Root Apex Cognition: From Neuronal Molecules to Root-Fungal Networks

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What we see is the blossom, which passes. The rhizome remains.
Jung (1963)

Abstract Plant roots are generally hidden from our sight, growing and living underground in alliances with symbiotic fungi. In order to find enough water and critical mineral nutrients, they explore large areas of soil with their root apices acting as plant cognition-based brain-like organs allowing them to use kin recognition, self/non-self recognition as well as swarm intelligence. Importantly, fungal hyphae integrate root systems into huge root-wide webs which allow not only the sharing of water and mineral nutrients, but also support long-distance chemical and electric signals. Roots use neuronal molecules such as glutamate and GABA supported by their specific receptors, as well as actin-based synapses and the plant-specific action potentials, to perform all their social activities and cognitive navigation for soil exploration.

1 Introduction

Plants conquered land in a tight co-evolution with symbiotic fungi, especially with the soil-borne members of the phylum Glomeromycota: arbuscular mycorrhiza (AM) fungi which teamed up with plant roots some 400 million years ago (Selosse and

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https://doi.org/10.1007/978-3-030-84985-6_25

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S. Mukherjee and F. Baluška (eds.), *Rhizobiology: Molecular Physiology of Plant Roots*, Signaling and Communication in Plants,
https://doi.org/10.1007/978-3-030-84985-6_1

Le Tacon 1998; Redecker 2000; Selosse et al. 2015; Remy et al. 1994; Field et al. 2015; Hoysted et al. 2018). These so-called endomycorrhizal fungi were followed in evolutionary history by ectomycorrhizal (ECM) fungi, which grow as saprotrophs in soil and enter into mutualistic symbiosis with many trees by enveloping their root tips with mycelial mantles (Bonfante and Genre 2010; Genre et al. 2020). Whereas hyphae of the AM fungi enter root cells and form intracellular arbuscules, hyphae of the ECM fungi remain outside of root apex cells, forming Hartig nets and mantles surrounding the root apices (see Fig. 1 in Bonfante and Genre 2010; Genre et al. 2020). A unique feature of AM fungi is that the hyphae of their extraradical mycelium typically interconnect several root apices not only of the same plant, but also different plants of different species, forming 'common mycorrhizal networks' also known as the 'wood-wide-web' (Simard et al. 1997; Read 1997; Giovannetti et al. 2006; Beiler et al. 2010; Rog et al. 2020; Gorzelak et al. 2020). Besides plants specialized for either AM or ECM symbiosis, there are also so-called dual-symbiosis plants capable of associating their root apices with both the AM and ECM fungi (Brundrett and Tedersoo 2018; Teste et al. 2020).

2 Root Apex Transition Zone: Oscillatory Brain-Like Cognitive Organ in Soil Exploration

Evolution of roots in land plants was accomplished via root-fungal co-evolution when the first ancient plants succeeded in overcoming the difficult transition from sea to land (Taylor et al. 1995; Redecker 2000). This is obvious not only from paleontological records but also from the root-fungal symbiosis found in the earliest plant lineages of evolutionary ancient plants including Lycophytes, Liverworts and Hornworts (Rimington et al. 2020). Although it is generally accepted that the roots of vascular plants evolved later than their shoots (Raven and Edwards 2001), the lower capacity of roots to fossilize make this scenario less stringent. Furthermore, several extant plants lacking roots lost them secondarily, making it difficult to properly evaluate fossil plants lacking roots as this may also be the derived condition (Raven and Edwards 2001). Regardless, it is clear that the evolution of roots was accomplished in a stepwise manner with numerous progressive changes culminating in the generation of complex root systems found among contemporary flowering plants (Kenrick and Strullu-Derrien 2014; Hetherington and Dolan 2017, 2018; Hetherington et al. 2016; Fujinami et al. 2020).

In 1880, Charles Darwin suggested that the root apex acts as a brain-like organ, '*…brain being seated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements*' (Darwin 1880; Baluška et al. 2006a, 2009a; Barlow 2006). This surprising claim received severe criticism from Julius Sachs, an influential contemporary botanist who accused Charles Darwin and his son Francis of performing flawed experiments in their country house (Heslop-Harrison 1980; de Chadarevian 1996; Ayres 2008). This dispute was a crucial crossroads in plant science, which was won by Julius Sachs not with scientific arguments but rather using his scientific political influence as leading figure in the field of plant physiology at that time. He asked his technical assistant Emil Detlefsen to repeat the experiments involving the surgical removal of maize root caps (originally reported by Ciesielski 1872) but he was not able to repeat this rather simple experiment properly (Detlefsen 1881), even though he was a skilled assistant of Sachs. However, strong support in favour of Sachs also came from Julius Wiesner, professor of plant anatomy and physiology at the University of Vienna (Wiesner 1881, 1884a, b). Now we can only speculate what would have been the outcome for plant science if Julius Sachs and Julius Wiesner would have accepted that even experiments performed in a country house can produce good results. Later, Francis Darwin and Wilhelm Pfeffer published data confirming that maize roots, with the caps cleanly removed, are well-suited for experiments and that the allegedly flawed Down House root experiments outcompeted the laboratory experiments of Sachs and Detlefsen (Krabbe 1883; Heslop-Harrison 1980; de Chadarevian 1996; Ayres 2008; Kutschera and Briggs 2009). Currently, the removal of maize root caps is accepted methodology and removed root caps regenerate completely within 30–40 h (Juniper et al. 1966; Barlow 1974; Barlow and Sargent 1978; Barlow and Hines 1982; Bennet et al. 1985; Iijima et al. 2003; Feldman 1976). The roots of dicot plants such as pea and arabidopsis are also capable of root cap regeneration (Barlow and Hines 1982; Sena et al. 2009; Efroni et al. 2016). For example, when plant regeneration is accomplished using callus tissue then it occurs via root development pathways (Sugimoto et al. 2010, 2011).

In 1997, we succeeded at immunofluorescence labelling of F-actin cytoskeletons in the intact root apices of maize (Baluška et al. 1997a), the same model structure which caused the severe dispute between Sachs and Darwins in 1880. This was the first time the actin cytoskeleton was visualized not in protoplasts or isolated plant cells, but in cells organized intact within tissues of the root apex. Abundant F-actin meshworks were found to be associated with the non-growing end-poles/cross walls of the transition zone cells (Baluška et al. 1997a, 2000, 2003a). In 2003, we outlined the plant synapse concept for the first time (Baluška et al. 2003b, 2005). Our data showed that this F-actin-based recycling of vesicles, including cell wall components, especially pectins, allows for effective cell–cell communication in the root apex (Baluška et al. 2002, 2003a, b, 2005, 2009b). Later studies revealed that this endocytic vesicle recycling is linked with the polar auxin transport accomplished via PIN-based export of auxin out of cells in root apices (Šamaj et al. 2004; Mancuso et al. 2005; Baluška et al. 2009b, McLamore et al. 2010). The same situation was found also for the transition zone in *Arabidopsis thaliana* roots (Verbelen et al. 2006; Schlicht et al. 2006; Mancuso et al. 2007; Dhonukshe et al. 2009; Mettbach et al. 2017). Later it emerged that this is part of the actin-auxin oscillator that drives polar trans-cellular transport of auxin through plant tissues (Holweg 2007; Nick 2007; Nick et al. 2009; Baluška and Mancuso 2013a, b, c).

There are several critical features suggesting that the root apex transition zone represents the root *brain* as proposed by Charles and Francis Darwin in 1880 (Darwin 1880; Baluška et al. 2006a, 2009a). First of all, cells in this developmentally unique zone are not distracted by any obvious tasks. They are neither dividing nor rapidly elongating, which allows them to focus on sensory integration tasks. They are located in very close proximity to phloem unloading sites which means that they are flooded with abundant levels of sucrose (Complainville et al. 2003; Ross-Elliott et al. 2017). This is associated with high activities of cell wall invertase, an enzyme which cleaves sucrose to hexoses (Hellebust and Forward 1962; Giaquinta et al. 1983; Roitsch and Gonzales 2004). Moreover, a high level of apoplastic sucrose induces osmotic stress which is relieved via induction of the fluid-phase endocytosis in cells close to phloem unloading sites (Baluška et al. 2004d). Another way to relieve this stress due to high sucrose levels is to synthesize large starch grains within the amyloplasts of the root apex transition zone cells (Fig. 6 in Baluška et al. 1993a and Fig. 2 in Baluška et al. 1993b).

This exceptional status of the transition zone cells allows them to focus mainly on cognitive tasks, resembling the situation of neurons of the central nervous system (CNS) seated within animal brains. Moreover, similar to CNS neurons, cells in the root apex transition zone also require greater levels of nutrient resources and oxygen (Baluška and Mancuso 2013a, b, c) in order to produce the ATP molecules necessary to drive the energetically demanding endocytic vesicle recycling and to support abundant and synchronized electrical spiking activities (Masi et al. 2009, 2015). This view is supported by a study reporting high cytosolic phosphate (Pi) concentrations in the transition zone for both epidermal and cortical cells of *Arabidopsis thaliana* root apices (Sahu et al. 2020). Pi is critical for ATP synthesis in mitochondria and for the synthesis of membrane phospholipids. In roots facing low levels of Pi in their environment, root caps act as the sensing organ which promptly stops root growth under Pi deficiency (Svistoonoff et al. 2007; Kanno et al. 2016). In this sensory circuit, the STOP1 transcription factor and ALMT1 anion/GABA (Ramesh et al. 2015, 2017, 2018; Žárský 2015; Kamran et al. 2020) act together to stop root growth (Abel 2017; Balzergue et al. 2017; Godon et al. 2019). ALMT1 also acts as a GABA receptor when, as in animal and human neurons, GABA lowers excitability of the plasma membrane (Žárský 2015).

There are intriguing similarities between animal brains and plant root apex *brains*: both enjoy uniquely protected as well as privileged locations within animal and plant bodies. Animal brains are protected mechanically within the skull, provided preferentially with nutrition and oxygen. Animal brains are free to perform only activities relevant to the control of cognitive behaviour of animals. Similarly, the Darwinian root-apex *brains* are positioned between the dividing cells of the root apical meristem and rapidly elongating cells pushing the whole root apex forward. In both maize and arabidopsis root apices, the size of the transition zone is similar to the size of the apical meristem, and unloading phloem elements define the basal border of the transition zone (Baluška et al. 1990, 1996a, 2001a, b; Verbelen et al. 2006). Finally, the brain is the only animal organ which is not in direct contact with blood. In fact, blood is toxic to neurons, and the blood–brain-barrier (BBB) effectively prevents direct contact of brain neurons with blood (Hagan and Ben-Zvi 2015; Righy et al. 2016; Abdullahi et al. 2018; Madangarli et al. 2019; Nian et al. 2020; Segara et al. 2021). Intriguingly, the etymological origin of the term neuron comes from the ancient Greek, meaning 'vegetal fibre' (Brenner et al. 2006; Mehta et al. 2020). More importantly, the allegedly unique features of neurons, formulated and popularized as the 'Neuron Doctrine' by Wilhelm Waldeyer in 1891 (Shepherd 1991; Jones 1994), are no longer considered to be so unique (Gold and Stoljar 1999; Guillery 2007).

Rather surprisingly, many so-called neuronal features are present in plant cells, especially in the transition zone of root apices (Baluška 2010). Recent advances in plant cell biology have revealed that plant cells, especially those located in the root apex transition zone, show almost all of the features which were defined, according the 'Neuron Doctrine', to be neuron-specific (Baluška 2010; Baluška et al. 2005, 2009a, b; Masi et al. 2009). As noted by Rainer Stahlberg, nerves in animals and vascular bundles in plants share analogous functions of conducting rapid electric signals (Stahlberg 2006a, b). Similar analogies to the cellular basis of plants and animals resulted in the acceptance of the Cell Theory. Therefore, it is puzzling that plant electrophysiology is considered to be esoteric (Alpi et al. 2007; Taiz et al. 2019). The most significant differences between plant and animal cells are associated with their different extracellular matrices, and their interactions with the plasma membrane and elements of cytoskeletal polymers (Reuzeau and Pont-Lezica 1995; Baluška et al. 2003b, Seymour et al. 2004; Halbleib and Nelson 2006; Campbell and Humphries 2011). For example, sodium is the major ion driving action potentials in animals but it is toxic for plants with pectinic cell walls (Feng et al. 2018; Verger and Hamant 2018), which rely instead on calcium fluxes (Hope 1961; Beilby and Coster 1979; Beilby and Al Khazaaly 2016; Hedrich and Neher 2018; Iosip et al. 2020). While plant cell walls pose additional problems for the excitability of plant cells and tissues, they also provide them with additional layers of signalling complexity (Baluška et al. 2003b; Ringli 2010; Wolf et al. 2012; Wolf 2017). Our discovery that cell wall molecules, such as calcium, boron cross-linked pectins and xyloglucans, are actively recycled from cell walls via endosomal vesicles (Baluška et al. 2002, 2009a, b; Dhonukshe et al. 2009) is crucial for our conceptual advancement of plant-specific synapses in the root apex transition zone.

3 Neuronal Molecules Relevant for Root Apex Cognitive Navigation and Soil Exploration

Plant root apices are supported via numerous molecules which were originally characterized as neuronal molecules. Among these, we will briefly discuss glutamate and GABA with their receptors, which control the electrical properties of the plasma membrane. Importantly, in both neurons as well as in plant cells, glutamate stimulates and GABA inhibits excitability of the plant plasma membrane. Although there are some differences in their receptors, especially with respect to GABA (Ramesh et al. 2015, 2017; Žárský 2015), the electrophysiological impacts on plasma membrane potentials and excitability are very similar. The same is true for another neurotransmitter, glutamate, in that the glutamate receptors of plants are very similar to those of animal brains (Weiland et al. 2016; Wudick et al. 2018; Qiu et al. 2020).

Evolutionary analysis even suggests that plant glutamate receptors might predate the animal glutamate receptors of the NMDA class which have a central role in the control of the brain's synaptic plasticity (Stroebel and Paoletti 2020). Importantly, both glutamate and GABA shape action potentials (APs) in plants, partially through their control of voltage-gated potassium channels (Cuin et al. 2018; Adem et al. 2020; Koselski et al. 2020). Similar to the neuronal APs in humans and animals, plant-specific APs are also blocked by diverse anesthetics and this prevents the movements of plant organs (Yokawa et al. 2018, 2019; Pavlovič et al. 2020; Baluška and Yokawa 2021).

4 Synaptic Principles Relevant for Root Apex Cognitive Navigation

Root apex cells located in the transition zone are unique with respect to their cytoarchitecture, endocytic vesicle trafficking, arrangement of actin cytoskeleton elements, polar transport of auxin, and bioelectric activities of their plasma membranes. In 1987, we discovered that the actin cytoskeleton is organized via unique bundles of F-actin anchored at the cellular end poles (cross-walls) which are densely populated with plasmodesmata (Baluška et al. 2000, 2003a, b; Baluška and Hlavacka 2005). Later, the plant-specific myosin VIII was discovered in plants and was also localized abundantly to these cross-walls (Reichelt et al. 1999). It emerged that myosin VIII supports plasmodesmata structure and function, anchoring the F-actin cables at the cross-walls, and driving endocytosis and endocytic vesicle recycling (Baluška et al. 2000; Volkmann et al. 2003; Baluška and Hlavacka 2005; Golomb et al. 2008; Sattarzadeh et al. 2008; Haraguchi et al. 2014). Importantly, myosin VIII-based end-poles of cells in the transition zone assemble cell–cell adhesion domains which fulfil several synaptic criteria and support the brain-like status of the root apex transition zone (Baluška et al. 2005, 2009a, b; Baluška and Mancuso 2013a, b, c). Auxin emerges as acting not only as a plant hormone but also as a plant-specific neutrotransmitter-like molecule which is integrating sensory inputs into the context of root tropism outputs (Baluška et al. 2005, 2008, 2009a, b; Baluška and Mancuso 2013a, b, c; Schlicht et al. 2006; Baluška et al. 2008). Interestingly, the root apex transition zone acts as the specific target of aluminium toxicity (Sivaguru and Horst 1998; Kollmeier et al. 2000; Sivaguru et al. 1999, 2000, 2003a; Illés et al. 2006; Yang et al. 2014; Li et al. 2018). The central role of aluminium toxicity in the transition zone is especially relevant for the basipetal (shootward) flow of auxin driven via the PIN2 auxin efflux transporter (Kollmeier et al. 2000; Shen et al. 2008; Yang et al. 2014; Wu et al. 2014, 2015), and is mediated by the activity of plant glutamate receptors (Sivaguru et al. 2003b).

5 Transition Zone Energides in the Driver's Seat to Control Root Apex Navigation

One of the most prominent features of cells in the root apex transition zone is the fact that the nucleus is centralized and suspended in dynamic cytoplasmic strands organized by cytoskeletal polymers (Baluška et al. 1990, 1997a, 2000, 2001a, b, 2003a, 2006b, 2010). Whereas the F-actin bundles are organized conically between cellular end-poles and are the most prominent structure, the dense F-actin baskets that suspend the centrally positioned nuclei and perinuclear radiating microtubules are also important for the integral roles of these cells in sensory signal perception and integration, resulting in adaptive root tropisms (Baluška et al. 2004a, 2006a, b, 2009a, b, 2010; Baluška and Mancuso 2013a, b, c). The current version of the Cell Theory is facing skepticism due to the existence of multinuclear coenocytic (cell division not followed by cytokinesis) and syncytia (fusion of cells) cellular assemblies. In fact, almost all plant cells have free cytoplasmic channels known as plasmodesmata. We have extended and fully developed the Cell Body concept which was originally proposed by Daniel Mazia in 1993, and correlates well with the Energide concept of Julius Sachs from 1891 (Baluška and Barlow 1993; Baluška et al. 1997b, 1998, 2001b, 2004b, c, 2006a, b). The Energide-Cell Body is the smallest unit of cellular life originating from still unknown ancient and centrin-based archaea with microtubular flagella (Baluška and Lyons 2018, 2021). It is hypothesized that the cytoplasmic strands, supported by vibrating and oscillating F-actin cables and microtubules (Tuszyński et al. 2004; Cifra et al. 2010; Kučera and Havelka 2012), are transmitting sensory signals received at the plasma membrane to the central nuclei (Matzke et al. 2019). Similar neuronal synapse—nucleus communication is involved in the formation and maintenance of neuronal circuits (Saha and Dudek 2008; Cohen and Greenberg 2008). Action potentials seem to have originated from the repair of damaged plasma membranes of ancient cells and contributed to preservation and homeostasis of plasma membrane and cellular integrity (Goldsworthy 1983; Steinhardt et al. 1994; Brunet and Arendt 2016; Baluška and Mancuso 2019).

6 Changing Metaphor for Transition Zone Energide: From 'Bug in Cage' to 'Spider in Web'

In 2004, we proposed the metaphor *Bug in Cage* for the Cell Body/Energide enclosed by the plasma membrane and cytoplasm (Baluška et al. 2004b). The idea behind this metaphor was that the symbiotic evolutionary origin of the Cell Body/Energide implies its semi-autonomous nature and biological agency behind its organization and behaviour (Baluška et al. 1997b, 1998; Baluška and Lyons 2018, 2021). The Cell Body/Energides in the root apex transition zone cells are acting as navigators of root apices (Fig. 1, Baluška and Mancuso 2018) in their search for water and critical mineral nutrients and avoidance of toxic soil patches. They can act as kind of sensitive radar for both acoustic and chemical cues (Falik et al. 2005; Schenk 2006; Gagliano et al. 2012a, b; Yokawa et al. 2014; Rodrigo-Moreno et al. 2017).

Our proposal here is that the Nuclei/Energides suspended within the cytoskeleton-supported cytoplasmic strands (Fig. 1a, b) of the root apex transition zone are perfectly suited to control the root apex navigation *akin* to navigators seated in the driver's seat (Fig. 1c). As the F-actin cables enclosing the nuclei are anchored at the root synapses (Baluška et al. 1997a, 2000, 2005, 2009b; Baluška and Hlavacka

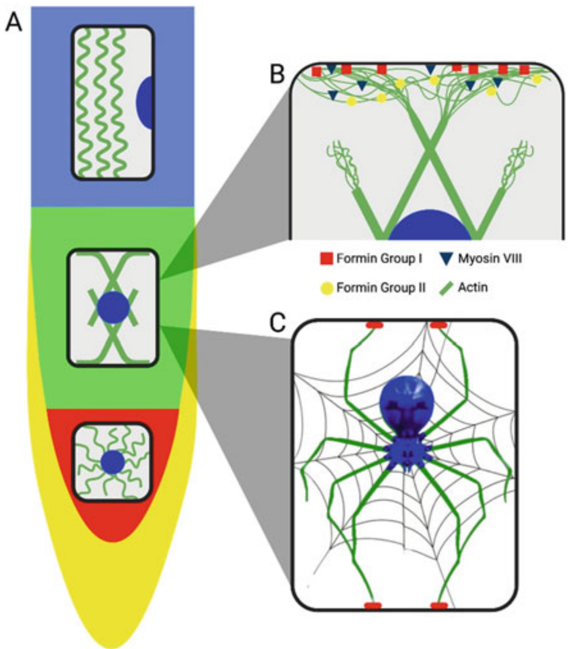

Fig. 1 Schematic Overview of the Root Apex Zones Relevant for Root Apex Navigation. **a** The root cap (yellow) encloses the apical meristem (red) and the transition zone (green). The zone of rapid cell elongation (blue) follows, which pushes all the other more apical zones forward. The nucleus (in blue) is enclosed by F-actin elements (in green) in the form of a meshwork (cells in meristem) or conical bundles anchored at the synaptic end poles (cells in transition zone). In cells of the rapid cell elongation zone, the nucleus is pushed to the cell periphery by the large central vacuole and relaxed F-actin bundles are organized longitudinally. **b** Detail of the two conical F-actin bundles organized at the synaptic cell periphery by actin-binding formins and myosin VIII. **c** Hypothetic scenario of root apex navigation via the transition zone Cell Bodies/Energides, depicted metaphorically in the form of a spider-in-web. For more details, see Baluška and Hlavacka 2005; Baluška and Mancuso 2013a, 2013b, 2013c, 2018; Baluška and Lyons 2018, 2021)

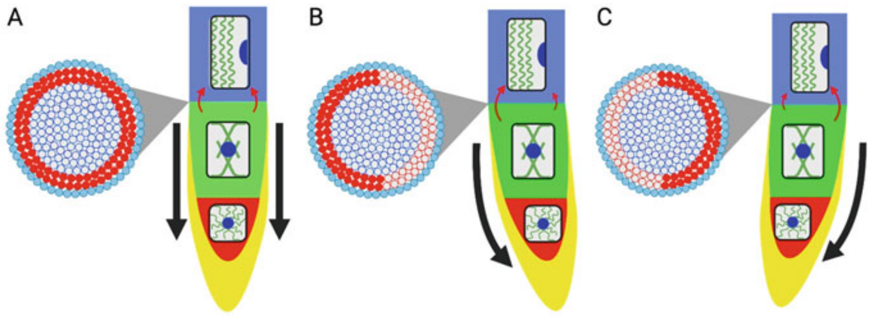

Fig. 2 Smart Border at the Basal Limit of the Transition Zone. The transition zone Cell Bodies/Energides control root apex navigation through their contacts at the synaptic end-poles of cells at the basal limit of the transition zone. This translates sensory perceptions into motoric root apex tropisms at this smart border between the basal limit of the transition zone. **a** If there is no relevant cue registered by the Cell Body/Energide, then all the transition zone cells are released into the rapid cell elongation zone in a coordinated fashion. **b, c** Differential release of cells from the transition zone into the rapid cell elongation zone allows root tropisms which are finely-tuned by relevant cues. The most critical cells for root apex tropisms are PIN2 expressing cells (shown as red circles) at the root periphery. **b** Repelling cues slow-down (small red arrow) the release of PIN2 cells (unfilled red circles in the root cross-section view) from the transition zone (green) into the region of rapid cell elongation (blue) at the opposite side of the root apex periphery. Attracting cues speed-up (large red arrow in the root cross-section view) the release of PIN2 cells (filled red circles) from the transition zone (green) into the region of rapid cell elongation (blue) at the opposite side of the root periphery

2005), the Nuclei/Energide are optimally placed to navigate root apex trajectories. The most effective means to control root tropisms is to manipulate the onset of rapid cell elongation in a coordinated fashion across the root epidermis and cortex (Fig. 2). In the maize root apex, there are hundreds of cells located at the basal limit of the transition zone that are primed for rapid cell elongation. Their Energides give their 'yes' for the burst-like onset of the rapid cell elongation (Fig. 2) which is under the control of auxin, calcium, ethylene and actin-myosin forces (Baluška et al. 1993a, b, 1996a, 1997a, 2000, 2001a, b). On the other hand, microtubules are not involved in this developmental switch as maize root tropisms are completed with all microtubules depolymerized (Baluška et al. 1996b). In some way, the active Energides of the transition zone cells resemble spiders sitting within their webs (Fig. 1c), feeling web vibrations to inform them of the presence of prey, as well as of other relevant cues from their environment (Mortimer 2019; Mortimer et al. 2019). This sensitive cytoarchitecture would explain the surprising ability of growing roots to respond to specific acoustic signals via positive root phonotropism (Rodrigo-Moreno et al. 2017) or to recognize barriers from distance (Falik et al. 2005; Schenk 2006).

How could the Energide sense relevant sensory signals and integrate this information to control root cell elongation? Here the 'Plasma Membrane Control Centers' (Pickard and Ding 1993; Pickard 1994, 2013; Gens et al. 2000) and the 'Hechtian Growth Oscillator' (Lamport et al. 2014, 2018, 2020) concepts are relevant. For the root apex, important cues are water and critical minerals which, when perceived, are associated with changes in tension and vibrations of the cytoplasmic strands (Fig. 1). The contact of F-actin and myosin VIII with the critical plasma membrane domains can control the ion fluxes across the plasma membrane. Interestingly, the conical bundles of F-actin that enclose nuclei are straight and thick, as if under tension, in the transition zone; in contrast, they instantly appear thin and wrinkled as root cells initiate their rapid cell elongation (Baluška et al. 1997a, 2000; Baluška and Hlavacka 2005).

Such sensitive and vibrating networks could allow effective perceptions from the root apex rhizosphere, including possible sound waves bouncing back from soil portions ahead of the growing root apices. For example, maize root apex generates sound waves in regular frequencies (Gagliano et al. 2012a, b). Analysis of growing roots of arabidopsis revealed that they are attracted by sound waves of 200 Hz which are close to the sound waves generated by streams of water (Rodrigo-Moreno et al. 2017). This root phonotropism can be expected to be useful for roots in their search for water (Rodrigo-Moreno et al. 2017; Fromm 2019). Acoustic root navigation, resembling bat echolocation, would also allow recognition of physical barriers in advance (Falik et al. 2005; Schenk 2006).

7 Evolution of the Root Apex Brain: From Ancient Roots Towards Complex Root Systems

In early root evolution, some 400 million years ago, ancient roots teamed-up with symbiotic AM fungi and have tightly co-evolved ever since (Pirozynski and Malloch 1975; Selosse and Le Tacon 1998; Selosse et al. 2015). Moreover, roots also attract specific bacteria which help roots to cope with diverse stresses. In order to control their rhizosphere, roots release large amounts of exudates and diverse infochemicals (Baluška and Mancuso 2020, 2021). These substances help them not only to develop the surrounding soil as their living niche but also to enjoy complex social lives with the roots of neighbouring plants (Baluška and Mancuso 2020, 2021). Roots are territorial (Schenk 2006; Novoplansky 2019). They discriminate self—non/self roots and apply the kin recognition (Bais 2018; Novoplansky 2019) in their behaviour (Baluška and Mancuso 2021). The root apex transition zone plays a central role in this social aspect of root life. Auxin transport via neurotransmitter-like modes based on synaptic-like vesicle recycling is critical aspect of root behaviour. In the evolution of roots, the auxin-transporting synapses (Baluška et al. 2005, 2008, 2009b) have been proposed to evolve from the ancient symbiotic synapses (Baluška et al. 2005; Kwon et al. 2008; Lima et al. 2009; Baluška and Mancuso 2013c).

Plants compete for light, water and mineral nutrients (Craine and Dybzinski 2013). In shoots, the shade avoidance syndrome is behind the light competition between neighbour plants (Smith and Whitelam 2007, Keuskamp et al. 2010; Martínez-García et al. 2010, 2014). In plant roots, fierce competition for water and critical minerals shapes root behaviour (Gersani et al. 2001; Schenk 2006; McNickle et al. 2009; Farrior 2019). Root apices apply their plant-specific perception, cognition and intelligence in order to succeed in their difficult task of finding sufficient water and mineral nutrients (Hodge 2009; Barlow 2010a, b; Gruntman et al. 2017; Baluška and Mancuso 2018; Fromm 2019; Novoplansky 2019; Parise et al. 2020). In plant evolution, roots evolved from structurally and cognitively simple rhizoids up to the complex root systems of contemporary flowering plants which enjoy complex foraging behaviour. Plants use their root systems for plant-plant communication of sensory and stress cues (Falik et al. 2012; Elhakeem et al. 2018; Novoplansky 2019; Volkov and Shtessel 2020; Yamashita et al. 2021).

8 Root-Fungal Networks Control Underground Supracellular Life

Plant root evolution started with the earliest colonization of barren land with help from symbiotic AF fungi some 400 billions of years ago (Pirozynski and Malloch 1975; Remy et al. 1994; Heckman et al. 2001; Schüßler and Walker 2011; Feijen et al. 2018). Roots are hidden underground in the soil, leading to the prevailing view of plants as simply green organisms which flower when mature. As an example, the value of the largest living organism on Earth, the giant sequoia tree, is generally based on its shoot parts, while its root parts are ignored. However, the true nature of plants and trees is based on the fact that their roots are structurally and functionally connected through fungal hyphae networks. In some sense, these networks are analogous to our human invention of the internet because the latest advances suggest that they serve not only for exchange of nutrients and water, but also for chemical and electrical long-distance signaling (Simard et al. 1997; Song et al. 2010; Barto et al. 2012; Gorzelak et al. 2015, 2020; Sasse et al. 2018; Simard 2018; Volkov et al. 2019; Volkov and Shtessel 2020). Obviously, the true nature of plants is hidden underground, which would explain why plants are generally considered to be devoid of agency, cognition, and intelligence. The aboveground parts of plants, visible to us, are just support organs specialized for photosynthesis and sexual reproduction (Baluška and Mancuso 2021). Roots demonstrate kin recognition, self/non-self recognition and swarm intelligence (Baluška et al. 2010; Ciszak et al. 2012; Baluška and Mancuso 2018, 2020, 2021). They invest their carbon-based photosynthetic substances to control the rhizosphere microbiota communities and soil as a life-friendly biotop (Barlow 2010a, b; Barlow and Fisahn 2013; Novoplansky 2019; Baluška and Mancuso 2020, 2021). Future experimental studies will focus on the ecological, cognitive and electrophysiological aspects of the root-wide-web (Simard et al. 1997; Lee et al. 2013; Simard 2018; Giovannetti et al. 2006; Fukasawa et al. 2020; Volkov et al. 2019; Volkov and Shtessel 2020; Kokkoris et al. 2021) spanning large areas of the Earth surface. Unfortunately, these intact forest areas are shrinking and this has serious consequences for the life-friendly climate (Baluška and Mancuso 2020).

Circadian clocks have emerged as critical players in decoding sensory information obtained from the environment (Hearn and Webb 2020; Koronowski and Sassone-Corsi 2021), which is crucial for cognitive aspects of all organisms. With respect to plants, which live both above-ground (shoots) and below-ground (roots), the situation is unique (Baluška and Mancuso 2018, 2021; Lee et al. 2019). Although the shoot clock was proposed to be the primary plant clock and the root clock is viewed as a simplified slave-like version of the shoot clock (James et al. 2008), recent studies revealed that the root clock coupling strength is extraordinary especially in the root apex (Gould et al. 2018; Maric and Mas 2020). Light can reach the root apices via internal tissues down to under-ground roots (Mandoli and Briggs 1984; Lee et al. 2016). This then allows them direct light-mediated entrainment of the root clock (Nimmo 2018; McClung 2018). As the AM fungi have their own circadian clocks (Lee et al. 2018, 2019), it can be expected that the huge symbiotic root—AM fungi networks are integrated via their supra-organismal circadial clocks (Lee et al. 2019). Similar trans-kingdom clocks are found in animals and humans (Thaiss et al. 2014; Page 2019). We can look forward to future studies in this newly emerging field of supra-organismal chronobiology.

9 Conclusions and Gaian Outlook

Land plants are decisive organisms with respect to the Earth's climate ever since they evolved from rather simple and small predecessors living in seas. The first terrestrial plants cooled the Ordovician Earth (Lenton et al. 2012). Their roots, in co-operation with symbiotic AM fungi, generated soil as a central habitat for terrestrial ecosystems (Rillig and Mummey 2006; van der Heijden et al. 2008). Ever since then, land plants have been integral in establishing and maintaining the climate of the Earth (Beerling 2019). Tree root systems are integrated and networked with the symbiotic fungal hyphae into huge super-organismal phenomenon known as wood-wide-web (Simard et al. 1997; Helgason et al. 1998; Giovannetti et al. 2006; Simard 2021). This wood-wide-web participates in homeostatic processes (Power et al. 2015) also known as the Gaia hypothesis proposed by James Lovelock in 1972 (Lovelock 1972, 1979, 2019: Lenton and van Oijeb 2002; Lenton and Latour 2018, Lenton et al. 2018). In this respect, although this seems to be counter-intuitive, plants are socially and cognitively active mostly underground as only roots, but not shoots, can enter into the long-lasting symbiotic interactions (Baluška and Mancuso 2018, 2020). There are examples of plants and even trees (Henschel and Seely 2000; Maurin et al. 2014) that live underground, and numerous myco-heterotrophic plants that are not green at all, obtaining all their food from fungal partners (Bidartondo 2005; Merckx et al. 2009). It is possible that future studies will reveal even more surprising connections between roots, fungal hyphae and microbial populations which control the terrestrial ecosystems and the Earth's climate. If we would like to solve the current climatic crisis and better understand the Earth's ecosystems, we should focus more on the underground life which is dominated by plant roots and their AM fungal partners. Here is where the key to our future life on the planet Earth is hidden.

Acknowledgements FB and FY acknowledge support from the Stiftung Zukunft jetzt! (Munich, Germany).

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