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Plant immunity is compartmentalized and specialized in roots

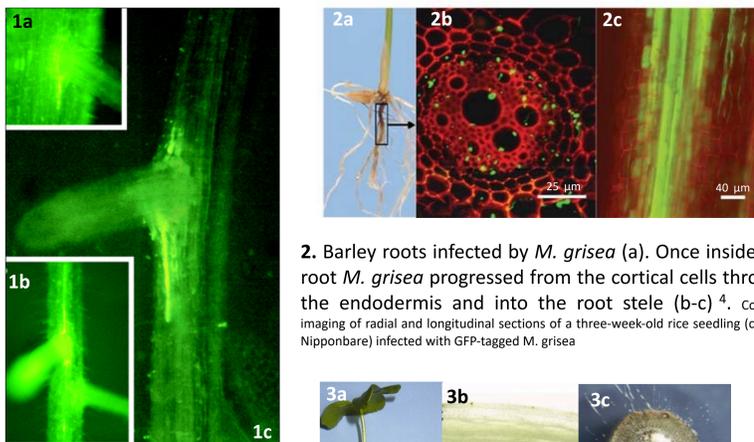
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Introduction

Roots are essential for maintaining plant fitness and survival. In recent years, differences between roots and shoots regarding plant defense strategies have been highlighted. Some gene markers of defense responses in leaves are often not relevant in the root system and sometimes are not even expressed. Furthermore, immune responses in roots appeared to be tissue-specific suggesting a compartmentalization of defense mechanisms in this organ.

The root system : an important opportunistic entryway



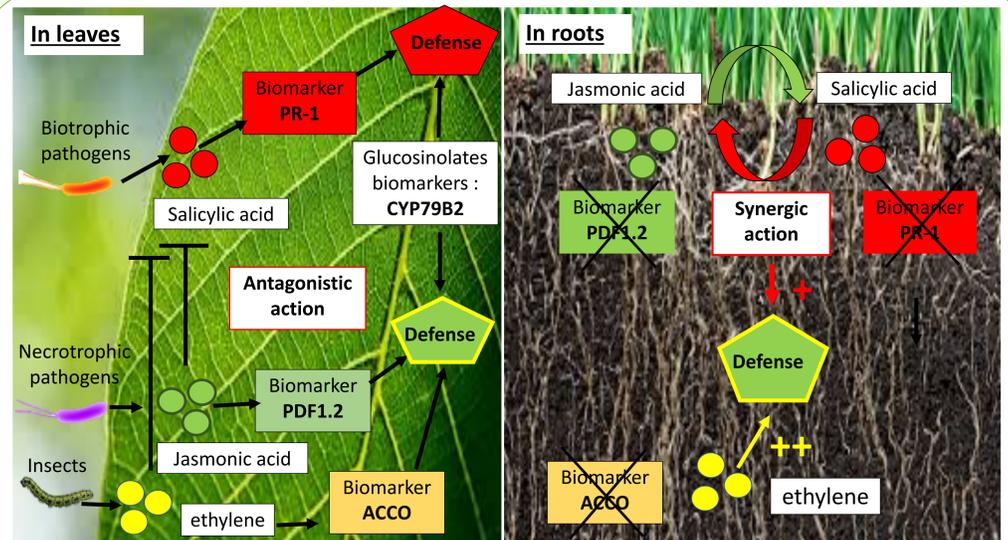
1. Colonization of natural apertures (epidermal cracks) (a, c) and within the entire (b) root tissue of rice forming intercellular lines of GFP-labelled *Rhizobium* bacteria³.

2. Barley roots infected by *M. grisea* (a). Once inside the root *M. grisea* progressed from the cortical cells through the endodermis and into the root stele (b-c)⁴. Confocal imaging of radial and longitudinal sections of a three-week-old rice seedling (cultivar Nipponbare) infected with GFP-tagged *M. grisea*

3. Cotton root infection with *Fusarium sp.* (a). Once inside the root, *Fusarium sp.* infect the aerial part of the plant (hypocotyl) through the vascular tissue (b-c)⁵.

Aerial disease can be related to root infection

Hormonal pathways: Which markers in *Arabidopsis thaliana* roots ?

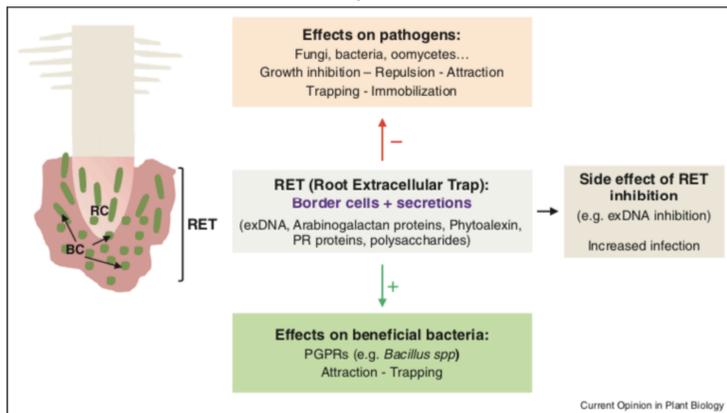


Defense biomarkers mainly found in leaves are SA markers (pathogenesis related proteins PR-1), JA markers (plant defensin: PDF1.2), ET markers (amino-cyclopropane-carboxylate oxidase myrosinase binding protein: ACCO), glucosinolate markers (enzyme involved in glucosinolate biosynthesis: CYP79B2). These biomarkers are not significantly induced in *Arabidopsis* roots^{6,7,8}. Furthermore the antagonistic action between salicylic acid and jasmonic acid that occurs in leaves is not always reported in roots. ethylene seems to play a major role in root defense.

Gene biomarkers differ both according to the plant species and the organs (e.g., aerial or belowground organs)

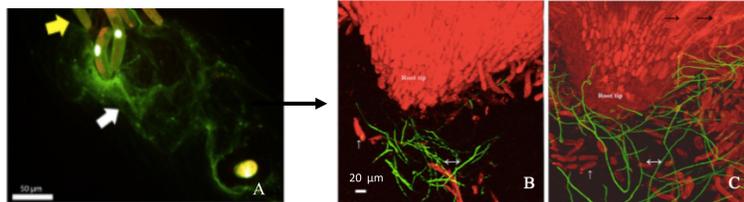
Root extracellular trap : a unique feature of the root

What is the root extracellular trap ?



Root extracellular trap (RET) is formed by border cells and root secretions (mucilage). Experimental evidences indicate that RET is able to alter microbial behavior in many ways to ensure root protection and create stable changes within the rhizosphere. Inhibition of RET formation results in root infection⁹. BC, border cells; ExDNA, extracellular DNA; PR proteins, pathogenesis-related proteins; PGPR, plant growth promoting rhizobacteria; RC, root cap.

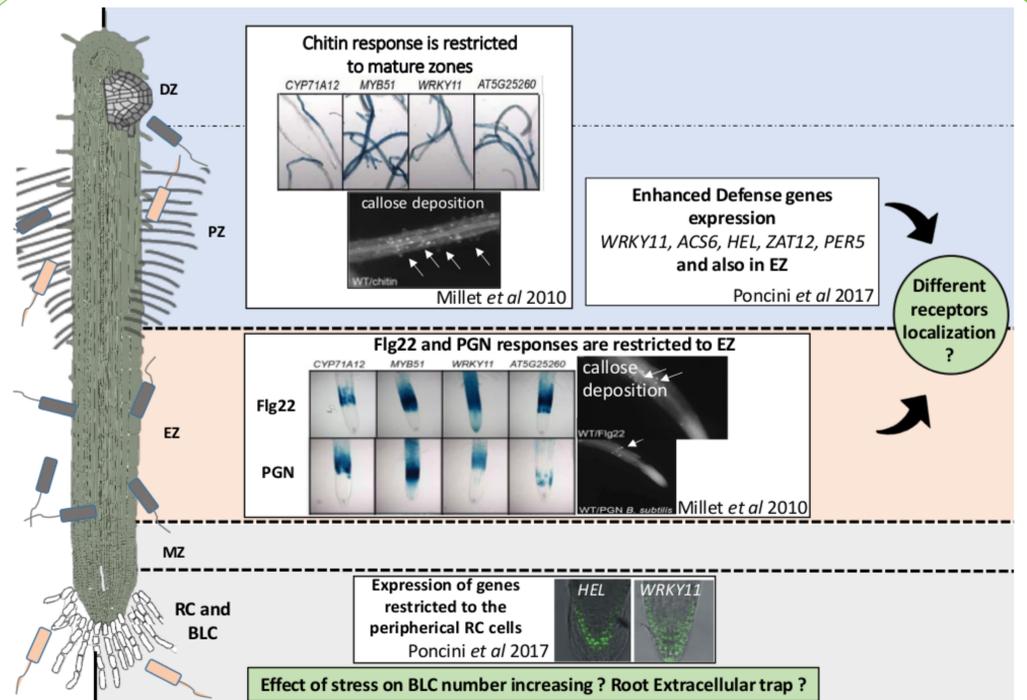
One example of RET protection



(A) Fluorescence microscopy images of pea root border cells (yellow arrow) releasing extracellular DNA (white arrow)¹⁰. (B) Fungal hyphae growth (green) is limited at distance from root tips (red). (C) In root treated with DNase I, fungal hyphae (double white arrow) proliferate among border cells (white arrow) and penetrate the root tip epidermis (black arrows)¹¹.

RET protect the root tip from pathogenic infection

Tissue-specific defense responses in *Arabidopsis thaliana* root



Promoters of defense gene in fusion to GUS were used to evaluate defense gene expression in the different root zone after elicitor treatments. In response to chitin, gene expression occurred in the entire mature zones (DZ and PZ). In contrast, with Flg22 and PGN, the response is restricted to EZ (*idem* callose). In root caps, expression of defense genes (WRKY11/HEL) was restricted to the peripheral RC cells. This compartmentalized response suggest tissue-specific elicitor receptors localization or difference in the amplitude of response within tissue¹². DZ, differentiation zone; PZ, root hair zone; EZ, elongation zone; MZ, meristematic zone; RC and BLCs, root cap and border-like cells CYP71A12, Cytochrome P450 family 71 polypeptide; MYB51, Transcription factor involved in indole-glucosinolate biosynthesis; WRKY11, Negative regulator of basal resistance; AT5G25260, Nodulin-like protein of unknown function; ACS6 : 1-aminocyclopropane-1-carboxylate synthase 6; HEL, Hevein-like protein; ZAT12, Zinc-finger protein; PERS, Peroxidase superfamily protein; Flg22, Flagellin; PGN, peptidoglycan

PTI induction is restricted to specific root zones that are critical for successful infection by invading pathogens

Conclusion

Root immunity is far from being fully understood and so many questions remain regarding mechanisms at the cellular and molecular levels.

- Root defense response to elicitors and/or pathogen attacks exhibit tissue specificity. How such compartmentalization occurs in root defense as compared to leaves is still unclear. Is it due to distinct localization of signal receptors or only due to differences in the amplitude of responses in each tissue?
- Root border cells are particularly important in root defense against pathogens. In *A. thaliana*, root border-like cells (BLCs) are likely to be key elements in defense as they perceive elicitors and display defense mechanisms responses.

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