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Root tips moving through soil

An intrinsic vulnerability

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Root elongation occurs by the generation of new cells from meristematic tissue within the apical 1–2 mm region of root tips. Therefore penetration of the soil environment is carried out by newly synthesized plant tissue, whose cells are inherently vulnerable to invasion by pathogens. This conundrum, on its face, would seem to reflect an intolerable risk to the successful establishment of root systems needed for plant life. Yet root tip regions housing the meristematic tissues repeatedly have been found to be free of microbial infection and colonization. Even when spore germination, chemotaxis, and/or growth of pathogens are stimulated by signals from the root tip, the underlying root tissue can escape invasion. Recent insights into the functions of root border cells, and the regulation of their production by transient exposure to external signals, may shed light on long-standing observations.

...The evidence suggests that there has evolved within plants, mechanisms for extremely rapid adjustment to changes in the soil environment. The logical conclusion is that plants can and do selectively manipulate the ecological balances within the rhizosphere to their own advantage.[1]

"Sloughed root cap cells" that detach from the root tip were long presumed to be moribund tissue serving to lubricate passage of the elongating root.[2] The discovery nearly a century ago that these cells from *Zea mays* L. and *Pisum sativum* L. can remain 100% viable for weeks after detachment into hydroponic culture did not alter this perception.[3] In recent decades, studies have shown that the cells from root caps of most species are metabolically active and can survive even after detachment into the soil.[4] Moreover, the cell populations express distinct patterns of gene expression reflecting tissue specialization and were therefore given the name root 'border' cells.[5] Like 'border towns' that exist at the boundary of disparate countries and cultures, border cells are part of the plant and part of the soil, yet distinct from both.

The soil is a dynamic environment whose pH, surface charge, water availability, texture and composition can range markedly on a large and small scale.[1,6,7] The concept of a 'microniche' emphasizes that the biological requirements for a particular soil microorganism may be met within one site but not another site only a micron away.[8] Thus, the rhizosphere—the region adjacent to root surfaces—can support much higher levels of microorganisms than bulk soil a few millimeters distant.[9] This phenomenon is recognized to be driven by an increased availability of nutrients released from plants into the external environment.[10] Less well recognized is the dynamic variation that occurs along the root surface, and its significance in patterns of disease development. As roots emerge and the new tissue differentiates progressively through stages from root cap, root apical meristem, elongation zone, and finally mature roots with lignified cell walls, the material released into the environment also changes.[11-13] More than 90% of bulk carbon released from young roots of legumes is delivered by the root cap, a 1 mm zone at the apex.[14] Some pathogens are attracted specifically to the root tip region, presumably in response to such exudates.[15,16] For example, instantaneous

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swarming occurs when a cotton root is placed into a suspension of *Pythium dissotocum* zoospores (**Sup. Fig. 1**). This host-specific attraction is specific to the root tip region where border cells are present (**Sup. Fig. 2**). Border cells remain attractive to zoospores when removed from the root (**Sup. Fig. 3**). The nature of the attractant is not known, but its impact is localized and transient (**Sup. Fig. 4**).

Newly generated tissue is highly susceptible to infection by pathogens, in general, so elongating root tips would be predicted to be vulnerable to invasion. And yet, root apices repeatedly have been found to escape infection and colonization.[17-19] Recent discoveries about parallels between mammalian white blood cells and root border cells may provide new insight into this apparent conundrum.[20] Neutrophils, a type of white blood cell, are produced in response to infection. Neutrophil extracellular traps (NETs) then attract and kill the invader through a process that requires extracellular DNA (exDNA) and an array of extracellular proteins.[21,22] Border cell production, like that of neutrophils, also is induced in response to signals from pathogens and root tip resistance to infection requires exDNA and an array of extracellular proteins.[20,23] Root tip specific chemotaxis, like that seen with Pythium zoospores, has been presumed to involve steps in a process of pathogen invasion.[15,16] It may, instead, involve a process of extracellular trapping and killing by cells designed to protect root meristems from invasion, in a manner analogous to that which occurs in mammalian defense. If tests confirm this model, the mystery of how root tips escape infection by soilborne pathogens they attract could be resolved.

Conclusions and Perspectives

Soilborne pathogens are a perennial threat to crop production worldwide. The fact that many species can remain in a dormant or quiescent state for years, with reactivation in response to signals released from emergent roots, makes control difficult using classical approaches such as crop rotation. Plants express complex and variable defense pathways that can take minutes to hours to deploy.[24,25] Under dynamic soil conditions, the defenses that occur in the earliest moments of root-pathogen contact may be most important in disease prevention and avoidance.[26] For decades, fumigant pesticides like methyl bromide that obliterate soilborne microbial populations within the soil have nearly eliminated the threat of some root diseases. With continuing efforts to implement the phaseout of methyl bromide due to its toxicity to beneficial microorganisms as well as animals, a renewed research focus on root-microbe dynamics is warranted.[27]

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Note

Supplemental materials can be found at: www.landesbioscience.com/journals/psb/article/15107

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