Review

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Root apex transition zone: a signalling–response nexus in the root

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Longitudinal zonation, as well as a simple and regular anatomy, are hallmarks of the root apex. Here we focus on one particular root-apex zone, the transition zone, which is located between the apical meristem and basal elongation region. This zone has a unique role as the determiner of cell fate and root growth; this is accomplished by means of the complex system of a polar auxin transport circuit. The transition zone also integrates diverse inputs from endogenous (hormonal) and exogenous (sensorial) stimuli and translates them into signalling and motoric outputs as adaptive differential growth responses. These underlie the root-apex tropisms and other aspects of adaptive root behaviour.

Unique root apex organization and distinct zonation

Roots explore soil in their search for nutrients. To perform this task efficiently, roots need large volumes of soil due to the patchy nature of water and nutrient distributions [1–5]. The only way for roots to move in the course of this exploration is by means of growth during which complex root systems are generated [3,4]. Growing roots show complex patterns of behaviour with indications of animal-like features such as decision-making, sensory-motoric circuits, search and escape movements, as well as self–non-self and kin recognition [5–10].

Whereas shoot apices are covered and protected by young leaves, root apices are covered by only a root cap [11] (Box 1). The remainder of the root apex, behind the cap, shows a distinct zonation, or longitudinal 'segmentation', which is comprised of a distinct meristem, and a zone of rapid cell elongation separated by a transition zone [12–16] (Box 1 and Figure 1). Another feature of root apices is that the meristematic zone is usually devoid of any additional organogenesis (in the sense of visible primordia of new lateral organs) except for making the primary apex itself. Secondary or lateral root initiation starts only at the base of the elongation region, from sites deep within the root body, at the cortex–stele interface [17] .

Here we review the anatomical and functional aspects of root apex organization, especially the polar auxin transport circuits within the transition zone (Figures 1 and 2), which underlie the signalling and behavioural complexity of plant roots.

Transition zone of the root apex: brief historic overview

The root transition zone concept, in its original sense, states that root cells leaving the apical meristem need to accomplish a transitional stage of cyto-architectural rearrangement, especially of the actin cytoskeleton, in order to perform rapid cell elongation [12,13,18]. Cells of this zone also have unique functional and sensorial properties [14,19,20]. Looking more deeply into the history of plant science, one can find the first recognition of the existence of such a zone in the famous book by Charles and Francis Darwin 'The Power of Movement in Plants' [21]. The Darwins stated that a zone 1.0–1.5 mm from the root tip of maize (*Zea mays*), which corresponds to the location of the transition zone in this root [12], is the most sensitive zone of the root apex with respect to reaction to stimuli (page 192 in [21]). The unique nature of this zone was also recognized, but not further elaborated upon, by Julius Sachs [22]. In the recent literature, this zone was at first termed 'postmitotic isodiametric zone' [12,13,23]. Then, it was renamed the 'distal elongation zone' [24], and later still the 'transition zone' [13–16,18]. Terms like 'basal meristem' [25–28], 'distal root meristem' [29] or 'zone of competence' [26], were also introduced for this same zone, and have often been used in the contemporary literature. These alternative appellations make the whole topic perplexing since it is not obvious whether or not these different names refer to the same zone. Although the original transition zone concept was elaborated for maize roots [12], it proved valid also for *Arabidopsis* roots [15]. The rapid cell elongation starts abruptly, not at the rather ill defined basal border of the meristem, but at a relatively sharp border at the base of the transition zone [12,15] (Figures 1–3 and Box 1). Since cell divisions are exceptional in this postmitotic root apex zone [12,15], the 'transition zone' appears to be the most suitable name for what turns out to be a rather unique portion of the root apex.

Hormonal network integration at the transition zone

The transition zone has received much attention in studies of roots devoted to the action of auxin, cytokinin, ethylene, gibberellins and brassinosteroids. Hormonal crosstalk has been shown to determine developmental cell fates as well as mediating rectilinear root growth and the differential growth of tropisms [30–33]. Firstly, cytokinin was discovered to act specifically in vascular cells of the transition zone where it controls the growth and fate of cells of all other root tissues via a regulatory circuit converging on

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Box 1. Root apex *versus* shoot apex

Besides the discussed differences in zonation, organogenesis and transcellular auxin transport complexities, there are also other profound differences between root and shoot apices. As all these are interrelated, and therefore relevant for the special status of the root apex transition zone, we list in this Box the most important root–shoot apex differences.

1- The outer–inner polarity of the plant body [43]: the inner pole (stele) is dominant in the root whereas the outer pole (cortex) dominates in the shoot [43,44].
2- The inner pole (stele) reaches to the very tip of the root apex but not to that of the shoot apex [44].
3- There is a fundamental difference in the root and shoot stem cells. Whereas the root apex stem cells specify the three major ground tissues of the plant body (dermal, ground and vascular tissues), the shoot apex stem cells specify the new leaf primordia (lateral organs).
4- Organogenesis is active at the shoot apex but absent (in the form of visible primordia) from the root apex [44].
5- Organogenesis is peripheral at the shoot apex, initiated in the epidermis; whereas the root organogenesis is endogenous, initiated at the endodermis/pericycle cortex–stele boundary.
6- Endodermis controls root growth, with a major impact expressed in the transition zone [37,38].
7- Epidermis controls shoot growth at the shoot apex [41,42].
8- Cell files are very regular within the root apex, but less so within the shoot apex [44].
9- PIN2 expression is root-apex-specific, with its maximum in the transition zone. PIN2 is essential for tropisms of the root, but not for those of the shoot.
10- Transition zone is very prominent in the root apex but is not obvious in the shoot apex [40].
11- There are two bending zones in the root apex. Besides the bending capabilities of the elongation region (present also in the shoot apex), there is also a root-apex-specific, PIN2-based bending in the transition zone of the root apex.
12- PIN1 and PIN7 are expressed in the epidermis of hypocotyl and shoot apex, whereas they are expressed in the endodermis and stele of root apex [64].
13- PINOID kinase targets PIN2 in cells of root apices [84], but it targets PIN1 in cells of shoot apices [99,110–112].
14- The gain-of-function mutant of PINOID kinase causes collapse of the root apex, whereas the loss-of-function mutant of PINOID kinase causes collapse of the shoot apex [110–112].
15- Root apex has two inverted fountains of polar auxin transport (Figure 2) converging on two different auxin signalling maxima (BA3 and DR5) ([65], discussed in [80]).
16- Root apex is covered by a root cap, a major plant sensory organ [44].

transcription factor SHORT HYPOCOTYL2 (SHY2) [34,35], a member of the auxin-repressor Aux/IAA family [36]. Cytokinin/auxin crosstalk is embedded within even more complex hormonal networks in the transition zone [29–33] which, in their turn, control diverse aspects of root biology such as tropisms, behaviour and communication [2–10,20]. Secondly, gibberellin signalling in the endodermis of the transition zone has been shown to control root meristem size [37] via targeting the degradation of DELLA repressor proteins (named after a highly conserved DELLA amino-acid motif in their N-terminal domains) [38]. DELLA-dependent mechanisms are relevant also for regulating cell cycle activities in the root meristem [39] and help define the border between the basal meristem and distal portion of the transition zone [40]. The endodermis is present within the transition zone and acts as major gibberellin-responsive tissue regulating the cell expansion necessary for root growth [32,37,38]. It is interesting to note that, in shoots, the control of growth does not reside at the endodermis but at the epidermis [41]. In this case, brassinosteroid signalling underlies the epidermal growth control [41,42]. This reversed outer–inner control tissue phenomenon resembles the concept of outer–inner polarity of the plant body with respect to hormone sensitivities proposed by Si-Jiu Liu and Elisabeth Tillberg [43]. In this concept, the inner pole is represented by the vascular tissues of the central cylinder whereas the outer pole is represented by the cortex tissues and the epidermis (Box 1). In shoots, the outer pole predominates whereas in roots the inner pole is dominant [43,44]. In accordance with this model, it is known that the shoot-derived auxin controls root apices and the root-derived cytokinin controls shoot apices [45–47].

Another important hormone with respect to cell fates and growth control is the volatile hydrocarbon, ethylene, which interacts with all other hormones [29,48]. Ethylene–auxin crosstalk is relatively well understood and is relevant for both root apex patterning and control of root growth. Ethylene regulates root growth via its impact on both auxin biosynthesis and polar auxin transport [29,48,49]. Transition zone cells play a critical role in this respect for they respond to increased ethylene levels with an increased level of PIN2 production and a stimulation of basipetal auxin transport [48], specifically in outer tissues of the root apex [43]. In the elongation region, the response to an increased ethylene level is different because cell growth here becomes rapidly and irreversibly inhibited [50,51].

Two coordinated bending zones drive root tropisms

Gravitropism is one of the many tropisms displayed by growing roots in which physical as well as biological cues operate [6,52,53]. The transition zone initiates a growth differential between the upper and lower parts of a horizontally gravi-stimulated maize root [24]. Here, the growth differential is not due to disparate cell growth rates but to a shifting of the location where cells will begin passage into and through the transition zone [13,54]. Cells on the upper part of the root advance their passage through the transition zone into the zone of rapid cell elongation (i.e. they spend a shorter period in the transition zone) whereas the lower side cells are retarded in this developmental transition [13,23,54]. Importantly, the differential progression of cells through the transition zone is independent of the microtubular cytoskeleton [54]. Other studies have shown that the actin cytoskeleton is also not needed [55,56] for this differential cell growth which drives gravitropism of roots [57,58]. Interestingly, there are two distinct growth (bending) regions, corresponding to the transition zone and elongation region (see the arrows in Figure 1), which drive the differential growth of root electrotropism [59]. Root tropisms as well as shoot tropisms, are based on polar auxin transport affected by proteins of the PIN family, as well as by members of the PGP/ABCB family of ABC transporters [60–62].

PIN2 helps to distinguish root apex from shoot apex

Shoot and root apices differ in the expression of the auxin transport-facilitator protein, PIN2 (Box 1). This protein is

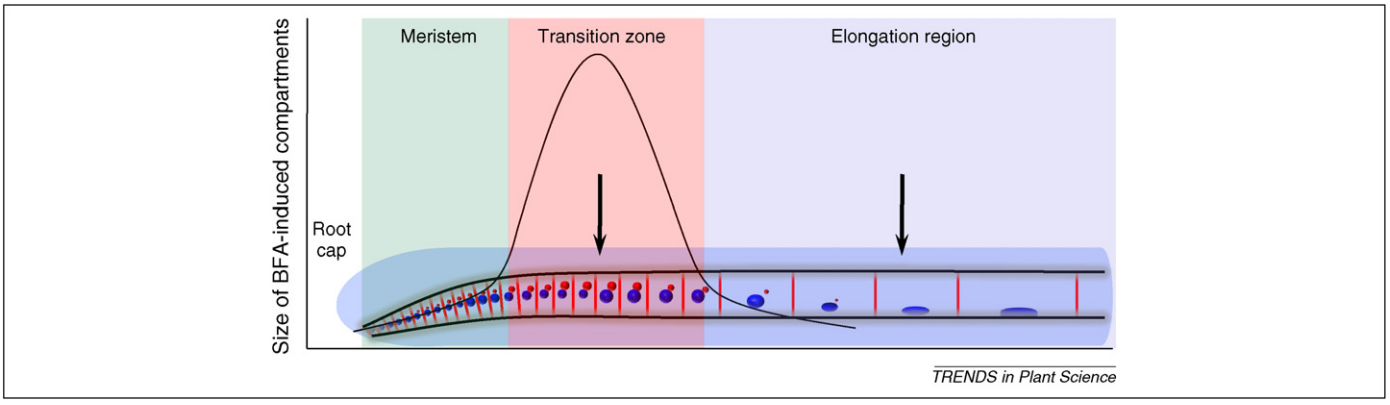

Figure 1. Root apex zonation. Bending of the transition zone is related to vesicle recycling rate which shows a peak in this zone, as visualized by the size of BFA-induced compartments. BFA treatment prevents this transition-zone root bending. Blue structures are nuclei, red structures represent BFA-induced compartments. Size of these endocytic compartments [78,82] is proportional to the endocytic vesicle recycling rate (for further details see [20,50,74,75,78,79,81–83,107,109]). Arrows indicate the two bending zones.

essential for root tropisms but not for shoot tropisms. In root apices, PIN2 is responsible for the backward (towards the root base) auxin flow in the epidermis and outer cortex (in the case of maize roots), as well as for the second inverted fountain of auxin flow at the basal border of the transition zone (Figure 2). PIN2 is essential for gravitropism and phototropism of root apices, whereas both these behavioural processes are performed in the absence of PIN2 in shoot apices (Figure 2 and Box 1). In the case of root tropisms the PIN2 protein is tightly linked with the outer-pole backward stream of auxin (Box 1).

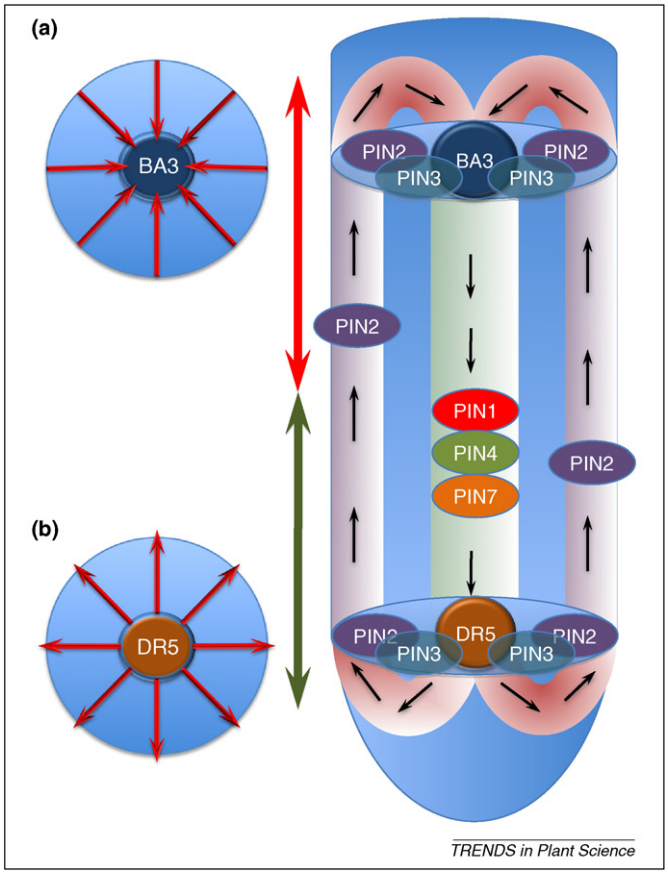

Figure 2. Two inverted fountains of the polar auxin transport at the root apex. **(a)** The basal 'outside-in' fountain, generated by concerted actions of PIN2 and PIN3, localizes to the basal limit of the transition zone and is visualized via the BA3 construct activity [65]. **(b)** The apical 'inside-out' fountain, generated by concerted actions of PIN1, PIN7 and PIN4, localizes to the quiescent centre and root cap initials and is visualized via DR5 construct activity. The apical meristem is indicated by the green bar, the transition zone by the red bar. For further details see [15,16,29,31,33,60,61,63,65,67,75,81,94].

PIN2 mutant lacks the transition zone bending

In contrast to shoot apices, where only PIN1 is expressed, polar auxin transport in root apices is driven by activities of five PIN proteins (PIN1–4 and PIN7), as well as by other auxin transporters from the ABCB family, such as ABCB1, ABCB4 and ABCB19 [28,60,61] and reviewed in [62–64] . This complexity contrasts with the apparent simplicity and regular anatomy of root apices [15,20]. In a root apex growing downwards along the gravity vector, the acropetal (towards the root apex) streams of auxin form a symmetrical fountain focusing upon the quiescent centre (Figure 2). Then, this stream loops backwards, travelling through the epidermis and outer cortex (in maize roots). At the basal border of the transition zone, the basipetal auxin stream loop reverses its direction, thus making an inverted fountain as it loops back again into the acropetal stream in the stele [28,64] (Figure 2). Root apices differ from the shoot apices by having two bending zones supported by two fountains of the polar auxin streams (Box 1, and Figures 1 and 2). Interestingly, whereas the acropetal inside-out fountain is associated with the DR5-based auxin-signalling maximum, the basipetal transition-zone-based outside-in fountain (Figure 2) is associated with the BA3-based auxin-signalling maximum [65]. Whereas PIN1, PIN4 and PIN7 feed into the DR5 maximum, PIN2 and PIN3 feed into the BA3 auxin-signalling maximum (Figure 2). The symmetry of these two 'auxin-stream' fountains is sensitive to physical signals such as gravity, light, temperature, humidity, oxygen concentration and several other stimuli [2,6,52,53,66]. As a result of such stimulation, root apices initiate either positive or negative tropisms, according to the vectors, gradients and strengths of these environmental stimuli [52,53] (Box 1).

PIN3 mutant lacks the elongation region bending

Similar to PIN2, PIN3 has a unique status amongst PIN proteins. Whereas all other PINs drive the auxin streams along the axes of plant organs, PIN2 and PIN3 are responsible for lateral auxin flows within both the statocytes of the root cap [64,67] and the cells of epidermis and cortex

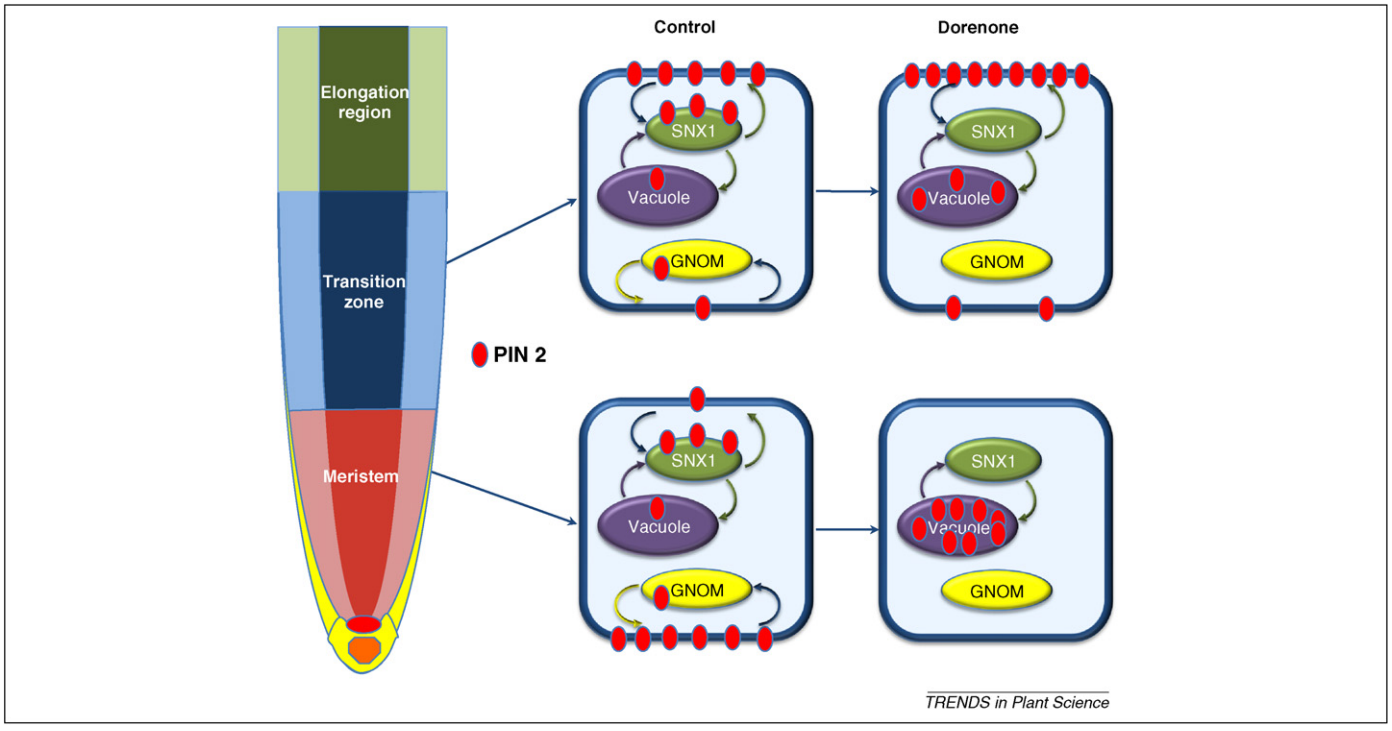

Figure 3. Subcellular zone-specific PIN2 targeting via endosomes in cortical cells. Apical targeting of PIN2 molecules (red structures) via the GNOM-based endosomes, and basal targeting via the SNX1-based endosomes which control the subcellular fate of recycling PIN2 molecules in cells of the meristem and the transition zone (for details see [95–106,110–112]). D'orenone specifically affects PIN2 in these two zones [73]: PIN2 is degraded in vacuoles in cells of the meristem and stimulated (higher gene expression and more PIN2 molecules) at the basal-end portion of the plasma membrane in cells of the transition zone (for further details see [73]).

(PIN2) as well as the endodermis/pericycle of the transition zone (PIN3) [28,35,60,67,68] (Figure 2). In fact, PIN3 is expressed in the endodermis (see Box 1) throughout the plant body and effects lateral auxin transport into the stele [63,69]. This endogenous lateral auxin flow is joined by the sensorially-induced lateral auxin flow resulting from either gravi-stimulation or light-stimulation and thereby initiates organ tropisms [63,69,70]. While the production or expression of PIN2 is downregulated at the basal border of the transition zone, the expression of PIN1, PIN3 and PIN7 continues throughout the elongation region (see the Figure 2 in [71]). Importantly, a recent study of a *pin3* mutant line revealed that, although it has normal root bending in the transition zone, it failed to bend in the elongation region [68]. Obviously, the lateral auxin transport supported by PIN3 is essential for the differential growth in this second root-bending zone in the elongation region (Figure 1) but is not required for the bending at the transition zone [72,73]. *pin2* roots are almost insensitive to ethylene [72]; however, although they fail to respond to internally generated auxin, they respond normally to externally applied auxin [72].

The transition zone is the most active zone with respect to auxin flux

In order to understand *in vivo* auxin transport, a crucial technique is one which monitors auxin fluxes in real time. To achieve this, auxin fluxes were monitored within intact plant organs using non-invasive carbon nanotube-modified and self-referencing, auxin-specific microelectrodes [74]. A surprising result was the finding of a peak of auxin flux in the distal portion of the transition zone, which, in large maize root apices, extends over the distance of 0.9–1.8 mm from the root tip [74]. These cells show fluxes significantly higher than those in the more apical cells of the root cap and root meristem, or in the more basal cells of the elongation region (see the Figure 3 in [74]). A similar pattern of auxin flux has been measured also for roots of *Arabidopsis* [75–77]. All this suggests that, in both dicots and monocots, this distinct peak of auxin flow is inherently related to cellular and subcellular processes specific to the distal portion of the transition zone.

Transcellular auxin transport in the transition zone is driven by vesicle recycling

The peak in auxin flux is very sensitive not only to the classical inhibitors of polar auxin transport such as N-1-naphthylphthalamic acid (NPA) and 2,3,5-triiodobenzoic acid (TIBA), but also to brefeldin A (BFA; Figure 3 in [74]). All these inhibitors affect auxin flux via an inhibition of vesicle trafficking [78,79]. This indicates that PIN proteins support auxin flux via vesicular secretion of auxin based on the endocytic vesicle recycling. Immunolocalization of auxin in maize root cells confirms auxin enrichment in the endosomes that participate in polar auxin transport [80]. In further support of this neurotransmitter-like mode (i.e. secretion via endocytic vesicle recycling) of auxin transport by cells of the transition zone [81], is the very close correlation between the rate of vesicle recycling and the auxin flux in the transition zone [82–84] (Figure 1). However, there is no clear correlation between the number of PIN molecules at the plasma membrane and the auxin flux [80,83,84].

Vesicle recycling peak corresponds with peaks of auxin flux and electrical activity

Studies devoted to expression and activities of phospholipase Dζ2 (PLDζ2), which produces the second messenger, phosphatidic acid (PA), revealed that *Arabidopsis* PLDζ2 regulates vesicle trafficking and is required for an auxin response [85–87]. Interestingly, PLDζ2 (and PLDζ1) is different from the other 10 PLDs in *Arabidopsis* in that it resembles mammalian PLDs with respect to its PX and PH domains; moreover, it is strongly expressed in roots, especially in transition zone cells [75,85,88]. Overexpression of PLDζ2, as well as the addition of PA, stimulates vesicle recycling and auxin transport in the transition zone [75]. Here, the peak in the polar auxin transport is based on the high rate of BFA-sensitive endocytic vesicle recycling, supporting the neurotransmitter secretion model for auxin transport [75,85,87] (Box 1). Furthermore, a *pldzeta2* mutant [75,85,88] shows inhibited auxin secretion in the transition zone, and the *pldzeta* phenotype can be mimicked following exposure to the general PLD activity inhibitor, 1-butanol [75]. Importantly, PLDζ2 is expressed specifically in cells of the transition zone [75,85].

Besides being a site of a high rate of endocytosis-based vesicle recycling, which in some obscure way is linked to the auxin transport peak, the transition zone of the root apex shows exceptional behaviour regarding electrical activity. Using a 60-channels multielectrode array (MEA), spatiotemporal characteristics of the electrical network activity of the maize root apex were analyzed [89]. Data obtained by this means revealed synchronous and oscillatory electric activity in the transition zone only, supporting the concept that this zone of the root serves some, so-far unknown, but apparently specific purpose for the integration of internal and external signalling. Interestingly, these cells are also very effective in supporting coherent transcellular calcium waves spanning the whole root apex after mechano-stimulation (see Figure 3d in [90]) and in the touch-induced ATP release from cells into extracellular space [91]. These phenomena are relevant for cell–cell signalling and obstacle-avoidance behaviour of growing root apices [90,91].

Unique nature of PIN2 polarity in the transition zone

The PIN2 protein does not belong to any of the multiple PIN subclasses: one subclass encompasses PIN1, PIN3, PIN4 and PIN7, whereas a second subclass contains PIN5, PIN6 and PIN8 [92]. PIN2 is unique amongst PINs in supporting basipetal (against the gravity vector) transport of auxin. In the *pin2* mutant line, PIN1 can partially replace PIN2 [93,94]. PIN2 undergoes a shift in its intracellular localization in root cortex cells; mitotic cells target PIN2 acropetally, whereas the transition zone cells, and the cells of epidermis, target it basipetally [95] (Figure 3). Recent reports indicate that PIN2 is targeted to the apical (facing the root apex) pole of the cell via the GNOM-based endosomal recycling pathway, whereas sorting nexin 1 (SNX1) endosomes link PIN2 polarization to the opposite basal pole of the cell [96–99] (Figure 3).

PIN2 is a general stress target and underlies avoidance and escape tropisms of roots

Mutant roots devoid of PIN2 are not only inferior in their gravitropic and phototropic responses, but they are also extremely sensitive to diverse environmental cues and stress situations. Firstly, PIN2 rapidly associates with endosomal compartments in cells at the lower, slowly expanding part of gravi-stimulated root apices [100]. SNX1 emerges as a marker of these elusive endosomes responsible for control of localization and fate of PIN2, at least in cells of root apices [101–103]. Enrichment of PIN2 in these endosomes is also a feature of all cells in the transition zone when roots are kept in darkness [104] – the normal situation of plant roots growing in their natural soil habitat. Next, PIN2 is targeted into endomembrane compartments and is selectively degraded in salt-stressed root cells [105]. The functional disassembly of this gravisensitive network based on PIN2 allows roots to deviate from the gravity vector and to accomplish salt-stress avoidance tropism [106]. A similar situation, when PIN2 is rapidly degraded in cells of the meristem, was reported for *Arabidopsis* roots exposed to D'orenone, an early cleavage product of β-carotene *en route* to trisporic acids [73] (Figure 3).

Transition zone PIN2 emerges as the aluminium-toxicity target of root apices [83,107]. Intriguingly, in this stress situation, PIN2 endocytosis is inhibited [105]. As a result of this, the amount of PIN2 at the plasma membrane was increased, whereas PIN2 was depleted from the endosomes [83]. Similarly, cold-stress inhibited recycling of PIN2, and of PIN3 also, and kept almost all PIN2 molecules at the plasma membrane [108]. Cells of the transition zone are also unique with respect to both PHOT1-based sensing of blue light and the negative phototropism of root apices [109]. Illuminated roots grow quicker and perform enhanced vesicular recycling of both PIN1 and PIN2 [104]. This response has been proposed to constitute a new kind of root tropism – the light-escape tropism [66].

Conclusions

The transition zone of root apices is a unique part of the whole plant body. Apart from tip-growing cells, such as root hairs and pollen tubes, the cells of the transition zone have the highest rate of vesicle recycling activity, and their auxin transport shows the highest degree of activity. In this root apex zone, auxin is secreted across the recycling and F-actin–myosin VIII-based cell–cell adhesion domains in a neurotransmitter-like fashion [81] which is driven by PLDζ2 activity [75]. This is the only zone in the whole plant body for which synchronized electrical activity has been reported [89]. The activity of auxin-secreting domains of the transition zone is sensitive not only to internal developmental cues but, importantly, also to environmental inputs such as light and gravity. The transition zone integrates the sensory-motoric circuits, allowing diverse root tropisms. Importantly, the natural environment for roots is darkness, and illumination of *Arabidopsis* roots activates a light-escape tropism [66]. Consequently, conclusions reached from numerous already published *in vivo* data obtained using illuminated roots may require fundamental re-interpretations.

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