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Review Paper

The roles of root border cells in plant growth and development: a review

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Abstract

Competency of root tips to grasp and move towards water and nutrients in the soil is the major factor influence on the sustainable survival and development of plants. Enormous population of separated somatic cells which known as Root border cells. Root tips are the part which covered by these Root border cells and those are play a major part in plant health. These Root border cells can active for few days after detachment from the root cap in the rhizosphere. Amount of border cells being detached from the root tip is depend on the species of plant. Further Root border cells are thought to play a key role in root defense and plant growth. The detached active cells may share many functions including physical, chemical and biological activities. Numerous discoveries showed the benefits of root border cells in growth and development of plant. Therefore, greater discharges of border cell production may have the possible to stimulate plant growth and development to the highest degree, and to contribute a selective advantage in certain soil atmospheres. While border cells may offer an appropriate mechanism for compound distribution to soil, further deep-seated research works are necessary to characterize the metabolic and proteomic expression arrays in comparison to other root cells to grasp and capitalize on their unique attributes at species level.

Keywords: Mucilage: Root, Root border cells, Root cap, Plant.

Introduction

The absorption of nutrients by the roots from the soil is influenced on generation of domestic signals which plays a crucial role in plant growth developmental process. Thus, it is believed that availability of nutrients is the key factor to plant growth in numerous environments of the world. Rhizosphere is the place through which larger amount of nutrients can obtain by the plants due to the microbial interaction with plant products in root exudates and plant spend huge amount of energy to produce border cells, which facilitate the root's ability to engineer the chemical, physical and biological properties of the peripheral surroundings.

Practically, the soaking of roots with water can be facilitated the discharge of cells in to suspension and these cells are referred as border cells[1].

The discharged cells remain adhered to the root tip when the free water is absence. Traditionally, Root border cells have been considered as dead cells that become detached from the root cap. It is now well recognized that these cells show a key function at the root–soilinterface and provide to the properties of the root environment[2] and can thrive for ten days[3]. An individual border cell is delivered to its definite destination out of root with time, it has already eased several tasks, such as mucilage secretion[4-6], the sensing of gravity and other environmental signals[7], interact with soil microorganisms[8].

Characteristics of Root border cells

The majority of border cells are in oblong or rectangular shape. The width of which ranges from approximately 20-25µm, and the length ranges from 50-80µm[9]. Like other cells, border cells have intact peripheral cytoplasm and 'normal' organelles[10]. It is often undergoing modifications in morphology and gene expression. The cells produce lignified secondary walls and excrete proteins into the surrounding soil environment when they tend to elongated[11]. In many of species, the detached root cap cells remain viable once they are shed into the outside environment. Further, they can remain alive for up to 3 months on agar[12] and for one week or more in the rhizosphere[10,3]. Border cells of maize and pea grown hydroponically can remain viable for more than three months[13].

Separation and development of root border cells

Root border cells found a distinctively differentiated and basically unrecognized area of the root system of many higherplants[14]. Every day, many of root border cells which are uniquely differentiated are synthesized and instructed to detach from the root caps (the region at the tip housing the apical meristem and root cap) of higher plants[1,8]. In root tips, they are originating from root cap cells. Mitosis converts stem of root cap meristem in to root cap cells followed by the steps forward through a sequence of different developmental stages such as stage of starch synthesis, stage of gravity sensing and stage of mucilage secretion, as a final point these cells detach from the side-line of the root cap to produce border cells. The final stage of root cap cell development is separation of border cells. After the separation, the root border cells and mucilage accumulate on the root tipin the absence of free water. As soon as the root tip is submerged in the water, the mucilage surges dramatically and border cells scatter quickly into suspension within 30-60s[15]. Brigham *et al*. It has been, stated that shortly after border cell separation, they are more metabolically active than their originator and the mRNA differential display showed that array of gene expression in border cells is notably different from that in root cap cells[16]. Contemporary outcomes have shown that a severe transformation in gene expression take place upon differentiation of root cap cells into border cells, with choosy yielding of many distinct proteins and cost of many others[17].

Factors affecting border cell separation

Hawes and Lin stated that border cell separation is a self-demarcated progression that is directed in response to developmental and environmental signals[18]. The border cells separation involves the complete disconnection of individual cells from each other and from root mass. The cell wall-degrading enzymes that solubilize cell wall connections between cells are essential for this border cell separation. In addition to that, mechanical effects also influenced on this process[4,19]. Further, water from the soil and, obviously, also by phytohormones[20]. An investigation of factors affecting on border cell separation of maize revealed that, properties of root cap such as size, shape and differentiation including the release of border cell are controlled by phytohormones including auxin and ethylene[20]. Experiments have been showed that, correlation between pectolytic enzyme activity in root cap tissue and cell separation from the root cap. This activity allows the hydrolysis of polygalacturonic acid and is detectable several hours before cells can dissociate from the root[18]. Pectin dimethyl esterification is the process that has been shown to contribute to border cell separation is catalyzed by enzyme called Pectin Methyl Esterase (PME)[21,22]. In pea root caps, a six-fold increase in PME activity occurs during border cell separation compared with that measured after completion of the process. Environmental factors such as bacteria, fungi, nematodes, and CO_2 also coordinated the process of border cell production. They could directly and indirectly regulate the production of border cells[15]. Hawes and Lin have observed that border cell development is a temperature-sensitive process that appears to be regulated independently of root elongation in pea plant[18].

Number of root border cells

Hawes *et al.* who reported that, the quantity of border cells per root changes among plant families: from about 100 (Solanaceae family) to several thousands (10,000 or more for the Pinaceae)[11]. Although species like Compositae, have border cells that die before detachment. Upland cotton (*Gossypium hirsutum)* belongs to Malvaceae family, discharges 8000–10 000 border cells per 24 hours while turnip (*Brassica rapa*) belongs to Brassicaceae family discharges no border cells[11]. Groot *et al*. stated that, all species exhibiting open RAM (Root Apical Meristem) organization produced at least an order of magnitude more border cells in the same time period (24 hours) than those with closed root apical meristem organization[23]. For example, Pea(*Pisum sativum*) (Fabaceae), a species with open RAM organization, produces on average of 4500 border cells per day, and up to 10 000 border cells are shed daily from the cap of *Gossypium hirsutum*, a plant with intermediate-open RAM organization[24]. A plant such as tobacco (*Nicotiana tabacum*) belongs to solanaceae family roots have closed type of RAM construction, release 100 Border cells daily; in the case of *Arabidopsis thaliana* (Brassicaceae), only small amounts of cells, which remain attached to each other, have been shown to be released[25]. The detached number of root border cells for each crop is a significant factor as stated by Iijima *et al*. proposed that the number of border cellsformed has been shown to correlate with their role in diminishing mechanical impedance[26]. Cultivars of rice belongs to upland / lowland (eco type) and japonica / indica (sub species) also showed differences in production of number of root border cells[5].

Mucilage secreted by root cap cells and border cells

Root cap cells and border cells secreted some substances which high in molecular weight called as mucilage and it is accumulated surrounding the root tip as mucilage layer. Hawes *et al.* and Zhao *et al*. reported that the mucilage layer comprises a diverse array of extracellular chemicals produced by border cells containing low molecular weight protein, aminoacids, sugars, phenolic and flavonoid antibiotics, anthocyanins and special enzymes such as peroxidase and galactosidase and cell wall degradation products during separation of border cell and both of them were reported that some specific chemicals secreted by border cells can either hinder or endorse the growth of microorganism and other organisms in the rhizosphere[27,7]. Hawes and Brigham stated as initiation of mucilage production by border cells is not a common reaction to toxins or pathogens, but rather a specific reaction to certain stress elements. For example, border cells of pea produced a mucilage layer in response to *Agrobacterium tumefaciens*, but not in response to *Escherichia coli*[1].

Functions of root border cells

Reduction of physical stress to root growth by root border cells: The growth and development of root in the soil is often checked by a combination of soil physical stresses, including mechanical impedance, water stress, and oxygen scarcity. Position of the root in the soil profile, the existing soil water conditions, and the extent to which the soil has been compacted are the factors determining the period of stress expressions. By modulating the properties of the external environment surrounding the growing root tip, the regulated production of border cells could, directly or indirectly, manipulate almost all of the physical and chemical properties (i.e. pH, nutrient solubility or soil structure) of the root-soil environment. Biochemical and physical properties of soil are changed with the secretion of organic and inorganic substances by roots cells when plants are in the stage of ordinary growth and development[28]. Many functions such as lubrication of the root tip, maintenance of root-soil contact, protection of roots from desiccation, stabilization of soil micro-aggregates, and selective adsorption and storage of ions have been attributed to root cap exudation[29,27]. Physical protection for the apical meristem is provided by root cap[30]. The border cells and their associated mucilage were long presumed to provide lubrication for the passage of the root cap[5].

Ijima *et al*. stated that de-capping of maize slowed the root elongation by about 47%, and it was linked with an increase of about 67% in the root penetration resistance (pressure exerted by the root to penetrate the soil) and also stated that in compacted soil, the root diameter increased significantly for de-capped roots[19]. Furthermore, it was also suggested that roots were undergoing greater mechanical impedance in the absence of root cap. Non availability of root cap border cell production and exudation of mucilage are the possible reasons for increase in root penetration resistance.

Further, Iijima *et al*. assessed that the whole surface of the root cap might be covered in separated border cells in compacted sand[4]. Because, exudation of mucilage may also be increased by soil compaction[31,32,4]. By detaching the bulk of the root cap, including the cap meristem, border cell and mucilage production is effectively limited to the small portion of the remaining lateral cap[33]. From this, the most likely explanation is that border cells were representing as a low-friction sleeve around the root cap and decreasing the root penetration resistance.

Influence of root border cells on soil organism

It is well known that, plant health and crop productivity are critically controlled by status of microbial population in the rhizophere, stimulated by exudates from plant root[34,35,5]. Border cells help plants by enabling roots to defense their own ecosystem. These distinct dead ‘sloughed cells’ were initially released inactively into the rhizosphere to offer mechanical defense as the root tip grows within soil. But, a wide range of studies has confirmed that plant wellbeing and continued existence by protecting the root meristem from pathogenic infection controlled by border cells[36]. In recent times it has been proposed that border cells may act as decoys for pathogenic organisms in the rhizosphere, shrinking the possibility of pathogen attack on the root tip.

The best characterized properties of border cells involve their specific recognition and responsiveness to soil borne microflora[1,8] and it has also been presented that border cells have different responses to microorganism infection[25]. Border cells control the ecology of the rhizosphere by the distinct discharge of biologically energetic chemicals that control growth and gene expression in microbes based on their selective interactions with soil-borne microorganisms[18,1,14], for example, much of evidence recommends that root border cells are involved in root–microorganism interactions in peas[16,36-38].

Moreover much greater significance of these cells is the ability to release specific signaling compounds that manipulate the activities of soil organism. They produce and quickly export some particular extracellular chemicals such asantibiotics, anthocyanins, antibiotics, special enzymes and sugars, which either obstruct or encourage the growth of other beings in the rhizosphere such as bacteria, fungi, viruses, parasites, nematodes, mites, insects and other invaders and which neutralize some toxic chemicals around the root in the soil[27,8,1]. Based on the genetic constitution, border cells can attract zoospores, synthesize defensive structures in response to fungal attack[39], deter or fix pathogenic bacteria and control growth and gene expression in symbiotic bacteria.

Cannesan *et al.* proposed that, besides changing their morphology border cells respond to pathogenic encounter and producinga significant volume of pisatin which expresses antifungal activity[40]. Furthermore, stimulation of border-cell production upon inoculation was found to appear proportionately with the number of oospores inoculated and further stated that root border cells in pea are involved in local root defense against pathogen attack both mechanically and chemically. For instance, pea border cells, the utmost generally used plant model for border cell studies. They are capable of barring growth of the fungus *Nectria haematococca in vitro*[36]. They also have the potential to repulsing the fungus, thus preventing infection of the root tip[37]. They seem to do so by encasing the hyphae in a kind of layer, and immediately the layer is removed the root tip remains free of infection[41]. In vitro, for example, border cells can hugely and specifically modify the dispersal of fungal zoospores on the root within minutes[42].

Secreted mucilage from border cells can also keep away pathogenic bacteria. It has been shown that border cells of plants belong to legumes export a large number of proteins (the secretome) during their detachment from the root cap[38]. The primary protective constituent of root cap is secretome which contains many antimicrobial enzymes, including chitinase, peptidase, and glucanase[38,43]. Border cells of legumes and cereals produce mucilage layer in response to co-cultivation with pathogenic bacteria, except in response to *E. coli*[9]. Because of such chemicals into the rhizosphere makes them a possibly important associate in the Rhizobium-legume interaction[14].

In addition to this, Hawes and Pueppke proposed that root border cells, which are sloughed from the root cap, may offer roots defense mechanism from disease causing nematodes by performing as decoys dispersed in the soil around the elongating root tip[9]. This is a pretty good recommendation, as very large numbers of cells may be disconnected during the life of a root tip[8], and the cells remain effective in the soil for up to seven days after detachment[10]. Recent efforts also suggest that deploying the capacity of roots to slough off border cells, which then operate as a decoy to the nematode, can considerably diminish damage to the roots.

For border cells to act as decoys in the rhizosphere they necessitate to mark the direction and promptness of movement of their target nematodes and if they have to act as successful deterrents to nematodes, they must exert a pull on nematodes away from the root and hold them in thelocality of the cells for some predetermined time. Thus the border cells, ormucilage, have to act as an attractant by releasing chemicals into the soil system, setting up a chemo attractant gradient that guides nematodes to them[44]. Once nematodes are make contact with border cells, nematode activity should be altered to prevent further migration in the direction of vulnerable root tissues.

Experimentally, the root border cells are acting as both an attractant and a deterrent to the root-knot nematode *Meloidogyne incognita*. Nematode attraction assays to border cells exposed that nematodes were attracted significantly but comparatively weakly to border cells[45] and remarkably, for the first time, localized chemo tactic attraction of nematodes by border cells from pea roots has been detected by Zhao *et al.*[7]. However, the degree and rate of attraction of nematodes to detached cells has not been investigated till, and this is vital in determining the possible effect of such phenomenon in field conditions where nematodes would have to be decoyed away from growing roots.

Therefore, border cells most likely have numerous biological functions in enhancing root growth and development, modifying populations of soil borne microflora in the rhizosphere and protecting plant roots from all kinds of risks.

Protein synthesis by root border cells

Brigham *et al.* who reported that, border cell separation in pea root cap release a collection of newly synthesized proteins which are free from microbial contamination[16]. Further, it produces at least a subset of the secretome into suspension. Proteins produced in border cells exhibit profiles that are very distinct from those of the root tip (root cap, root meristem, and adjacent cells)[16]. In vivo-labeling experiments reveal that 13% of the proteins that are rich in preparations from border cells are invisible in root tip preparations. Root border cells from pea secrete specific sets of proteins while they are detached from the root tip as compared with the root cap and the rootsystem[16]. Border cells synthesize and discharge 100 proteins into the extracellular environment including defense-related proteins such as proteases and peroxidases[16,38,46].

One of the most interesting recent results related to border cell function is that, in pea, they secrete extracellular DNA[17], which is responsible in root tip resistance to fungal infection. Hawes *et al*. proposed that root tips produce extracellular root slime ‘traps’ involving extracellular DNA (exDNA) and proteins that modulate adhesion and aggregation of the pathogens and contribute to root cap protection[46]. The presence of exDNA in root border-cell exudates was found to contribute to the root cap protection against *Nectria haematococca*. In peas, the digestion of exDNA from root border-cell exudate using enzymes such as DNase I results in loss of root tip resistance to *Nectria haematococca* infection[47].

Reduction of Alminium (Al) toxicity by root border cells

The root tip is the main site where Al toxicity is accessed in higher plants[48]. Longer phrase Al-prevention mechanisms that defend the apical root meristem may be more crucial for constant root growth. Root border cells play an important role in regulating the root context[49,38]. A number of border cell characteristics established that they have the control to shelter plant health by preparing the environment of the budding root tips[1].

Fiskesjo revealed that, the exposure to Al resulted in cytoplasmic structures in onion root cap and she proposed a novel hypothesis that toxic Al could be removed by split-up of root border cells from the cap[50]. For instance, they are involved in Al detection and tolerance[51]. Release of Al-binding mucilage by border cells could play a crucial role in protecting Al-induced cellular damages of root tips[51]. Brigham *et al.*, expressed that border cells respond keenly and increase the mucilage production to the presence of Al and their occurrence reduces the amount of Al reaching to the root tip of pea plants[16]. Horst *et al*. reported that mucilage of an Al-tolerant cultivar of cowpea bound more than one-half of the total Al content of the apical one cm of root tips, and its removal depressed root elongation in the presence of Al[52]. Li *et al.* also have demonstrated that Al binds strongly to maize mucilage[53]. Miyasaka and Hawes have examined the effect of Al toxicity on the viability of detached Border cells from different Al-tolerant snapbean cultivars[51]. Their results also indicated that border cells have the capacity to protect root tips from Al toxicity.

Conclusion

Border cells, also called sloughed-off cells are the cells that separate from the outer layers of the root cap, which is always has the capacity to renewed. The frictional force which experienced by the root tip during border cell production controlled by degree of detachment of the border cells. The rate of border cell detachment is exceptionally variable among plant species, from none to tens of thousands with discharge rates highly dependent upon the prevailing environmental conditions. Once detached from the cap, border cells remain lively in the soil for few days and they are bounded by the mucilage which binds heavy metals away from the root meristem. Border cells also generate signal compounds involved in the safety of meristem against pathogens and in the promotion of symbiosis. While border cells may offer a suitable mechanism for compound delivery to soil, further deep-seated research works are necessary to characterize the metabolic and protein encoded genome expression arrays in comparison to other root cells to understand and capitalize on their unique attributes at species level.

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