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Abstract

As sessile organisms, plants have evolved sophisticated mechanisms of gene regulation to cope with changing environments. Among them, long non-coding RNAs (lncRNAs) are a class of RNAs regulating gene expression at both transcriptional and post-transcriptional levels. They are highly responsive to environmental cues or developmental processes and are generally involved in fine-tuning plant responses to these signals. Roots, in addition to anchoring the plant to the soil, allow it to absorb the major part of its mineral nutrients and water. Furthermore, roots directly sense environmental constraints such as mineral nutrient availability and abiotic or biotic stresses and dynamically adapt their growth and architecture. Here, we review the role of lncRNAs in the control of root growth and development. In particular, we highlight their action in fine-tuning primary root growth and the development of root lateral organs, such as lateral roots and symbiotic nodules. Lastly, we report their involvement in plant response to stresses and the regulation of nutrient assimilation and homeostasis, two processes leading to the modification of root architecture. LncRNAs could become interesting targets in plant breeding programs to subtly acclimate crops to coming environmental changes.

KEYWORDS: long non coding RNA, root growth, root development, plant nutrition, stresses

Introduction

The development of next generation sequencing methods to analyze transcription in multiple cell types and conditions revealed that more than 90% of the eukaryotic genome generates transcripts, a large proportion of which are the so-called non-coding RNAs. Despite the weak coding potential of these molecules, some were shown to produce small peptides (1). From mammals to plants, this tremendous quantity of enigmatic non-coding

transcripts has been intensively studied, revealing novel regulatory ways to fine-tune gene expression. Regulatory non-coding transcripts are divided into two main groups based on their size. First, the small RNAs (sRNAs), which are less than 200nt in length, include the small-interfering RNAs (siRNAs), the micro-RNAs (miRNAs) and the phasing-siRNAs (phasiRNAs). These sRNAs regulate gene expression at the transcriptional or post-transcriptional levels through RNA-dependent DNA methylation (RdDM), transcript cleavage or inhibition of translation (2). Notably, the RdDM-acting siRNAs arise from genes transcribed by either Pol II or Pol IV and after processing are recruited to their target loci with the help of a Pol V long non-coding RNA (lncRNA) acting as a scaffold (Reviewed in (2)). More generally, lncRNAs form the second group and are non-coding transcriptional units longer than 200nt in length. Similarly to coding RNAs, the majority of lncRNAs are transcribed by Pol II, poly-adenylated and subjected to splicing events (3). However, compared to coding genes, lncRNAs are more specifically expressed, at certain stages during developmental processes, in specific tissues or in response to environmental stimuli (4). In addition, they are generally shorter in length and contain fewer introns, thus generating a lower number of isoforms compared to coding transcripts (5–7). Even though lncRNAs are mainly enriched in the nuclear fraction of the cell, regulating gene transcription there, some are translocated to the cytoplasm and regulate gene expression at the post-transcriptional level (8).

Thousands of lncRNAs are transcribed within eukaryotic cells, manifesting their likely participation in a wide range of biological processes (8). For example, in arabidopsis, the *ELENA1* and *SVALKA* lncRNAs are directly involved in the plant response to pathogen and cold stress, respectively (9,10); *COOLAIR*, *COLDAIR* and *COLDWRAP* lncRNAs mediate the epigenetic silencing of the *Flowering Locus C* (*FLC*) gene facilitating vernalization (11–14); the *LAIR* antisense lncRNA, transcribed from a *Leucine-Rich repeat receptor Kinase* (*LRK1*) genomic region, is important for rice grain yield (15). Generally, plant lncRNAs are involved in stress signaling, photomorphogenesis, fertility and plant growth and development (3). This review focuses on the influence of lncRNAs on root growth and development both during normal growth conditions as well as in response to environmental stresses and their relevance on key root-mediated assimilation of soil nutrients.

Influence of lncRNAs on root growth and development

Root growth and development are tightly regulated by phytohormones. Among them, auxin regulates cell division and elongation and is described as a positive regulator of root growth (16). Nuclear Speckle RNA-binding Proteins (NSR) proteins are a class of protein involved in Alternative Splicing (AS) and auxin-related developmental processes, such as the development of lateral roots (LR) (17) (**Figure 1)**. The *nsra/nsrb* double mutant is less sensitive to auxin and presents a lower number of LR in response to auxin application (17). Interestingly, the lncRNA *Alternative Splicing COmpetitor* (*ASCO*) is able to physically interact with the NSR proteins modulating AS during auxin signaling and modifies auxin-related root growth and development (17) (**Figure 1**). As a result, plants overexpressing *ASCO* exhibit an increased sensitivity to auxin. More recently, immunoprecipitation of the NSRa protein followed by a transcriptomic analysis has served to identify multiple NSR-dependent spliced mRNAs. Strikingly, many lncRNAs, other than *ASCO*, were shown to also interact with NSRa,

suggesting that they could also modulate NSR-dependent AS and subsequently impact root architecture (18), even though further investigations are needed.

Auxin transport within the root also shapes root architecture by modifying the distribution of auxin inside root tissues. For example, mutants impaired in auxin transport exhibit a significant reduction of root length and meristem size (19). The *PINOID* (*PID*) kinase is a key regulator of auxin transport as it phosphorylates the PIN proteins directly involved in this process. As might be expected, *PID* repression leads to a reduced sensitivity to root gravitropism (20). Curiously, auxin signaling disrupts a chromatin loop encompassing the *PID* promoter and its neighboring gene, the lncRNA *AUXIN-REGULATED PROMOTER LOOP* (*APOLO*), and induces the transcription of both *PID* and *APOLO* genes through ARF transcription factors (TFs) (21). Following that, *APOLO* physically interacts with the LIKE HETEROCHROMATIN PROTEIN 1 (LHP1) chromatin looping protein, closing again the chromatin loop and subsequently repressing *PID* gene activity. In addition, *APOLO* is able to trigger DNA methylation and the deposition of the H3K27me3 repressive histone mark in this *PID-APOLO* region, driving it into a repressive state (**Figure 1B**). Not surprisingly, *APOLO* downregulated lines exhibit a reduced sensitivity to root gravitropism, just as the *pid* mutant (21). More recently, it has been observed that the *APOLO* promoter is active during LR development, a process controlled by auxin (22). In the same study, it was shown that the *APOLO* RNA is able to recognize multiple loci in *trans* through the formation of R-loops, directly influencing the local chromatin conformation and gene activity of several auxin-responsive genes (22). Notably, a significant proportion of *APOLO*'s target genes, in addition to being responsive to auxin, are also involved in LR formation (**Figure 1B**). For example, the *LEUCINE-RICH REPEAT/EXTENSIN2* gene which is involved in cell wall remodeling during LR emergence (23), is targeted by *APOLO*. In agreement with this, seedlings overexpressing *APOLO* present a significant increase in LR density in response to auxin (22).

In arabidopsis, the *TRANS-ACTING SIRNA 3* (*TAS3*) lncRNA also participates in LR development through ta-siRNA production after *miR390* cleavage (24). Notably, the *miR390* is specifically expressed at the sites of LR initiation, triggering the processing of *TAS3* into ta-siRNAs that mediate inhibition of transcription factors of the ARF family, *ARF2*, *ARF3* and *ARF4.* Through this mechanism *TAS3* and its derived ta-siRNAs promote LR growth (24) (**Figure 1C**).

In addition to auxin, another phytohormone directly involved in shaping the root architecture such as cytokinin (CK), described as an inhibitor of root growth and widely used for plant regeneration to inhibit adventitious root formation (25). Essential for shoot meristem activity, leaf growth and senescence, CK are mainly produced in root tip, but are also synthesized in the plant aerial parts (26). The locus of the *Sho* gene from petunia, involved in CK biogenesis, also produces an antisense non-coding transcript (27). The expression of *Sho* and of the antisense lncRNA seems to be positively correlated and leads to the production of 24nt small RNAs in most tissues. This suggests a role of *Sho* antisense transcript to fine tune the accumulation of its sense transcript (**Figure 1D**). Strikingly, roots are the only tissue where the 24nt were not detected, suggesting that *Sho* is not degraded in this compartment. This mechanism would allow the maintenance of a high level of CK synthesis in the root compared to other organs. Thus, the *Sho* antisense lncRNA could be involved in the organ-dependent control of CK biogenesis in petunia (27).

Another factor influencing root development is the *SCARECROW* (*SCR*) gene, required for the asymmetric cell division occurring within arabidopsis roots (28). Similarly, SCR-like TFs (OsSCL) are a family of proteins found in rice and critical for proper root development (29). More precisely, in non-root organs, such as shoots and flowers, *OsmiR171* is acting as an inhibitor of *OsSCL* genes. A non-coding transcriptional unit, named *MIKKI* ('decoy' in Korean) and derived from a retrotransposable element, indirectly controls *OsSCL* gene expression through the inhibition of the *miR171* activity (**Figure 1E**). This inhibition is mediated through target mimicry (30), the *MIKKI* non-coding transcripts binding to the *miR171* but showing a loss of base pair complementarity at the cleavage site. This avoids *MIKKI* cleavage and leads to the sequestration of miR171, acting as a miRNA sponge, preventing this miRNA from cleaving *OsSCL* mRNAs. The root length was significantly reduced in plants overexpressing the *MIKKI* transcripts (29), demonstrating a functional role of this *miR171-MIKKI-OsSCL* regulatory node. Altogether, lncRNAs constitute emerging regulators of root growth and development through their participation in plant hormone signaling pathways and through the regulation of key root-related genes.

LncRNAs and stress-affected root growth

The increasing world population and concomitant climate change has resulted in an unsustainable path for global food security. To address these challenges, new strategies are required that may allow us to prepare crops against environmental constraints linked to climate change. For example, many lncRNAs are activated upon biotic and abiotic stresses, underpinning that certain lncRNAs may be involved in plant stress resilience. Although stresses affect various organs of the plant, the root compartment is particularly sensitive to adverse environmental conditions such as osmotic-related stresses and cold or pathogen attacks that have a strong negative impact on root growth (31). Large variations in lncRNA expression have been linked to environmental stresses in multiple model and crop plants. In this section, we will discuss the roles of lncRNAs in responses to deleterious environmental events for root growth and development, beginning with abiotic stresses (including drought, salt and cold) and ending with biotic stresses.

Transcriptomic analyses revealed that more than one hundred lncRNAs are differentially expressed upon drought stress in arabidopsis (32), poplar (33), millet (34), cassava (35) and rice (36). For example, two rice Natural Antisense Transcripts (NATs), *Os02g0250700* and *Os02g0180800,* may be involved in the transcriptional regulation of their overlapping coding genes (*late embryogenesis abundant* (*LEA*) and *cinnamoyl-CoA reductase* (*CCR*)), both participating in plant drought tolerance (36), even though such an assumption is only based on correlation analyses (**Figure 1F**). In arabidopsis, the overexpression of the *DRought-Induced lncRNA* (*DRIR*) regulates a subset of genes involved in ABA signaling and water translocation, of particular relevance for plant drought stress resilience. *DRIR* also seems to directly regulate the transcriptional activity of *FUCOSYLTRANSFERASE 4* and of the TF *NAM/ATAF/CUC3,* potentially modulating the plant tolerance to drought and salt stresses through the associated pathways (37) (**Figure 1G**).

Salt stress also disturbs accumulation of a number of lncRNAs in various plant species, including arabidopsis (38), soybean (39), medicago (40), tea bush (41), cotton (42), sorghum (43) and poplar (44). The cotton *lncRNA973* regulates a subset of genes of the salt-stress

signaling pathway, mainly participating in scavenging reactive oxygen species (ROS), directly fine-tuning plant salt stress tolerance (42) (**Figure 1H**). Remarkably, ectopic overexpression of the cotton *lncRNA973* within arabidopsis significantly increased the plant salt tolerance from germination to seedling establishment, whereas reducing the *lncRNA973* through virus-induced gene silencing (VIGS) in cotton significantly reduced the plant's tolerance to salt stress. Additionally, according to sequence and expression-based data, the *lncRNA973* may also act via target mimicry for the *miR399* (45), a well-known miRNA regulating root phosphate (Pi) assimilation and homeostasis (46–49), although *miR399* has not been linked so far to salt stress. Similarly, the root crop cassava may regulate drought and cold stress responses through the *lncRNA340* acting as another target mimicry for *miR169*, even though functional genetic analyses have not yet been conducted (35) (**Figure 1I**).

Low temperature is another stress preventing normal root growth and development. For example, it has been noticed that prolonged cold exposure increases root hair growth, presumably participating in plant cold acclimation. Strikingly, plantlets with reduced or increased levels of *APOLO* lncRNA transcripts constitutively produced more root hairs compared to WT (50). Furthermore, plants with a modified level of *APOLO* show an increased level of *ROOT HAIR DEFECTIVE 6* (*RHD6*) transcripts, a key gene involved in the regulation of root hair formation. That same work also showed that *APOLO* controls *RHD6* transcriptional activity during cold stress through the recruitment of the WRKY42 TF to its promoter region (50) (**Figure 1B**).

Moving on now to biotic stresses, roots subjected to such stresses generally undergo significant changes in their coding and non-coding transcriptome. Particularly, flagellin is one of the best characterized bacterial effectors (51); its detection by the root triggers a series of signaling events that restricts the pathogen propagation and inhibits root growth (52). Deregulation of the *ASCO* lncRNA significantly affects the activity of genes involved in flagellin response in addition to the auxin-related genes (53) (**Figure 1A**). Curiously, most of these "biotic stress" genes affected by *ASCO* knock-down in root tissues do not overlap with the deregulated genes detected in *nsra*/*nsrb* mutants, suggesting an alternative role of *ASCO* for plant biotic stress response. Indeed, recently *ASCO* has been shown to also interact with PRE-MRNA PROCESSING 8 (PRP8a) and SILENCING MOVEMENT DEFICIENT 1 (SmD1b), in addition to NSRs. These proteins are central spliceosome components involved in the splicing of several flagellin-responsive genes. Accordingly, plants with a reduced level of *ASCO* transcripts are hypersensitive to flagellin as indicated by the reduction of primary root growth and root apical meristem size when they are treated with flagellin (53).

Other pathogens that profoundly affect root growth include the Root-knot nematodes (RKNs) that are some of the most destructive pests for agriculture, due to their large spectrum of plant hosts and the major decrease in yield they provoke upon infection (54). More than 500 lncRNAs are differentially expressed upon RKNs infection of roots, hinting that these molecules may be involved in the nematode stress response, even though genetic-based approaches are needed to specifically identify the lncRNAs involved in this process (55).

Collectively these results show that lncRNA expression is highly sensitive to environmental cues and that lncRNAs are emerging as novel components in the plant response to biotic and abiotic environmental stresses.

LncRNAs-mediating nutrient homeostasis and coordination of root growth

For the assimilation of minerals and to overcome nutrient limitation, plants evolved sophisticated mechanisms to adapt their root growth to the soil mineral content and environment. Here, we describe the role of lncRNAs in perception and signal transduction occurring during the acquisition of two essential micronutrients: nitrogen (N) and phosphate (Pi).

Application of nitrogen (N)-containing fertilizers significantly participates in increasing cereal yield and has a strong impact on root architecture, a trait influencing efficiency of nutrient uptake. Notably, N-dependent changes in root architecture are found in many plant species (56) and this has consequences on other root-dependent traits such as water acquisition. Concomitantly, it has been observed that N starvation changes the expression of multiple lncRNAs in arabidopsis (57), poplar (58), barley (59), maize (60) and rice (61). For example, two antisense lncRNAs are significantly induced in rice roots upon N starvation (61) and may regulate the *AMMONIUM TRANSPORTER 1* (*AMT1*) gene that participates in N assimilation (62). Furthermore, the *T5120* lncRNA is directly regulated by *NIN LIKE PROTEIN 7* (*NLP7*), a master regulator of the N signaling pathway, and it has been suggested that *T5120* might participate in *NITRATE TRANSPORTER 1.1* (*NRT1.1*) gene activation (63) (**Figure 1J**).

In contrast to other plants, legumes are able to develop nodules, a unique organ on their roots in which symbiotic N^2-fixing *rhizobia* capture the atmospheric N (64). Hence, legumes can have a major impact on soil nitrogen content and are key components of environmentally friendly agricultural practices (65). The *EARLY NODULIN 40* (*ENOD40*) lncRNA participates in legume nodulation (**Figure 1K**) and certain sequences of this gene are also conserved in non-legume plants (66). RNAi-mediated silencing of *ENOD40* in *Lotus japonicus* suppresses nodule formation (67). Strikingly, it has been proposed that the legume *ENOD40* lncRNA presents a dual function: on the one hand it can act as a lncRNA involved in nucleocytoplasmic trafficking of *NUCLEAR SPECKLES RNA-BINDING PROTEIN 1* (*MtRBP1*), a key regulator of gene expression (68), on the other hand it can lead to the production of two small peptides interacting with the sucrose synthase protein and participating in sucrose mobilization during nodulation (69). In medicago, a short variant of the *TAS3* lncRNA, known to be involved in LR growth in arabidopsis (see above, (24)) is induced in response to *rhizobia* and participates in nodule formation. An interesting variation in regulation occurs in this legume plant: this short variant of *TAS3* acts as a target mimicry of *miR390* due to specific nucleotide changes inhibiting *miR390* action in the production of the ta-siRNAs RNA targeting *ARFs* (tasiARFs) (70). Thus, the implication of lncRNAs for the regulation of N signaling pathway, assimilation and nitrogen-fixing symbiosis strengthens the relevance of the non-coding transcriptome for a proper N homeostasis in different plants.

In addition to N, phosphate (Pi), is another mineral essential for plant growth and development. Pi starvation triggers major changes of root architecture together with changes of gene expression within the root to increase P-nutrient acquisition from the soil

environment. For example, primary root growth of the arabidopsis Col-0 ecotype is immediately interrupted upon Pi starvation through a Fe-dependent mechanism (71). However, this response is not conserved across all arabidopsis accessions, such as the L*er* ecotype (72). Notably, it has been observed that the non-coding transcriptomes between Col-0 and L*er* ecotypes during early Pi starvation are strongly different when compared to the coding transcriptomes (73). Strikingly, in only one hour of Pi starvation, many lncRNAs are differentially regulated within arabidopsis root tips of these ecotypes (73). In the same study, the authors showed that *NPC48* and *NPC72*, two lncRNAs enriched in L*er* and Col-0 ecotypes respectively, significantly reduced the main root growth when overexpressed in Col-0. Further work is necessary to identify the root-related regulatory networks modulated by *NPC48* and *NPC72*. Note also that *NPC48* disturbs the transcriptional activity of key root growth regulators such as *ROOT MERISTEM GROWTH FACTOR 7* (*RGF7*), *BIG*, *RECEPTOR-LIKE PROTEIN KINASE 2* (*RPK2*) and *CASPARIAN STRIP MEMBRANE DOMAIN PROTEIN 5* (*CASP5*) (73) (**Figure 1L**), providing further support that lncRNAs are emerging regulators of root growth and suggesting a potential link with the differential responses to soil environmental conditions across ecotypes.

Plants have evolved many adaptive mechanisms to maintain a homeostatic level of Pi within their cells in soil environments with variable levels of combined Pi. For example, *PHOSPHATE 2* (*PHO2*) is involved in the Pi-starvation response, directly regulating the plant Pi homeostasis by controlling the degradation of *PHO1*, involved in Pi loading into the xylem (74). Coherently, the *pho2* mutant accumulates toxic amounts of Pi within the shoot, because of an uncontrolled Pi uptake and translocation into this tissue (75). Upon Pi starvation, *miR399* is induced and targets *PHO2* transcript, limiting Pi assimilation (30). Strikingly, two arabidopsis lncRNAs, *INDUCED BY PI STARVATION 2* (*At4*) and *INDUCED BY PI STARVATION 1* (*IPS1*), conserved in medicago, maize and tomato, are also induced within low Pi condition (76–78) and share a partial complementary sequence with *miR399*. Concomitantly, these Pi-induced lncRNAs act as miRNA sponges for *miR399,* affecting *PHO2* transcript level and thus Pi homeostasis (30,76–78) (**Figure 1M**). Similarly, *at4* mutants present a Pi homeostasis defect between the root and shoot compartment under Pi starvation (77,78). Other regulations may appear in other plant species that impinge on this regulatory module. For example, in rice, an antisense lncRNA of *OsPHO1;2* (*cis-NATPHO1;2*) participates in Pi homeostasis by promoting the translation of *OsPHO1;2* transcript (79) (**Figure 1N**). Notably, RNAi-mediated silencing of *cis-NATPHO1;2* decreases the quantity of OsPHO1;2 protein, reducing Pi content and grain yield. In contrast, *cis-NATPHO1;2* ectopic overexpression increased the OsPHO1;2 protein level (79). Hence antisense lncRNA regulation controls *OsPHO1;2* but this type of regulation is not conserved in arabidopsis or other species.

Altogether, there is growing evidence that lncRNAs are important regulators of various biological processes and stress responses. Interestingly, many lncRNAs show species or ecotype specific mechanisms (e.g. 73 and 79) suggesting that variation in their sequence or expression patterns may have consequences on the coding transcriptome and adaptation to different environments. Furthermore, many Genome Wide Association Studies (GWAS) for diverse agriculturally relevant traits have been mapped to intergenic regions containing lncRNAs, hinting at a potential function of lncRNA for root growth, development and responses to adverse constraints (80,81). Also, RNA molecules might be more attractive than proteins to modulate gene regulation as their effects may be more transient (82). Notably,

the use of nanoparticles enriched in lncRNA molecules may be used to directly control their targets, allowing plants to better cope with a transient adverse condition as recently shown in cotton (82). With less than 1% of the annotated plant lncRNAs functionally characterized, long non coding RNAs constitute an immense reservoir for discovering new gene regulatory mechanisms and may offer attractive targets for future plant breeding programs, in particular at the level of roots.

Perspectives

- Environmental changes disturb the root architecture and function, impacting water uptake, nutrient acquisition and plant anchoring. Unless cultivated plants acquire new adaptations, the foreseeable global changes will almost certainly decrease crop yield. In this context, the ability of lncRNAs to control root development and growth through the regulation of key root-related genes may open up new ways to breed plants for greater resilience and adaptation to local environmental conditions.

- All investigated crop transcriptomes show extensive variation in lncRNAs expression within the root compartment. Even though few plant lncRNAs have been functionally characterized to date, it is likely that their ability to modulate gene expression will make them key targets for plant improvement.

- We anticipate that new mechanisms of lncRNA-mediated regulation of gene expression will be discovered in the near future. Such discoveries may provide new strategies on how to incorporate these lncRNAs in plant breeding programs to subtly acclimate many crops to the coming environmental changes.

Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

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Abbreviations

ABA, abscisic acid; AMT1, AMMONIUM TRANSPORTER 1; APOLO, AUXIN REGULATED PROMOTER LOOP; ARF, AUXIN RESPONSE FACTOR; AS, Alternative Splicing; ASCO, ALTERNATIVE SPLICING COMPETITOR; CASP5, CASPARIAN STRIP MEMBRANE DOMAIN PROTEIN 5 ; CCR, CINNAMOYL-COA REDUCTASE; COOLAIR, COLD INDUCED LONG ANTISENSE INTRAGENIC RNA; COLDAIR, COLD ASSISTED INTRONIC NONCODING RNA; CK, Cytokinin; DRIR, DROUGHT-INDUCED LNCRNA; FLC, FLOWERING LOCUS C; IPS1, INDUCED BY PHOSPHATE STARVATION 1; LEA, LATE EMBRYOGENESIS ABUNDANT; lncRNA, LONG NON-CODING RNA; LR, Lateral Root; NRT1.1, miRNA, micro-RNA; N, Nitrogen; NITRATE TRANSPORTER 1.1; NSR, NUCLEAR SPECKLE RNA-BINDING PROTEINS; Pi, Phosphate; PID, PINOID; phasiRNAs, phasing-sirRNAs; PHO1/2, PHOSPHATE1/2; QTL, Quantitative Trait Locus; RGF7, ROOT MERISTEM GROWTH FACTOR 7; RHD6, ROOT HAIR DEFECTIVE 6; RPK2, RECEPTOR-LIKE PROTEIN KINASE 2; RKN, Root-knot nematodes; RdDM, RNA dependent DNA methylation; ROS, Reactive Oxygen Species; SCR, SCARECROW, siRNA, small-interfering RNA; sRNA, small RNA; VIGS, Virus-Induced Gene Silencing, Xist, X-inactive specific transcript; ZAT6, ZINC FINGER OF ARABIDOPSIS THALIANA 6.

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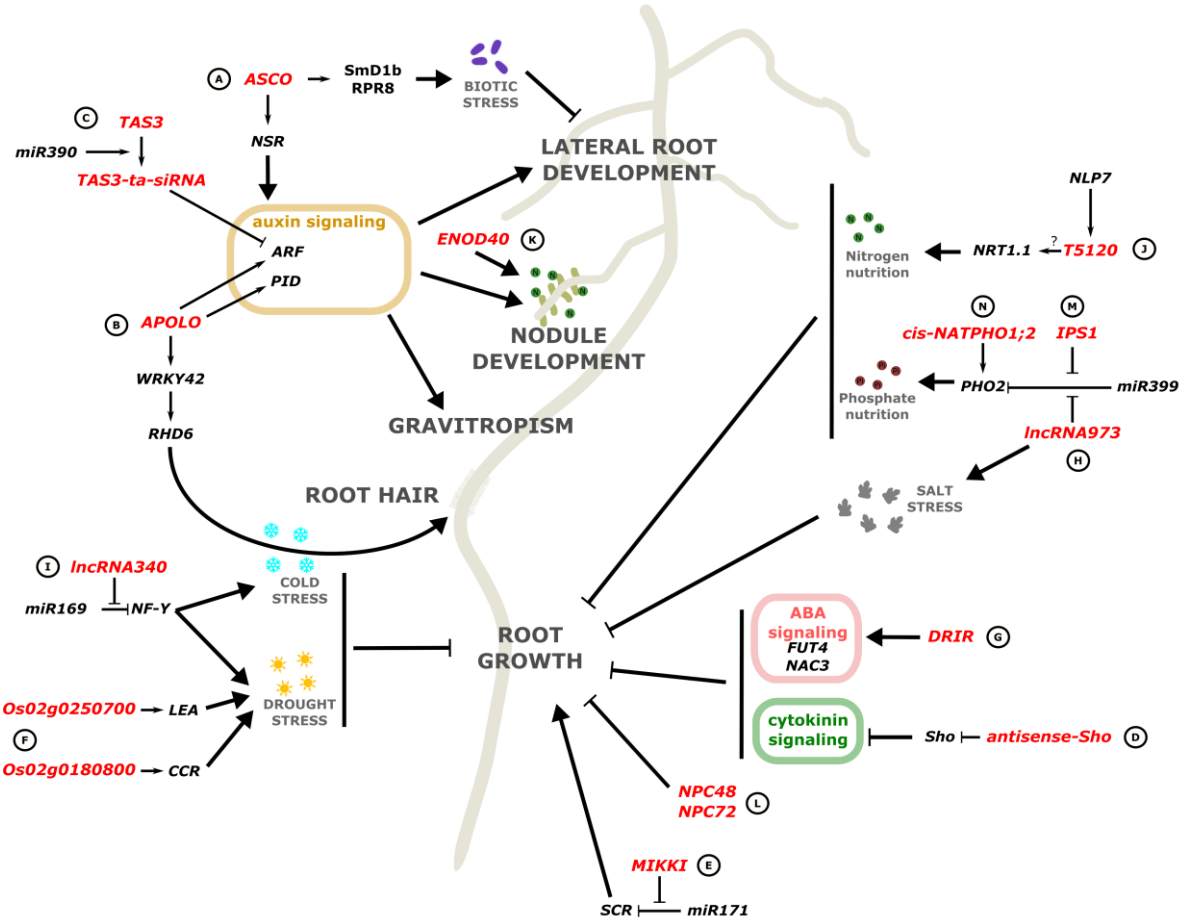

Figure 1. Involvement of lncRNAs in root growth, development and response to environmental stresses. A. The arabidopsis *ASCO* lncRNA modulates auxin induced lateral root growth and biotic stress responses through its interaction with NSR (17) and SmD1b-RPR8 (53), respectively. **B.** The lncRNA *APOLO* fine-tunes the expression of several auxin-responsive genes (22), regulating lateral root development and gravitropism in arabidopsis (21). In addition, it modulates the binding of the WRKY42 TF to the *RHD6* promoter, promoting root hair initiation under cold stress (50). **C.** The arabidopsis *miR390* processed the *TAS3* lncRNA into ta-siRNAs, mediating the inhibition of *ARFs* TF, positively influencing lateral root growth (24). **D.** In petunia, the cytokinin-mediated root growth inhibition is modulated by an antisense lncRNA of *Sho* gene, a repressor of cytokinin signaling (27). **E.** The rice *MIKKI* lncRNA shapes the root architecture through target mimicry of the *miR171-SCR* module (29). **F.** *Os02g0250700* and *Os02g0180800* are two antisense rice lncRNAs modulating root growth, improving plant drought tolerance through the regulation of *LEA* and *CCR* genes, respectively (36). **G.** *DRIR* is an arabidopsis lncRNA regulating a subset of ABA-related genes, including *FUT4* and *NAC3* (37). **H.** *LncRNA973* is a cotton lncRNA participating in salt stress responses of roots (42). It also acts as target mimicry of the *miR399-PHO2* module to control phosphate (Pi) homeostasis (30,46,47,49). **I.** The *lncRNA340* in the roots of the crop cassava acts as target mimicry of the *miR169-NF-Y* regulatory interaction, participating in cold and drought stress tolerance (35). **J.** The master regulator of nitrogen signaling *NLP7* in arabidopsis promotes the *T5120* lncRNA transcriptional activity, likely participating in *NRT1.1* gene activation known to be implicated in nitrogen assimilation (63). **K.** The medicago *ENOD40* lncRNA promotes nodule development (69). **L.** *NPC48* and *NPC72* are two arabidopsis lncRNAs whose overexpression inhibits primary root growth (73). **M.** The *IPS1* lncRNA acts as target mimicry for the *miR399-PHO2* module in arabidopsis, medicago, maize and tomato, participating in Pi homeostasis (30,74,77,78). **N.** In rice, an antisense lncRNA of *PHO1;2* (*cis-NATPHO1;2*) promotes *PHO2* transcript translation, participating in phosphate homeostasis (79).