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Root border cells and secretions as critical elements in plant host defense

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Border cells and border-like cells are released from the root tip as individual cells and small aggregates, or as a group of attached cells. These are viable components of the root system that play a key role in controlling root interaction with living microbes of the rhizosphere. As their separation from root tip proceeds, the cells synthesize and secrete a hydrated mucilage that contains polysaccharides, secondary metabolites, antimicrobial proteins and extracellular DNA (exDNA). This exDNA-based matrix seems to function in root defense in a way similar to that of recently characterized neutrophil extracellular traps (NETs) in mammalian cells. This review discusses the role of the cells and secreted compounds in the protection of root tip against microbial infections.

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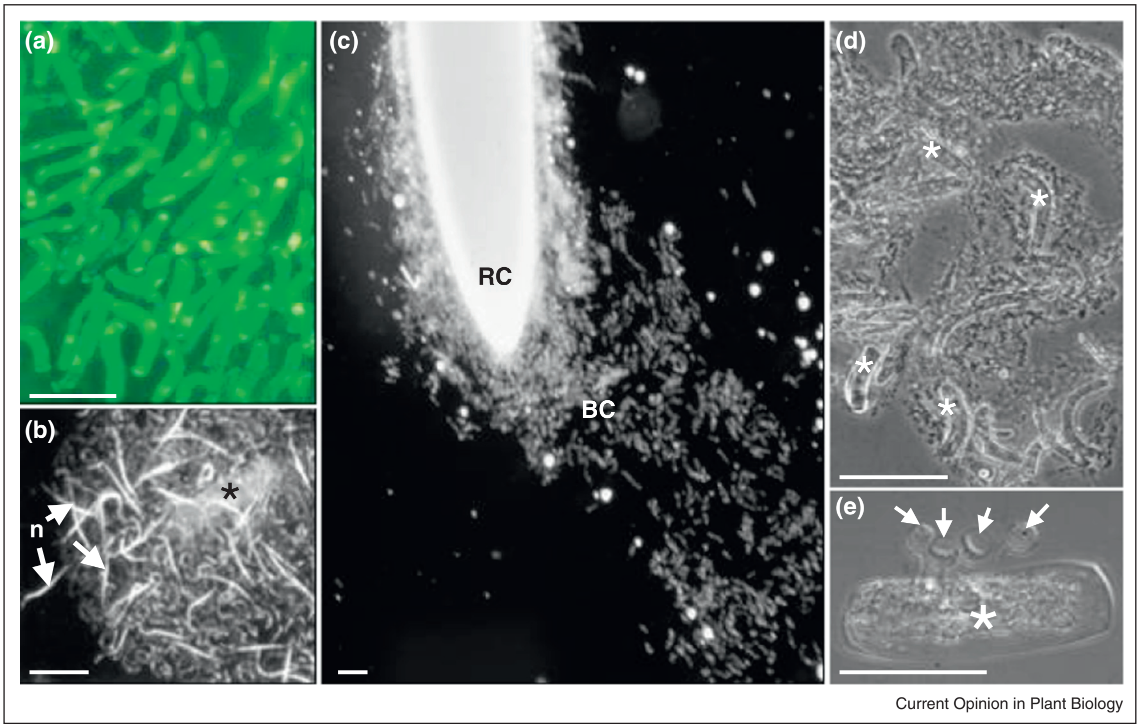
Introduction

Maintaining a healthy root within the soil is vitally important for plant growth and crop protection. During root growth, root cap turnover and programmed cell separation from the cap periphery results in the delivery of detached cell populations into the rhizosphere [1,2]. These are termed root border cells or root border-like cells depending on the pattern of their release and organization [3••,4]. Border cells are defined as cells that detach from the root cap as individual cells and small aggregates, whereas border-like cells are released as blocks or sheets of cells that remain attached to each other [1,4].

Interestingly, the production of border cells appears to be correlated to mycorrhizal associations with the root. Plant species that have a higher mycorrhizal propensity release larger numbers of border cells than those with lesser mycorrhizal propensity [5,6] although the role of border cells in the establishment of mycorrhizal colonization is not known. A number of studies have provided evidence that border cells (Figure 1a,c) can influence root-rhizosphere dynamics at the root tip. First, the number of border cells increases in response to pathogens and other stimuli including carbon dioxide, metals, soil type and secondary metabolites [2,8,9]. Second, border cells are capable of attracting or repelling pathogenic microorganisms including nematodes (Figure 1b), bacteria (Figure 1d) and oomycetes (Figure 1e). For example, instantaneous attraction of zoospores to border cells, but not root surfaces, occurs in a host–microbe specific manner (Figure 1e) (see [12], supplementary Figures 1–4). Exposure of pea roots to the pathogen *Nectria haematococca* results in the formation of a mantle of hyphae, mucilage and border cells that covers the root tip [13]. Remarkably, the moving root tip remains free of infection once the mantle has been detached and left behind. Third, border cells secrete antimicrobial proteins, phytoalexins, arabinogalactan proteins and pectins within the extracellular matrix or 'slime' [9,14,15,16••,17••]. The slime layer and its responses to stimuli can be visualized using India ink, which does not penetrate the matrix (Figure 2). Border cells from pea emerge from the root tip ensheathed within a slime layer measuring several millimeters in diameter (Figure 2b). Individual border cells from maize (Figure 2a) and pea (Figure 2c) respond to the presence of bacteria and germinating fungal spores by increased slime production [18].

It has been recently found that pea root border cells secrete DNA to the matrix (exDNA) much like the NETs 'neutrophil extracellular traps' reported by Brinkmann et al. in 2004 [19••] to be released by white blood cells in mammals [19••,20,21••,22]. ExDNA-based extracellular traps have now been shown to underlie critical aspects of mammalian immune responses ranging from infectious disease to lupus and other autoimmune disorders as well as heart attacks, stroke, and skin diseases (summarized in Table 1). These emerging discoveries offer revolutionary insights into previously unrecognized disease processes and offer new avenues for clinical approaches to human health and wellness [31,32••]. Here, we outline recent

Figure 1



Dispersal dynamics of pea border cells in response to immersion in water for 30 seconds **(c)**. Viability of border cells is shown using the vital stain fluorescein diacetate **(a)**. Root knot nematodes added to the suspension are chemotactically attracted to border cells, and form aggregates where nematode mobility ceases **(b)** [7]. *Agrobacterium tumefaciens* added to pea border cells **(d)**, and *Pythium dissotocum* zoospores added to cotton border cells exhibit similar behavior **(e)** [10,11]. Arrows in (b) point to nematodes and in (e) to zoospores attached to a border cell. RC, root cap; BC, border cells (also indicated by *); n, nematodes. Bars: 20 μm.

advances from studies on the role of these secretions on root health.

Secretion of high molecular weight cell wall glycomolecules, pectin and arabinogalactan proteins

Pectin impacts border cell separation. Release of border cells is dependent on the activity of pectin-degrading enzymes such as methylesterases and polygalacturonases responsible for their separation from the root tip [33,34]. The cells are released individually or as aggregates, depending on species, genotype, and environmental conditions [3••,30,35]. The cell walls of border cells and border-like cells contain significant amounts of pectic polysaccharides including homogalacturonan and xylogalacturonan [3••,17••,36]. Both pectin types are also found in the secreted mucilage surrounding the root cap. Interestingly, in the *Arabidopsis Quasimodo 1-1* mutant that is deficient in homogalacturonan biosynthesis, border-like cells are released as individual border cells further supporting the role of pectin in their attachment and separation. Border cells of *Quasimodo 1-1* mutant also secrete abundant mucilage in which they remain enclosed thus forming a matrix that resembles biofilm secretions of bacteria. Such a ‘border cell biofilm’ is also present in pea, rice, maize and other species [15,35,37,38]. The biofilm not only contains pectin, but also a number of antimicrobial proteins ([15] and see below). Xylogalacturonan is another pectic polysaccharide that is abundantly secreted by root cap and border cells [17••,36,39]. Structurally xylogalacturonan is a homogalacturonan in which the galacturonan backbone is substituted with Xyl residues. Xylogalacturonan is more resistant to digestion by pectin-degrading enzymes such as polygalacturonases known to be produced by plant pathogens during infection [40•]. This is most likely because of the xylose-containing side chains of the polysaccharide. Consistent with this is the observation that the expression of the XGD1 gene responsible for the addition of xylose to xylogalacturonan backbone increases in response to many pathogens including *Phytophtora infestans* and *Pseudomonas syringae* [40•].

Arabinogalactan proteins impact interaction with microbes. Border cells and border-like cells also make arabinogalactan proteins [3••,17••]. These are found in their cell walls but also abundantly secreted into the extracellular matrix [17••,36]. Plant arabinogalactan proteins