A critical appraisal of phloem-mobile signals involved in tuber induction

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The induction of tuber formation is a key developmental transition for the production of potatoes, one of the most important food crops. Understanding the regulation of tuber induction is essential to devise strategies to improve tuber yield and quality. During the last two decades we have started to comprehend this regulation, with the identification of genes that control tuberization (Jackson, 1999; Abelenda et al., 2011). This has been facilitated by the tremendous progress in understanding the control of flowering, which is similar to tuberization in aspects such as the response to photoperiod and the involvement of phloem-mobile signals (Suárez-López, 2005; Abelenda et al., 2011). This Perspective paper focuses on recent findings that suggest several molecules as candidates for systemic signals controlling tuber induction.

LONG-DISTANCE SIGNALS REGULATE TUBERIZATION AND FLOWERING

Short day (SD) photoperiods promote tuberization, whereas long days (LDs), high nitrogen levels and high temperatures inhibit or delay tuberization. Within the tuberization process, it is important to distinguish between tuber induction and tuber development and growth. Induction takes place when signals are produced in leaves and transported through the phloem to underground stems (stolons), or when mobile signals that inhibit tuberization are repressed (Jackson, 1999; Suárez-López, 2005). This leads to the initiation of tuber development and growth, which determines tuber shape, number, and weight. Although tuber yield is often used to assess tuber induction, changes in tuber yield can result from alterations in many different factors, including overall plant growth, photoassimilate partitioning, the strength of induction, tuber development, etc. (Dwing and Struik, 1992). The time of tuber initiation is therefore a much better indicator of tuber induction than tuber yield.

Grafting experiments using potato plants induced and non-induced to tuberize demonstrated the existence of transmissible substances decades ago (Gregory, 1956; Chapman, 1958), but the identification of these signals has proven difficult. Recent advances in the study of other developmental processes provide hints for finding long-distance tuberization signals. The intense search for a phloem-mobile flowering signal, called florigen, has led to the identification of several FLOWERING LOCUS T (FT) family members as leaf-produced proteins that travel to the shoot apical meristem, where they induce flowering (Fluck et al., 2008; Suárez-López et al., 2013). In Arabidopsis thaliana, FT expression is activated by the transcriptional regulator CONSTANS (CO) in leaf phloem cells in response to floral inductive photoperiods (An et al., 2004; Ayre and Turgon, 2004).

However, florigen is not a single molecule. Positive and negative transmissible regulators of flowering exist (Bernier, 1988; Matsukas et al., 2012). Several FT family members can perform these functions. In rice, Heading date 3a (Hd3a) and RICE FLOWERING LOCUS T 1 (RFT1) act as florigenic signals under different photoperiods (Tamaki et al., 2013). In Arabidopsis ATC acts as a mobile repressor or antiflorigen and TWIN SISTER OF FT (TSF) might function as a florigen...
StSP6A et al., 2011). The effect of StSP6A on tuberization is transmitted in potato. Indeed, several FT inductive LDs (Navarro et al., 2011; González-Schain et al., 2012). A potato CO-like protein that represses tuberization under non-inductive conditions, a role similar to that of FT in flowering control (Navarro et al., 2011). One of them encodes StSP3D, which mainly affects flowering, and another encodes StSP6A, which induces tuber formation in the potato (Li et al., 2009, 2011; Huang et al., 2012; Lu et al., 2012). Other reports indicate that translocation of the FT protein, but not the RNA, is required to promote flowering (Lischutz et al., 2006; Mathieu et al., 2007; Noguiguchi et al., 2008). These findings suggest that movement of the FT mRNA can help to induce flowering, but movement of the FT protein is much more crucial. In addition to FT proteins and RNA, other types of molecules, such as hormones and metabolites, have been postulated as long-distance floral signals (Turnbull, 2011; Dinant and Suárez-López, 2012).

IS FT A PHLOEM-MOBILE TUBERIZATION SIGNAL?

Transmissible signals for flowering and tuberization are interchangeable. Tobacco scions induced to flower promote tuberization when grafted onto potato stocks kept under non-inductive conditions (Chailakhyan et al., 1981). When a rice tuber-inducing condition is transferred from one species (Giavalisco et al., 2006; Lin et al., 2007; Aki et al., 2008), and in addition to FT proteins and RNA, other types of molecules, such as hormones and metabolites, have been postulated as long-distance signals (Turnbull, 2011; Dinant and Suárez-López, 2012).

There are similarities, but also differences, in the regulation of FT genes. SSSt6P64 is negatively regulated by StCO (Figure 1), a potato CO-like protein that represses tuberization under non-inductive LDs (Navarro et al., 2011; González-Schain et al., 2012). StCO does not seem to play a role under SDs (González-Schain et al., 2012). By contrast, Arabidopsis CO promotes FT transcription only under inductive photoperiods (Turck et al., 2008). In rice, Hda6 is repressed or activated by the CO-like protein Hdl under non-inductive or inductive conditions, respectively, and in addition RFT1 is up-regulated and promotes flowering much later under non-inductive conditions (Tsui et al., 2013). These differences stress the need to test hypotheses based on flowering-time models, rather than simply extrapolating them to tuberization. Demonstrations that SSSt6P64 moves are therefore eagerly awaited.

Two additional FT family members from potato, StTFL1 and StS6P65, might be related to the tuberization process. StTFL1 mRNA levels are high in stolons before induction and decrease at early stages of tuber development. Overexpression of StTFL1 causes an increase in the number of tubers produced (Gao et al., 2010), suggesting a role in tuber induction or development. The expression pattern of SSSt6P64 suggests that this gene might play an opposite role to that of SSSt6P64 in tuberization control (Navarro et al., 2011; Kloosterman et al., 2013); although a functional analysis of this gene has not been reported so far. Further analyses of StTFL1 and SSSt6P65 to determine their biological functions should be pursued, given that FT-related proteins affect other developmental processes aside from flowering and tuberization (Pin and Nilsson, 2012; Hiraoka et al., 2013). As many FT-like proteins are mobile, it would be worth testing StTFL1 and SSSt6P65 movement.

SBE5L AND POTH1 RNAs AS PUTATIVE TRANSMISSIBLE SIGNALS

Two mRNAs have been proposed as long-distance signals regulating tuberization. SBE5L and POTATO HOMEBOX 1 (POTH1) are homeobox transcription factors that interact with each other (Chen et al., 2003). Overexpression of POTH1 increases the number of tubers produced relative to wild-type (WT) plants in in vitro tuberization assays (Rosin et al., 2003). Overexpression of SBE5L enhances tuber formation under SDs and promotes tuberization under non-inductive LDs. SBE5L mRNA moves from overexpressing scions to WT stocks and movement correlates with increased tuber yield (Chen et al., 2003; Banerjee et al., 2006). Graft transmission of POTH1 mRNA has also been shown (Mahajan et al., 2012). Transcription of SBE5L and POTH1 in vascular cells (Banerjee et al., 2006; Mahajan et al., 2012) is consistent with movement of their transcripts through the phloem. Additional experimental approaches support translocation of SBE5L mRNA and have been previously reviewed (Han napel, 2010).

However, there are numerous caveats to be aware of when interpreting the movement of SBE5L and POTH1 RNAs, as well as their effects on tuberization. First, POTH1 has not been shown to affect tuber formation in soil-grown plants. Second, whether SBE5L and/or POTH1 are required for tuber induction in WT plants has not been demonstrated, as only overexpression alters tuber induction or development. Third, RNA movement has been shown from overexpressing plants, but not from WT plants (Banerjee et al., 2006; Mahajan et al., 2012), and it has not been tested whether movement is required for tuberization. Fourth, POTH1-overexpressing plants exhibit dramatic alterations in the vasculature (Rosin et al., 2003; Mahajan et al., 2012). It is possible that the tuber phenotype of POTH1-overexpressing plants and graft transmission of POTH1 mRNA are indirect consequences of these alterations. Fifth, both POTH1 and SBE5L are transcribed in stolons, with an increase in SBE5L transcription at early stages of tuber formation (Banerjee et al., 2006; Mahajan et al., 2012), casting doubts on the need of movement from leaves. Finally, it has not been excluded that movement of SBE5L and/or POTH1 proteins may occur.

Therefore, although SBE5L and POTH1 RNAs are able to move, further research is needed to demonstrate whether this has any biological relevance. This can be addressed by simultaneously silencing SBE5L and POTH1 or several SBE5L paralogs, which have been proposed to act redundantly (Chen et al., 2003). Whether the SBE5L protein moves should also be tested.
Suárez-López Phloem-mobile signals regulating tuberization

FIGURE 1 | Model for the regulation of tuber induction by phloem-mobile signals. The main candidates for mobile signals are the SIS6P6A protein, two RNAs – StBEL5 and miR172 – and GAs. The production, and possibly the movement, of these four factors is regulated by a complex genetic network. PHYB, StSUT4, and StCO repress tuberization in response to LDs. GAs also seem to act as repressors, whereas SIS6P6A and perhaps miR172 and StBEL5 act as tuberization promoters under inductive SD conditions. Under LDs, PHYB represses the expression of SIS6P6A and SIGA20ox1, which encodes an enzyme that catalyzes the conversion of GA3 to GA1, an active GA. StSUT4, StBEL5 mRNA, miR172, and GAs presumably translocate to stolons through the phloem. In the stolons, SIS6P6A promotes tuber development, at least in part through up-regulation of SIGA20ox1, which converts active GAs into inactive forms. miR172 up-regulates StBEL5, which together with POTH1 down-regulates SIGA20ox1, reducing the synthesis of active GAs, which repress tuber development. Under LDs, GA20 would move from leaves to stolons and would be converted to GA1, thus repressing tuber development. Under SDs, there would be less GA20 available and tuber development can occur. Thick gray arrows indicate RNA movement, and thick black arrows indicate protein or GA movement. Discontinuous lines indicate that movement or regulation has been suggested, but not demonstrated.

miR172 AFFECTS TUBERIZATION IN A GRAFT-TRANSMISSIBLE MANNER

To date, miR172, which regulates flowering in several species, is the only microRNA (miRNA) shown to affect tuber induction (Martin et al., 2009; Zhu and Helliwell, 2011). The effect of miR172 in potato has been reported in overexpressing plants, which form tubers under LDs, tuberize early under SDs and show up-regulation of StBEL5. Inactivation would help to confirm if miR172 is required for tuberization control.

There is growing evidence that small RNAs, including short interfering RNAs (siRNAs) and miRNAs, move cell-to-cell and systemically (Humber et al., 2003; Yoo et al., 2004; Lin et al., 2008; Pant et al., 2008; Chitwood et al., 2009; Carlsbecker et al., 2010; Dunoyer et al., 2010; Molnar et al., 2010). The effect of miR172 overexpression is graft transmissible, suggesting that this miRNA regulates long-distance signals that control tuberization or, alternatively, that miR172 itself is a mobile signal. In grafting experiments, miR172-overexpressing scions accelerated tuberization of WT stocks, but the reciprocal graft combination did not tuberize early. The simplest interpretation is that miR172 is required in aerial organs, rather than in stolons, to promote tuberization. However, increases of miR172 levels in stolons correlate with tuber induction, while changes in leaves do not (Martin et al., 2009). At least two hypotheses can explain this apparent contradiction: (1) overexpression of miR172 in scions might not be sufficient to counteract tuber-inhibiting signals derived from WT
ROLE OF GIBBERELINS IN TUBERIZATION

The plant hormones gibberellins (GAs) are present in phloem sap and seem to act as signaling molecules in some species (Eriksson et al., 2006; King et al., 2006, 2008). The last steps in the biosynthesis of active GAs are catalyzed by GA 20-oxidase (GA20ox1) and GA 3-oxidase (GA3ox). Biologically active GAs, including GA1, GA3, and GA4, are inactivated by GA 2-oxidase (GA2ox) enzymes (Hedden and Thomas, 2012).

Gibberellins are involved in the control of tuber induction or development. Different observations have led to the assumption that GAs inhibit tuberization under LDs. Tuberization would take place when GA levels decrease in response to SDs (Rodríguez-Falcón et al., 2006). This decrease seems necessary to arrest longitudinal stolon growth and allow stolon swelling (Jackson, 1999). But high GA levels really required to repress tuber induction under LDs? Silencing of a potato GA20ox (StGA20ox1) and manipulation of the levels of a GA3ox (StGA3ox2) do not induce tuberization under LDs (Carrera et al., 2000; Bou-Torrent et al., 2011). In addition, a GA20ox, StGA20ox1, affects tuberization in vitro, but not in soil-grown plants (Kloosterman et al., 2007), leading to the conclusion that StGA20ox1 is a tuber-identity gene rather than a regulator of tuber induction. Local up-regulation of StGA2ox1 in stolons by StSUT4 (Navarro et al., 2011) is consistent with this interpretation.

Moreover, the expression patterns of several GA biosynthetic enzymes and the phenotypes of plants with altered levels of these enzymes do not always fit with the hypothesis of GAs repressing tuberization. For example, although SGA2ox1 is down-regulated at the initiation of tuber development, StGA2ox1 and StGA2ox3 are up-regulated (Kloosterman et al., 2007). Both SGA2ox1-silenced lines and plants overexpressing StGA3ox2 tuberize earlier than WT plants under SDs, despite showing opposite changes in GA levels (Carrera et al., 2000; Bou-Torrent et al., 2011). As GA biosynthesis involves feedback and feedforward regulations (Hedden and Thomas, 2012), some of these contradictions can be explained through negative feedback regulation of StGA2ox1 genes by active GAs, but this still has to be demonstrated.

To explain some of these conflicting results, it has recently been proposed that GA2ox1 is the immediate precursor of GA1, which would be mobile, whereas GA2ox would not. In StGA3ox2-overexpressing plants, increased conversion of GA20ox to GA1 in aerial parts would reduce the amount of GA1 transported to stolons, resulting in low levels of GA1 in stolons and early tuberization (Bou-Torrent et al., 2011). This interesting hypothesis fits well with some observations.

However, as StGA2ox genes are expressed in stolons (Carrera et al., 1999), GA2ox is expected to be synthesized here. StGA3ox2-overexpressing plants would then have increased conversion of GA20ox to GA1 also in stolons, which should repress tuberization. Localized silencing of StGA20ox1 and StGA3ox2 in leaves and stolons and grafting experiments using plants with altered levels of these enzymes would help to elucidate the role of GA2ox and GA1. It will also be necessary to test GA20ox movement in potato plants and whether movement is required to prevent tuberization. More work is also needed to determine whether GAs play a role in tuber induction or they regulate tuber development by preventing stolons from being competent to respond to leaf-derived inductive signals. Nowadays it cannot be excluded that GAs perform both functions.

SUCROSE AND OTHER PUTATIVE LONG-RANGE SIGNALING MOLECULES

Sucrose is a metabolite, a source of energy and a signaling molecule and it has been proposed as a transmissible substance for tuberization and flowering (Sheen et al., 1999; Suárez-López, 2005; Ruan, 2012). Transcripts of sucrose transporters are phloem mobile in several species, including potato, which suggests a possible signaling role for these RNAs (Lesche et al., 2011). A potato sucrose transporter, SSUT4, is involved in flowering and tuberization control. Inhibition of SSUT4 induces tuberization under LDs. Graft transmission of this phenotype, together with an increase in sucrose export from leaves of SSUT4-silenced plants, suggest a role for SSUT4 in long-distance signaling at least in part via source to sink carbon flux (Chincinska et al., 2008). In addition, SSUT4 regulates the production of putative long-distance signals, such as SSP6A and probably GAs (Chincinska et al., 2008, 2013). There is additional evidence of a link between sucrose and GAs during tuberization. In vitro treatment with high sucrose concentrations, which induces tuber formation, reduces endogenous GA1 levels in stolons before tuber initiation (Xu et al., 1998). Exogenous GA treatment, conversely, up-regulates SSUT4 (Chincinska et al., 2008). Altogether these observations indicate a complex interplay between GAs and sucrose during tuber induction or development. Understanding the different roles that sucrose plays in tuber formation, as a starch precursor, energy source and signal, deserves further attention.

Other molecules, such as metabolites, hormones, and peptides have the potential to act as mobile signals, but their roles in tuberization are not yet clear (Jackson, 1999; Fernie and Willmitzer, 2001; Dinant and Suárez-López, 2012). Grafting of tomato mutants onto potato stocks has been proposed as a strategy to elucidate the role of hormones in long-distance signaling, although the results so far point to effects on assimilate distribution rather than on signaling pathways (Pérez et al., 2005).

THE ROLE OF PHYTOCHROME B IN REGULATING MOBILE SIGNALS

The photoreceptor phytochrome B (PHYB) plays an interesting role in the control of tuber induction, as it affects several putative systemic tuberization molecules. Grafting experiments using PHYB-silenced plants, which tuberize under LDs, led to...
We have recently witnessed substantial advances in our knowledge of alteration of GA homeostasis (Jackson et al., 2000). In potato, PHYB affects GA synthesis or signaling, as SAGA201 kRNA abundance is increased in PHYB-silenced plants, which show several phenotypes characteristic of alterations in GA homeostasis (Jackson et al., 2000). In addition, SSUT4 probably mediates some effects of PHYB on plant development (Chincinska et al., 2008). How PHYB regulates flowering by GAs (Lau and Deng, 2010) In potato, PHYB affects GA synthesis or signaling, as SAGA201 kRNA abundance is increased in PHYB-silenced plants, which show several phenotypes characteristic of alterations in GA homeostasis (Jackson et al., 2000). In addition, SSUT4 probably mediates some effects of PHYB on plant development (Chincinska et al., 2008). How PHYB regulates flowering by GAs (Lau and Deng, 2010). In potato, PHYB affects GA synthesis or signaling, as SAGA201 kRNA abundance is increased in PHYB-silenced plants, which show several phenotypes characteristic of alterations in GA homeostasis (Jackson et al., 2000). In addition, SSUT4 probably mediates some effects of PHYB on plant development (Chincinska et al., 2008). How PHYB regulates flowering by GAs (Lau and Deng, 2010).

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CONCLUSION AND FUTURE CHALLENGES

We have recently witnessed substantial advances in our knowledge of potato tuber induction. Although the identity of mobile

tuberonization molecules is yet unknown, they are probably involved in flowering. Several good candidates have been proposed (Figure 1) Further research should test whether they act as genuine potato tuberization signals.

Long-distance inferences the production of sig-
nals, but also requires phloem loading, transport and unloading, as well as the response of target tissues to these signals. Inter-}

specific grafting and experimental approaches used in other species, such as analyses of phloem sap composition, visualization of reporters fused to putatively mobile proteins and strategies to disrupt intercellular signaling, can be employed to address these questions.

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