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# Induced root-secreted phenolic compounds as a belowground plant defense

Arnaud Lanoue,[1,*] Vincent Burlat,[1-3] Ulrich Schurr[4] and Ursula S.R. Röse[5]

[1]Université François Rabelais de Tours; EA Plant Biotechnology and Biomolecules; Avenue Monge; Tours, France; [2]Université de Toulouse; UPS; UMR; Surfaces Cellulaires et Signalisation chez les Végétaux; Castanet-Tolosan, France; [3]CNRS; UMR; Castanet-Tolosan, France; [4]ICG-3 Phytosphere; Forschungszentrum Jülich; Jülich, Germany; [5]Department of Biology; University of New England; Biddeford, Maine, USA

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*Correspondence to: Arnaud Lanoue; Email: arnaud.lanoue@univ-tours.fr

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**Rhizosphere is the complex place of numerous interactions between plant roots, microbes and soil fauna. Whereas plant interactions with aboveground organisms are largely described, unravelling plant belowground interactions remains challenging. Plant root chemical communication can lead to positive interactions with nodulating bacteria, mycorriza or biocontrol agents or to negative interactions with pathogens or root herbivores. A recent study[1] suggested that root exudates contribute to plant pathogen resistance via secretion of antimicrobial compounds. These findings point to the importance of plant root exudates as belowground signalling molecules, particularly in defense responses. In our report,[2] we showed that under Fusarium attack the barley root system launched secretion of phenolic compounds with antimicrobial activity. The secretion of de novo biosynthesized *t*-cinnamic acid induced within 2 days illustrates the dynamic of plant defense mechanisms at the root level. We discuss the costs and benefits of induced defense responses in the rhizosphere. We suggest that plant defense through root exudation may be cultivar dependent and higher in wild or less domesticated varieties.**

Plants grow and live in very complex and changing ecosystems. Because plants lack the mobility to escape from attack by pathogens or herbivores, they have developed constitutive and in addition inducible defenses that are triggered by spatiotemporally dynamic signaling mechanisms. These defenses counteract the aggressor directly via toxins or defense plant structures or indirectly by recruitment of antagonists of aggressors. Whereas induced defenses are well described in aboveground interactions, evidence of the occurrence of such mechanisms in belowground interactions remains limited. The biosynthesis of a defensive molecule could be both constitutive and inducible with a low level of a preformed pool (**Fig. 1**). In addition, upon encounter of an attacking organism, those levels could be induced to rise locally to a high level of active compound that is able to disarm the pathogen.[2,3] Only a few examples show that root exudates play a role in induced plant defense. Hairy roots of *Ocimum basilicum* secrete rosmarinic acid only when challenged by the pathogenic fungus *Pythium ultimum*.[4] Wurst et al.[5] reported on the induction of irridoid glycosides in root exudates of *Plantago lanceolata* in presence of nematodes. In vivo labelling experiments[2] with $^{13}CO_2$ showed the induction of phenolic compounds secreted by barley roots after *Fusarium graminearum* infection and the de novo biosynthesis of root secreted *t*-cinnamic acid within 2 days. These results show that the pool of induced *t*-cinnamic acid originated from both pre-formed and newly formed carbon pools (**Fig. 1**), highlighting a case of belowground induced defense inside and outside the root system.

The concept of fitness costs is frequently presented to explain the coexistence of

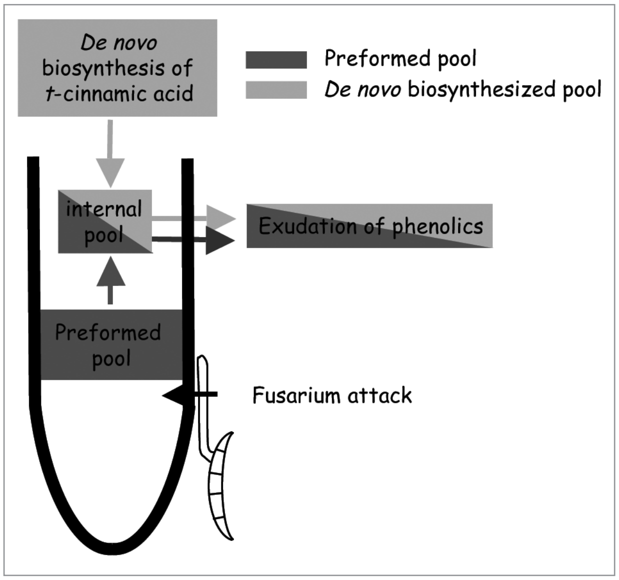


**Figure 1.** Suggested mechanisms for the induction of root defense exudates in barley in response to Fusarium attack. Upon pathogen attack by Fusarium, the initial preformed pool of phenolic compounds is increased by the addition of inducible, de novo biosynthesized *t*-cinnamic acid. Both, the preformed pool and the de novo biosynthesized pool fuel the exudation of defense compounds from infected roots.

both constitutive and induced defense.[6] In the case of induced defense, resources are invested in defenses only when the plant is under attack. In the absence of an infection, plants can optimize allocation of their resources to reproduction and growth to compete with neighbours.[7] Constitutive defenses are thought to be more beneficial when the probability of attack is high, whereas adjustable, induced defenses are more valuable to fight against an unpredictable pathogen. Non disturbed soil is a heterogeneous matrix where biodiversity is very high and patchy[8,9] and organism motility is rather restricted.[10] As a consequence of the patchiness, belowground environment is expected to be favourable to selection for induced responses.[11] The absence of defense root exudates between two infections may form an unpredictable environment for soil pathogens and reduce the chance for adaptation of root attackers. Plants may also use escape strategies to reduce the effect of belowground pathogens. Henkes et al. (unpublished) showed that Fusarium-infected barley plants reduced carbon allocation towards infected roots within a day and increased allocation carbon to uninfected roots. These results illustrate how reallocation of carbon toward non infected root parts represents a way to limit the negative impact of root infection.

We have demonstrated the potential of barley plants to defend themselves against soil pathogen by root exudation.[2] Even the barley cultivar 'Barke' used in our study, a modern cultivated variety, was able to launch defense machinery via exudation of antimicrobial compounds when infected by *F. graminearum*. We suggest that plant defense through root exudation might be cultivar dependent and perhaps higher in wild or less domesticated varieties. Taddei et al.[12] reported that constitutively-produced root exudates from a resistant Gladiolus cultivar inhibit spore germination of *Fusarium oxysporum* whereas root exudates from a susceptible cultivar do not affect *F. oxysporum* germination. Root exudates from the resistant cultivar contained higher amounts of aromatic-phenolic compounds compared to the susceptible cultivar and these compounds may be responsible for the inhibition of spore germination. Metabolic profiling of wheat cultivars, 'Roblin' and 'Sumai3', respectively, susceptible and resistant to Fusarium Head Blight, showed that *t*-cinnamic acid was a discriminating factor responsible for resistance/defense function.[13] Therefore it is likely that wild barley varieties hold higher defense capacities compare to cultivated varieties selected for high yield. In the future, plant breeders in organic and low-input farming could use root-system defense ability as new trait in varietal variation.

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