through the phloem and assist in their delivery to target tissues¹⁹. It is not yet clear if the mobile proteins are also transported as a complex similar to mobile RNAs. In potato, polypyrimidine tract-binding proteins (PTBs), StPTB1 and StPTB6 are the RBPs that

aid in the transport of mobile mRNAs (such as *StBEL5* and *POTH1*) to control tuber development. Moreover, it has been shown that potato plants with higher levels of StPTB1 or StPTB6 protein exhibit increased transport of *StBEL5* mRNA to stolon and produce enhanced tuber yield²⁰.

Why does the movement of StSP6A protein and *StBEL5* mRNA to below-ground stolon induce tuber formation? These mobile factors alter the expression of downstream target genes to trigger tuberization pathway at the stolon apex. For example, *StBEL5* along with its KNOX partner, *POTH1* alters the expression of the target genes associated with a plant hormone gibberellin (GA) and reduces the level of GA in the stolon, which is essential to trigger tuber initiation and swelling. Apart from contributing to reduced GA level in the stolon, a recent study showed that StSP6A interacts with a sugar transporter

StSWEET11 and this heterodimer helps to establish source–sink relationship during tuber swelling²¹.

This obviously raises the question whether we can employ the knowledge gained in potato to other storage root crops (Figure 1b). As the genomic sequences of many of the storage root crops are now available, use of genetic and bioinformatics approaches would enable us to explore the mechanism of storage root development. What made us believe that mobile RNAs/proteins and RBPs could have a role in storage root development? Our recent studies have shown that the orthologues of mobile RNAs and proteins as well as RBPs are present in several storage root crops, such as sweet potato, cassava, carrot, radish and sugar beet^{22,23}. The RBP-mediated mobile RNA transport mechanism also appears to be conserved in these storage root crops²². Moreover, regulation of key target genes by the BELL–KNOX

proteins is found to be conserved in these root crops, similar to tuber development in potato²³. Besides potato, FT proteins regulate storage organ development in onion²⁴ and turnip²⁵. Moreover, we could identify a high level of similarity between potato StSP6A and protein sequences of SP6A orthologues in several storage root crops²³, suggesting that these orthologues may regulate storage organ formation in root crops, similar to tuber development in potato.

Overall, these findings highlight that the orthologues of mobile factors StSP6A, StBEL5 and StPTBs are well conserved in storage root crops belonging to different families. Whether the long-distance signalling network is also functional in these root crops, remains to be studied. These mobile factors hold promise for storage organ development in root crops and only future research can answer the above-mentioned questions.

1. Corbesier, L. *et al.*, *Science*, 2007, **316**, 1030–1033.
2. Tamaki, S., Matsuo, S., Wong, H. L., Yokoi, S. and Shimamoto, K., *Science*, 2007, **316**, 1033–1036.
3. Cai, Q., Qiao, L., Wang, M., He, B., Lin, F., Palmquist, J. and Jin, H., *Science*, 2018, **360**, 1126–1129.
4. Hua, C., Zhao, J. H. and Guo, H. S., *Mol. Plant*, 2018, **11**, 235–244.
5. Buhtz, A., Pieritz, J., Springer, F. and Kehr, J., *BMC Plant Biol.*, 2010, **10**, 64.
6. Zhang, Z. L. *et al.*, *Nature Plants*, 2016, **2**, 16033.
7. Lucas, W. J. *et al.*, *J. Integr. Plant Biol.*, 2013, **55**, 294–388.
8. Turck, F., Fornara, F. and Coupland, G., *Annu. Rev. Plant Biol.*, 2008, **59**, 573–594.
9. Chailakhyan, M. K., Yanina, L. I., Devedjian, A. G. and Lotova, G. N., *Dokl. Akad. Nauk SSSR*, 1981, **257**, 1276–1280.
10. Banerjee, A. K., Chatterjee, M., Yu, Y. Y., Suh, S. G., Miller, W. A. and Hannapel, D. J., *Plant Cell*, 2006, **18**, 3443–3457.
11. Navarro, C. *et al.*, *Nature*, 2011, **478**, 119–122.
12. Mahajan, A., Bhogale, S., Kang, I. H., Hannapel, D. J. and Banerjee, A. K., *Plant Mol. Biol.*, 2012, **79**, 595–608.
13. Lu, K. J., Huang, N. C., Liu, Y. S., Lu, C. A. and Yu, T. S., *RNA Biol.*, 2012, **9**, 653–662.
14. Yoo, S. C., Chen, C., Rojas, M., Daimon, Y., Ham, B. K., Araki, T. and Lucas, W. J., *Plant J.*, 2013, **75**, 456–468.
15. Ghate, T. H., Sharma, P., Kondhare, K. R., Hannapel, D. J. and Banerjee, A. K., *Plant Mol. Biol.*, 2017, **93**, 563–578.
16. Winter, N. and Kragler, F., *Plant Cell Physiol.*, 2018, **59**, 1700–1713.
17. Xoconostle-Cázares, B. *et al.*, *Science*, 1999, **283**, 94–98.
18. Ham, B. K., Brandom, J., Xoconostle-Cázares, B., Ringgold, V., Lough, T. J. and Lucas, W. J., *Plant Cell*, 2009, **21**, 197–215.
19. Kehr, J. and Kragler, F., *New Phytol.*, 2018, **218**, 29–40.
20. Cho, S. K., Sharma, P., Butler, N. M., Kang, I. H., Shah, S., Rao, A. G. and Hannapel, D. J., *J. Exp. Bot.*, 2015, **66**, 6835–6847.
21. Abelenda, J. A. *et al.*, *Curr. Biol.*, 2019, **29**, 1178–1186-e6.
22. Kondhare, K. R., Kumar, A., Hannapel, D. J. and Banerjee, A. K., *BMC Genomics*, 2018, **19**, 1–13.
23. Natarajan, B., Kondhare, K. R., Hannapel, D. J. and Banerjee, A. K., *Plant Sci.*, 2019, **284**, 73–81.
24. Lee, R., Baldwin, S., Kenel, F., McCallum, J. and Macknight, R., *Nature Commun.*, 2013, **4**, 1–9.
25. Zheng, Y., Luo, L., Liu, Y., Yang, Y., Wang, C., Kong, X. and Yang, Y., *Plant Divers.*, 2018, **40**, 50–56.

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